Spider Webs: Design and Engineering

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'All things in nature,' said Sullivan, 'have a shape, that is to say, a form, an outward semblance, that tells us what they are, that distinguishes them from ourselves and from each other . . . .'. 'Whether it be the sweeping eagle in his flight or the open apple-blossom, the toiling work-horse, the blithe swan, the branching oaks, the drifting clouds, over all the coursing sun, form ever follows function, and this is the law.'

Joedicke, 1959

INTRODUCTION

The interdisciplinary approach of combining architectural and engineering knowledge with biological and ethological thinking can elucidate the reasons for the enormous variety in spider webs; and web analysis can teach us something about optimal forms for the construction of a functional building.

When a house is designed by an architect, various needs are taken into consideration. First, the site will always interact with the structure; for example, environmental conditions may demand a strong, or permit a more open design. At the same time, the building becomes an integral part of the environment, changing it in a way which may influence future building nearby. It makes a great difference whether structures are meant to stand over long periods of time, or whether they serve temporary needs, to be taken down after a few days.

Economy of material and labor influence the way in which a building is planned, and available material dictates the width, height and shape of rooms. Human buildings show wide variety in size, depending on whether they are meant to be inhabited by one individual, a single family, or a great number of people. If they have mainly a sheltering function, their form must be different from office and industrial structures. In addition, separate units are connected with each other by transportation networks of highways and railroads.

Spiders live in self-made structures too. There is an enormous variety in spider webs which is noticeable even to the casual observer. Near the ground there may be webs which contain dense tangles of threads or silken sheets; in high grass and in shrubs there are more elaborate three-dimensional structures, while up in the trees beautiful geometric orbs can be recognized. Some house only a single animal, others shelter a mother and her offspring, and still others are large communal complexes inhabited by hundreds of individuals.

A great variety of roles has been suggested for spider webs: some of the better known are network for movement and communication, silken trap, protective device, and platform for mating. In a number of instances we have experimental evidence for the part played by a structural detail, in others the function can only be surmised. In specific webs, the sticky catching thread is neatly separated from the dry silk of the framework, setting the catching function apart from that of support. Signal threads run unimpeded through open spaces to allow undampened transmission of information.

The resonant properties of webs filter out inappropriate signals, and specific thread patterns send information in many directions, so that a multitude of animals can be recruited for an attack on oversized prey. Orbs and tangles can be intermingled to form a composite functional habitat for a small group of spiders. Broad opaque silken bands protect builders from the eyes of predators. And the communal tangle built by some baby spiders creates a favorable environment for growing up.

We postulate that each structural feature in a web can be understood as part of a system of strategy for survival in the builder's own unique environment. We believe that the comparison of spider structures with human buildings (Fig. 1) will identify basic principles in design which serve similar purposes in two groups of otherwise dissimilar living beings, revealing the systems by which both modify their environment.

In the drawing opposite, Edward H. Williams, a Raleigh, North Carolina architect, superimposed various building designs discussed in the review: the floor plan of a family residence with side terraces, at bottom a suspension bridge, a clover leaf highway interchange at right, and the symmetric orb web of a spider, left top; all suspended in an irregular space structure. Each of these designs shows a solution to a problem in the builders' lives which is examined in the text of the review.

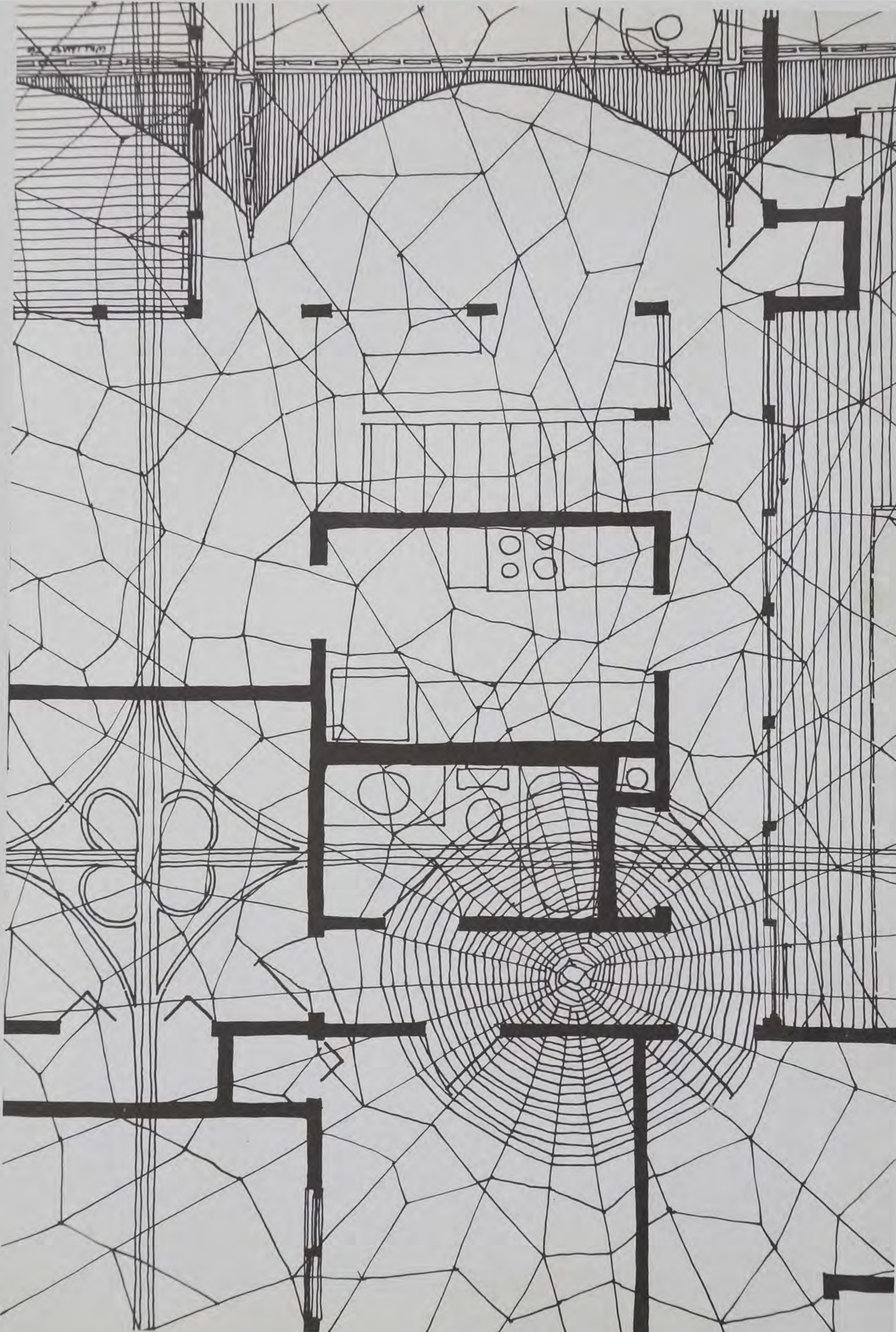

Figure 1. In this 16th/17th century Dutch print, a group of people consider how to lay out a city while they look at a spider web. The symmetric orb design of the web is reflected in many city plans, like the Place de l'Etoile in Paris, or the radial plan for Karlsruhe where the main streets begin at the centrally located castle of the prince. Such city plans permit the ruler to keep the citizens under control by positioning guns at the center, comparable to a spinder's control over prey in the web through the vibrating radii.

THE BUILDING SITE

In human affairs we are apt to consider man as a self-sufficient unit. Actually, people are not autonomous, but with their organizations and housing structures they form a total system from which no part can be separated. How complete is a man alone without his society or country? Similarly, a farm in the absence of the farmer, his family or the livestock does not function. In the same way, it is hard to talk about a spider without a web or the web without a spider.

The blind spider without a web is nearly helpless, unable to catch or even identify prey without vibration cues (Baltzer, 1923), and his hooked feet, adapted for hanging on silken threads, slip on smooth surfaces. Conversely a naked web will not catch or hold prey and quickly falls into disrepair. An even

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closer tie exists between spider and web: the silk is secreted by the body and eaten by some species in hard times to become part of the body again. In fact, orb weavers eat their webs regularly and secrete 95% of the same materials the next day (Peakall, 1971), simply transferring amino acids in and out of the body for utility's sake.

For these reasons we will think of web and spider (and architecture in general) as an integrated system. As such a complex, the web/spider unit can survive; it enters into the global exchange of energy and materials, and this is what biologists study. Products can be transferred within the complex, as when orb web building materials are secreted and reingested.

At the interface of the web/spider organism there are interactions with the environment, such as taking in food and oxygen and releasing carbon dioxide and faeces (Fig. 2). Again, some web/spider complexes might be likened to a farm, where an integration of sub-units, like cow, grass and farmer, function together. Here also, there can be intraexchange when the farmer milks the cow or spreads manure on the meadow. Interexchange occurs with the outer environment when the farmer buys hay for the cow or sells the milk. In fact, we are familiar with many systems which are like this.

A human city, for example, may provide its own services, such as garbage collection and fire protection, or generate its own electricity; interactions can occur involving transfer of energy and materials within the 'city/citizens' complex. For food or telephone service a city must rely on interexchange from outside its boundaries. If we integrate the city functions with a huge architectural structure, as proposed by Paolo Solari, we have an attractively close parallel to a spider colony. Still, in such a system no unit is self sufficient. Fires, trucks, buildings, food and firemen are interlocking parts in a complex which is successful in its ability to sustain itself and to replace its components over time.

With both the web/spider and the farm and city, however, it is not enough simply to bring the several sub-units together: success of the structure depends upon finding a good place to operate—a proper potential site. When ecologists talk of 'site selection' or 'site utilization' in spiders and other animals they are generally considering site to be an area of material resources. However, we prefer to look at the broader spectrum of interplay between an organism and its environment (Fig. 2).

In this way we avoid difficulty in discussing the web/spider complex, because the spider can set up housekeeping literally in thin air. G. C. Argon (1957) states this as a concept of design, that 'By joining with uninterrupted lines a number of points in space, the object claims a "site", and existence in undetermined space'. From the design view, all that we investigate in webs is a product of their creation in defining a site, and this has no relation with the formerly uncolonized area, except as a source in space in which to put a new object: the web. This is because all the site require-

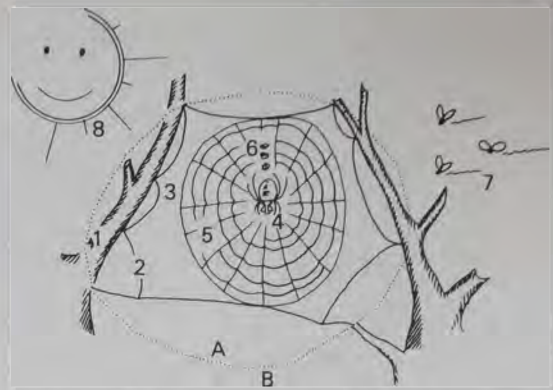


Figure 2. The site area defined by web/spider complex of *Araneus diadematus*. A. Site area, also web space; B. Non-site area or non-web space. Web/spider complex components: 1. Environmental structural components, nature's contribution to web site. Contribute potential and kinetic energy to complex. 2. Buffer zone, cushions and filters exchange with non-web space. 3. Web sector, permanent structural part, potential store of metabolic energy. 4. Spider sector, living part, potential store of metabolic energy. Constant material loss from body processes. 5. Web sector, temporary structural part, potential store of metabolic energy. 6. Stored prey, store of metabolic energy. Some loss through degradation. 7. Prey source, metabolic and kinetic energy input. Material input. 8. Environmental interface, source of material (water) input, heat energy, cooling forces, kinetic energy (wind) and other diverse inputs and losses.

The organization by the spider of previously existing and internally produced components into the site defines site (A) and non-site (B) areas. We call the material part of this organization a structure, which is an important part of the web/spider complex system. The web/spider complex system filters and buffers exchange with the non-site area, allowing necessary supplies to come in and wastes to pass out. Within the complex, the temporary web is built within a permanent structure, work is performed, energy is used and stored. This general model may be applied to other webs or other structures such as a human office building or bank.

ments of any web/spider complex, whether structural (strong supports, close twigs, open spaces in vegetation) or biological (rain water, sunshine, prey sources) only become functionally available with the establishment of the structure itself.

A corollary is that the first step in web system strategy is to modify the immediate environment. Other species may rely on morphological or physiological adaptation for survival, but spiders and man primarily adapt behaviorally by keeping their physical form and changing their surroundings. Environmental modification can come about through the active choice of the spider (Turnbull, 1973; Enders, 1974), or natural selection operating on large numbers of randomly placed offspring. One female *Araneus diadematus* can produce up to 1000 spiderlings, of these the few surviving to adulthood are found in predictable foliage and positions. They may have actively selected these spots, or have distributed randomly when only the well-placed would survive. In either case, the method is inconsequential for our consideration, as the result is the same.

Araneus diadematus orbs are primarily found high in trees and shrubs, and the same is true for the sheets of *Mallos gregalis* (Diguet, 1915), while *Cyrtophora* webs are found within 200 cm from the ground (Wiehle, 1928) on opuntiae and agaves. *Metepeira* webs are characteristically within a leafless open space in a bush or tree (McCook, 1889). Whatever the place or method of selection, the end result is to delimit characteristic 'web' and 'not-web' areas for each species. It is easy to imagine global creation of diverse sites, so that all heights, hosts and geographies are utilized with species living side by side. This is exactly what we see when we look at nature: these beautifully interlocking systems complement each other, allowing all 'niches' to be filled and every species to get its share of the biological pie. A comparison can be made with the view of the Earth presented to the passenger in an aeroplane: the landscape appears neatly divided into farms, cities, forests, and roads uniting various places. Such parallels will grow increasingly obvious as we consider the spiders' complex in more detail.

Figure 3. This geometric orb web of an adult female *Araneus diadematus*, or cross-spider, was built in a laboratory frame in about 30 minutes. The builder sits on the hub and pulls radii tight with its eight legs. A scale in the upper left corner indicates 20 mm in the original, and the direction of gravity, showing this to be a vertical orb web. A small wooden structure was deliberately introduced into the lower right part of the larger frame: the spider, which was prevented from leaving, has distinctly modified the spiral where it would have overlapped the frame.

THE SPIDER'S WEB

Components

For web components the following terms will be used in this review. The **geometric orb** denotes a two-dimensional cartwheel structure. It consists of radial spokes around a hub; the radii are crossed by spiral turns, and end peripherally in a complex frame. The area covered by the spiral structure is frequently elliptic rather than circular and the hub usually lies off-center. All known orbs are short term structures, and are repaired or renewed after a few days. Building time is short: one to two to a few hours. There are two different procedures for constructing the geometric orb:

In the vertical *Araneus* type web, which we will discuss in detail, all or nearly all radii are built first, the majority running all the way from hub to frame; later the spiral is laid across the completed radius structure from the outside in (Fig. 3). Under the microscope most thread crossovers look like integrally fused junctions. The meshes of the orb are rectangular. In *Araneus* webs, spiral threads are covered with drops of glue, whereas radii are dry (Witt, *et al.*, 1968).

In the *Cyrtophora* web, which is a compound structure, a horizontal geometric orb is only one component. When the orb is built, only a few radii (10–20) are laid at first, then additional radii are constructed as the spiral is laid from the hub outward, to a total radius number of 300 to 500 at the frame. This construction sequence is clearly explained by Kullmann (1958). Because radius and spiral threads run together briefly, the meshes have a hexagonal shape (Fig. 4E).

A **sheet web** is a two-dimensional structure, showing no symmetry. It either lies flat or is bowl-shaped, composed of long threads which frequently cross each other unfused. There can be oval holes in the sheet, which are lined with reinforcing thread, but otherwise the structure is uniform without subdivisions. All sheet webs we know form long-lasting structures, built intermittently over long periods of time.

The **space web** is three-dimensional, occurring either by itself or together with an orb or sheet. There are no clearly delineated substructures in a space web; however, during construction great care is taken that tension is evenly distributed in all directions (Holzapfel, 1933). Space webs show some woven parts, built with short strands which frequently are fused into Y structures; other sections of the space

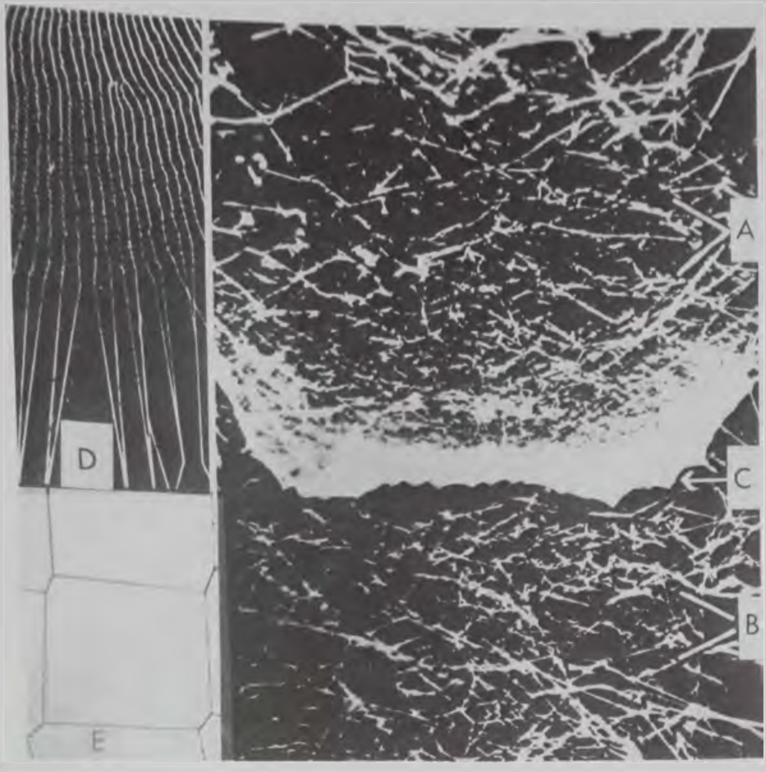


Figure 4. Web of *Cyrtophora citricola*, modified from Kullmann (1958). A shows the upper space web, which increases in density toward the center; B the lower space web, which is relatively wide-spaced on top. In the middle the bowl-shaped horizontal symmetric orb web C separates the upper from the lower part, provides running space for the spider at the underside, and acts as a receptacle for falling prey. D provides a look onto the orb from above, showing the increase in radial number toward the periphery, here at the bottom; E shows an enlarged mesh of the orb with its hexagonal shape.

web have wide open spaces, crossed by only a few silken lines. Space webs are usually constructed in the course of several days; the same web is used for weeks and months, sometimes throughout the life of the builder. Many space webs function as sites for communal life and cooperative prey-catching.

One or more of the above components appear in each of the four webs we selected, and in most other known webs. We do not examine the widely distributed single sheet webs of the Lyniphiid spiders, which are obvious on a dew-covered meadow; nor do we discuss the single-thread 'web' which the bola spider keeps in perpetual motion.

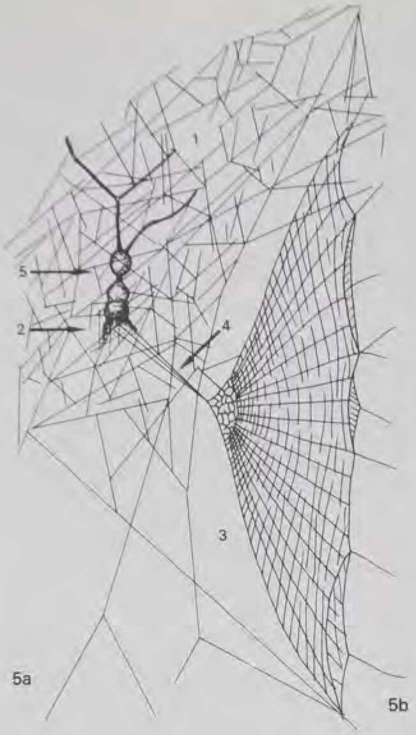
Web Examples

We discuss four types of web. Firstly we have the *Araneus* web (Fig. 3), typical of the many spider species which construct single verticle orb webs. All these webs are slight variations on the basic theme: a radial support structure, overlaid by a so-called catching spiral. The finished structure is particularly beautiful. There is a logarithmic decrease of interspiral distances from the periphery towards the center, and usually the radial threads are spaced at wider angles at the top than at the bottom. The spiral area is oval, with the long axis vertical; and there are circular as well as pendulum turns. In the middle are the hub and open zone; outside is the irregular frame area.

The frame is suspended on anchoring lines that form a buffer zone between non-spider built structural elements, like branches and walls, and the spiral area, which can have a number of individual variations. The single occupant sits either in the hub, or in a hiding place outside the web, holding a signal thread stretched to the hub. The web of *Araneus diadematus* Cl. (commonly called the 'cross spider') has been most thoroughly explored and recorded (for a recent review of *Araneus* web literature see Witt, *et al.*, 1968).

Then there is the *Metepeira* web (Fig. 5a and b), a composite web built by members of the genus *Metepeira* which is distributed world-wide. Two species in particular, *M. labyrinthea* and *M. spinipes*, show aggregations and a repertoire of interactions (McCook, 1889; Pickard-Cambridge, 1903). The web contains five distinct structural features, each of which has different physical properties as a result of different combinations of silk from the silk glands and thread laying behavior. These features are space-web, retreat, orb web, signal threads and egg sacs. Each is distinct and all are built in a fixed sequence. The orb component in *Metepeira* and *Araneus* has the same structure. Numerous *Metepeira* may inhabit a conglomerate of many webs, each animal building its own retreat and orb.

Next we have the *Cyrtophora* web (Fig. 4): the webs of *Cyrtophora citricola* and *C. moluccensis* appear the same, and have been described and analyzed by Wiehle (1928), Kullmann (1958), Blanke (1972), and Lubin (1973). They are three-dimensional structures, consisting of at least three easily distinguishable features: a space web on top and below, separated by a horizontal orb. The upper part is a three-dimensional, irregular mesh-work,



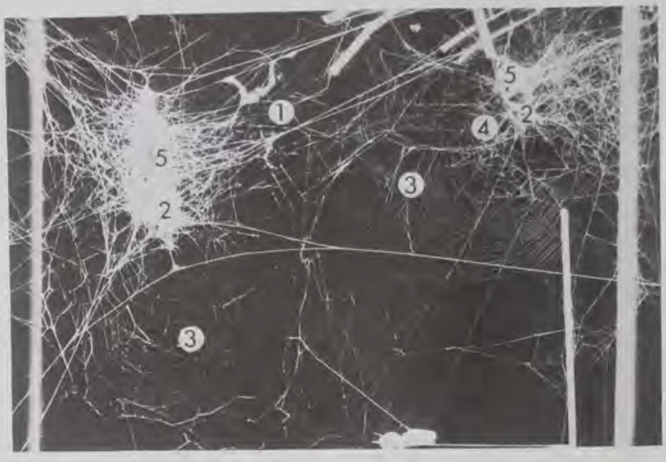


Figure 5a. One *Metepeira* compound web. First built is space web (1), where spider sits under retreat (2), separated from orb web (3), and holds connecting threads (4), above retreat; mature females may construct tiers of egg sacs (5). Woodcut by McCook 1889. These single web modules may be joined together for colonial living.

Figure 5b. On the left and right are retreat/egg sac combinations containing *Metepeira spinipes* individuals who have built webs sharing thread connections. Interactions occur in the permanent connected space web, while prey is caught by individuals in periodically built orb webs. In nature, many *M. spinipes* build webs together, sharing a single site. For explanation of numbers see Fig. 5a.

becoming increasingly dense toward the orb. A horizontal orb forms the middle part of the web and, in contrast to those of *Araneus* and *Metepeira*, has a great number of incomplete radii. The flat orb is distorted by strong vertical lines, so that it resembles a bowl with a raised center. The area directly under the orb is relatively open, permitting the single inhabitant to move around rapidly. Often many webs are built together (e.g., 200; Lubin, 1973) forming a colony in which the individual structures are connected through their space-webs and common mooring lines. In these large communities hubs maintain a minimal distance of 15 cm, and animals frequently exchange webs.

Finally there is the *Mallos gregalis* web (Fig. 6). These tiny spiders from central Mexico live together in the thousands. The colonies consist of a single, huge web on which all members coexist socially, hunting prey and feeding in groups. The web as a whole has the appearance of a grey mass, the newest part being pure white. Again the three-dimensional structure has three distinct features: the outermost surface or prey-catching sheet, usually studded with dead flies; the complex interior space web, honeycombed with tunnels; the internal chambers containing spiders and egg sacs. Like many other spiders forming complex societies, *Mallos gregalis* is prevalent in the tropics (Burgess, 1976), where webs are constructed far above the ground in trees or bushes. They are easy spiders to keep in the laboratory for they will accept a wide variety of supports (Diguet, 1915; Gertsch, 1949; Burgess, 1976).

Web Boundaries

These sites need not be thought of as static or isolated, any more than we consider a town as only an insular unchanging structure. On the contrary, they are transformed into a dynamic web/spider complex, capable of exchanging energy internally as well as

Figure 6. Section of a tree colony of *Mallos gregalis* observed near Guadalajara, Mexico. Spiders communally build webbing around branches and leaves; flying prey adheres to the sticky exterior sheet where communal feeding takes place. Spiders normally rest within the interior of the web structure. Note the openings in the covering sheet web, which give animals access to the web surface.

externally with their environment. *Araneus diadematus* builds a bridge thread and anchoring lines between branches or twigs. This defines the periphery of her solitary site, and also forms the buffer zone between non-spider built supports. Branches which were separate and formerly undefined now, as anchor points, become a dynamic part of the site system. The frame threads, comparable to the foundation of a house, modify the shape of these environmental supports to best suit the daily construction of an orb web; they also absorb kinetic stresses, forming a tension skeleton on which the orb hangs.

This system is reminiscent of Klee's sculpture: 'In this structure, the dual factor of a system of suspension and a system of support is certainly apparent, but the oblique planes have full freedom within the supporting framework to which are attached joints so delicate as to be mere meeting points' (Argon, 1957). We shall discuss temporary and permanent silk lines later, but it is important to note here that the bridge thread and the frame are frequently reinforced permanent parts of the orb web. They continuously demarcate and preserve the perimeters of the site, whether or not an orb is present. The frame silk may be relatively thick, and it represents a substantial energy expenditure, but the bridge and frame are long term investments, supporting the hypothesis that once sites are established they seldom change (Peakall, 1971).

Building-Time

Like humans, spiders build both temporary and permanent structures. While the silken material, as far as it has been analyzed, is similar in both web categories, the design in each shows distinct differences. Economy of labor and material is the outstanding characteristic of the short term, daily-renewed web, while more time, material and effort are expended on a structure which serves for weeks or months. Another interesting feature of the two design types is their functional separation: the temporary structure serves as a highly efficient trap which catches prey for one individual, while a web with a permanent design frequently serves several spiders for many functions, such as feeding, protection, or raising offspring.

The best representative of a short term building is the geometric orb-web of *Araneus diadematus*. It shows structural simplification through symmetry, which Nervi (1956) postulates for economy of material in building, and which is essential in a frequently renewed structure. It has been shown (Witt, 1952) that laying spiral sections perpendicular to the next radius, which results in a logarithmic spiral, constitutes the shortest and simplest route for the builder. If we think only of economy in material, the logarithmic spiral is wasteful, because a good device for catching and holding air-borne prey should have narrowly arranged spiral turns at the periphery where supporting radii are far apart; and a narrow spiral is really quite unnecessary near the hub. Evidently economy in movement and orientation are more important for the spider in a temporary structure than design features concerned with prey capture alone.

Each day *Araneus diadematus* constructs a large aerial net for flying insects. In comparison *Cyrtophora* web/spider complexes, which claim a smaller surface area, are built on a permanent basis. These are not merely chance variations in building, they represent two major strategies of architectural design and support. Norberg-Schulz (1945) concisely stated 'In principle, we may distinguish between two types of skeleton structures: embracing and repetitious. The embracing skeletons are used to span large continuous distances and mostly form a closed whole' (Fig. 7, and the Buckminster Fuller geodesic domes) (see *Interdisciplinary Science Reviews* **1**, 39 (1976)). The orb uses an embracing scheme: while spokes can be added to the cartwheel structure, the design cannot be changed without upsetting its symmetry. Repetitious skeletons, on the other hand, can be enlarged by adding units at the periphery without destroying structural integrity. This design allows flexibility and repeated additions, as represented in space and sheet webs.

So the orb web, in contrast to space and sheet webs, shows modules which consist of short sequences of thread-laying behavior which are repeated several hundred times whenever an orb is rebuilt. It is a good illustration for Marcel Breuer's words, that 'the search for simplification is, of course, connected with a view to finding a prototype for mass production'. The geometric orb, which covers the widest possible

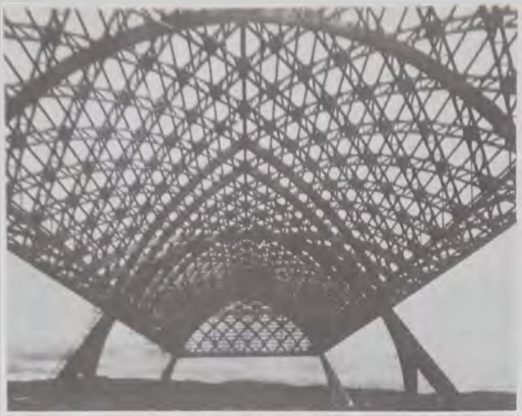


Figure 7. In building the exhibition hall in Turin, Pierre Luigi Nervi used a modular design, where precast structural elements are employed many times, for reasons of economy in material and labor. Though mesh size varies in the vertical geometric orb web, we can look at it as covering as large an area as possible with as little material as possible; construction is simplified by a behaviour module, which is coded in the central body of the spider's central nervous system.

area with the least material and effort, owes its harmony to 'the repetition of a module in such a way that all parts of the structure coexist in simple numerical relations' (Vitruvius, 1940).

We can imagine the evolution of the orb web as a refinement of the modular design; that is, as a short sequence of probing and thread positioning movements which can be repeated at rapid speed many times. As a matter of fact, the spiral-laying *Araneus diadematus* usually forms more than 1000 meshes in rapid sequence in less than 20 minutes, occurring as repeated execution of a relatively simple pattern of behavior which is programmed in the spider's central nervous system. Destruction experiments (Witt, 1969) have shown that the central body at the rostral-caudal end of the supraesophageal ganglion of *Araneus diadematus* may be the site of the modular code. Laser lesions here result in severely disturbed web regularity.

The exhibition hall in Turin is a human example of modular design. 'In the building of the Exhibition Hall in Turin (1948–49) Nervi employed precast units of reinforced concrete for the barrel-shaped vault of the hall, their maximum thickness being scarcely two inches. With these thin sectioned components he bridges an area 80 m long, an astonishing ratio between expenditure of material and performance. The corrugated arrangement of these prefabricated units forming the ribs of the roof gives them the necessary strength and at the same time solves most handsomely the problem of direct lighting' (Joedicke, 1959) (Fig. 7). For this structure, as well as for an orb web, the equivalent of a temporary scaffold is necessary.

Prospective Duration

Peakall (1971) describes another measure which *Araneus* uses to conserve energy and material in the frequently renewed orb-web. He placed 'cold' spiders on radioactive webs, which they readily accepted. After using the foreign webs for the rest of the day, they carefully took them down piece by piece and ingested the old silk, as this species usually does. In webs built subsequently the reappearance of the amino acids, the building stones of the old silk, could be quantitated by measuring radio-activity. In every case more than 90% of the old silk radioactivity was present in the web two days thereafter, illustrating the common use of recycled building material, and reminiscent of repeated employment of components of short term human structures.

When a backpacker buys a tent as a short term shelter, he selects a system with a short set-up time, and the equipment which permits quickest erection is frequently chosen over a more lasting model. In a similar way, *Araneus* lays its threads with enormous speed during the daily web construction, fusing one thread to another at about 2000 points in 20–40 minutes. For the human observer orb web building looks as if a well prepared plan is carried out in a systematic fashion, while space web construction follows a predominant trial and error procedure. In sheet and space webs, there does not seem to be a precoded neural template; both *Cyrtophora* and *Mallos* take several days to build their first web, then continue adding parts.

Cyrtophora changes between rapid positioning of a thread, extensive probing, and testing, and frequently separates an already positioned strand and fastens it a second or third time at a different place (Wiehle, 1928). Observers of *Cyrtophora* web building describe how old silk is discarded whenever repair or renewal takes place, rather than the web being reused. Thus, in the space and sheet web, short building time and reingestion of material are abandoned in favor of a more permanent structure. Even after a rainstorm sheet and space webs are still used, whereas orb webs are destroyed.

In the repetitious type, structures can be more flexible, and *Metepeira* and *Cyrtophora* show a wide variety of forms. Because of multi purpose flexibility, these systems can accomplish a diverse array of functions not available to the orb web. For one thing the spider can move in three dimensions while, for another, the tangle provides a degree of protection against predators for both spider and eggs. In addition the newly hatched young 'exercise' on the upper threads. Most importantly, the site is preserved on a permanent basis. Although one *Cyrtophora* may exchange webs with a conspecific, other spiders cannot colonize the now-occupied space.

We might consider the permanent strategy as a homestead. Once a squatter develops his property he forces others off and exercises control over its use. In this sense he has the advantage of a home base free from outside interference. If he then builds a basic home, like a log cabin, the settler will be able to occupy the simple structure and have the option of adding extra rooms as they are needed. This is one reason why many large American homes still have at their center a single room cabin or other primitive form of dwelling.

BEHAVIOR AND DESIGN

In our four spider species and their web complexes there is almost a continuum in the degree of social interaction. The orb web of *Araneus diadematus* appears to be designed for single occupancy; there is only one small area, the hub, from which the web can be monitored; the converging radii direct all vibrations and locomotor pathways to this single spot. Little intermember tolerance exists in this species. Whatever produces vibration in the web is attacked, be it a fly, a sibling, or a tuning fork.

Even solitary animals, however, have some contact with their species—minimally with mates and young. The web of *Araneus diadematus* is the substrate for courtship, initiated by the wandering males who pluck or strum with a leg on the periphery of the female's web. Before actual mating takes place the male connects its own thread to the web of the female, and so before two animals get together they must add another structural element. When hundreds of young hatch from their egg case they stay together for some time, not on an orb, but on a communally constructed sheet (McCook, 1889; Burch, in preparation). In every case the orb functions for a single spider, and the group interactions are relegated to another structure.

In contrast, *Cyrtophora* and *Metepeira* exhibit regular conspecific interactions, which take place on the usual web structures; additional features are not built. In *Cyrtophora*, if webs are found touching, neighbors may steal food or exchange webs, and predation on each other is possible but rare. When an egg sac hatches, spiderlings proceed directly to overhanging space webs. They build their own structures in the mother's web and animals within the complex remain tolerant for several days. They probably aggregate around webbing, rather than around each other. Courtship, however, is dependent on the presence of the female and not her web.

Like *Cyrtophora, Metepeira spinipes* are *always* found in groups, exhibiting characteristic spacing (Blanke, 1972; unpublished measurements by J. Wesley Burgess). The space web in *Metepeira* is the arena for social interactions. Webless males may wait here to steal food from neighbors' orbs, or descend to retreats for courtship and mating. Here the young go after hatching, and the space web also serves for the attachment of their first webs. Males may cohabit for days with unmated females, in the area above the retreat. Curiously, after mating, the egg sac is built above the retreat and this area is filled.

Because *Mallos* enjoys a wide spectrum of social interactions, the web forms a permanent substrate. As a product of communal spinning, the sheet allows aggregation, group predation, and the joint rearing of young. Tolerance is complete. Males approach females in a simple courtship and tiny immatures run on the web, feeding unmolested on prey caught by adults. It is not known yet how males and females select each other on the communal structure, where all animals appear in close contact at any time, but there may well be some undiscovered structural features which serve mate selection.

In both the sheet and space web the repetitive construction system is used, and there is an increase in web size for additional colony members. Similarly, instead of building a separate nursery for a family, an architect may prefer to provide regular adult-sized rooms with juvenile furnishing, knowing these rooms will serve many ages in the years to come.

Another way to look at social behavior is to find out how activities in a web/spider complex are organised. A single *Araneus diadematus*, conserving reusable structural material, may coordinate activities herself. Thus, the catching web, egg sac and retreat area, are well separated. Likewise *Cyrtophora* males are not dependent on web structure to mate but use cues directly from the female.

If the site regularly includes several members, however, it may be more efficient to coordinate group activities with something structural, such as the web itself. We might say that at home we know our way around very well, but in the expanse of a big city an individual's need for maps, direction signs and well marked roads becomes important.

The behavior of *Metepeira* is largely regulated by its web structure. Prey catching on the orb resembles *Araneus diadematus*, but distance between orbs is fixed by a permanent space web. Orientation of males to females, rather than taking place in the open, is directly channeled through the overhead roadway of the space web, which connects site members. As in *Cyrtophora*, dispersal of young *Metepeira* is directed by the space web, but the young stay around for a long time and may disperse over the entire colony-shared web. The locus of every spider action is thus preserved within the complex: the temporary orb is fixed to the permanent space web, while the retreat provides a resting point for the male and also preserves inner space for the egg sac. In a changing environment the web complex is its own urban zoning system, under a plan which was developed over time and is encoded in the spider's genes.

The *Mallos* plan is less flexible, turning most functions over to structural integration. On a shared web substrate site members travel on silk pathways laid down earlier, as the draglines of other walking colony members. Not only movements, but also communal predation signals are carried by the surface sheet, whose threads exhibit a resonance response, which mediates the predatory cue (Burgess, 1975). Within the web, chambers for egg sacs and pregnant females centralize some aspects of reproduction between many members. Because the sheet is asymmetric and continuous, groups of spiders can catch prey together. Flies are possibly attracted to the web (Diguet, 1915).

STRUCTURES OF COMMUNICATION

Animal communication is easy to talk about and hard to study, mainly because our everyday exchanges involve questions like 'who talks to whom?' or 'did I get through?' To investigate communication scientifically, we need something we can measure. Behavioral scientists may look at information transfer, which consists of any measurable communication units which are directed into the environment by an organism. In looking at information transfer, we implicate structure and design as substrate for transfer of communication units. Also, since signal energy deteriorates over distance, animals must arrange to be in resolving range. To widen this range they produce some signal transport network. Like a spider in her web, every human is surrounded by structural extensions of his senses; we are interconnected by telephone, and telex wires, radio waves, roadways, railways, postal ways and air ways. We call our neighbor up, send a letter, exchange books, or walk through halls and over roads to see him personally. We are directly tied to our conspecifics by the structural networks of our civilization.

Spacing is one social factor dependent on communication. Unless they distribute completely at random, animals either aggregate or spread apart, and these distribution patterns are dependent on information exchange between individuals. In this sense many apparently solitary animals communicate with their conspecifics, giving signals necessary to preserve distances. There is likelihood that this is so in the single orb web builders.

In order to eat, spiders must receive some information from their potential prey, usually in the form of thread vibration. Here the orb structure organizes the environmental information by filtering out only prey of appropriate size (Witt, 1975), and dampening low vibrations or aerial sounds (Fink, *et al.*, 1975; Szlep, 1964; Walcott, 1969). In a social context, the resonance of the *Mallos* web provides for communal predation, because the web carries a clear signal when a trapped fly buzzes (the communal predatory cue), but dampens the vibrations of walking spiders (Burgess, 1975).

Wherever web connections are shared between animals, some vibratory signals will be transmitted. Thus, while two touching *Araneus diadematus* orbs frequently result in cannibalism, orbs of the colonial *Metepeira* are separated by a tangle of space web.

These functions have many counterparts in the societies of other living beings. As a structure builder, man designs houses to connect the units of his family, but includes doors and walls to contain individuals and to provide needed privacy. A company building may be designed to channel people to the executive's office, but inevitably there is a secretary present, who coordinates and filters the flow of traffic. Streets with smooth surfaces connect human habitations and permit circulation in vehicles or with soled shoes. Silk lines connect spiders for movement on hooked feet.

FACTORS INFLUENCING DESIGN

Design in human buildings and spider webs reflects the immediate functional requirements as well as traditions. Houses in suburban developments must provide the inhabitants with shelter of the proper size and with a comfortable environment, but they also contain non-functional elements like white columns, ornamental trims and gables, which are reminiscent of Greek temples. Similarly, features in the design of spider webs are explainable either through 'tradition' or through the immediate advantage they offer the builder.

We are not sure that the term 'tradition', which Webster defines as 'designed with conscious adherence to architectural styles of the past', strictly applies to spiders. Another name sometimes used is 'genetic inertia'. Their central nervous system, which signals to the legs and the rest of the body to move in a specific way so that silk is laid to form the web pattern, develops according to a genetic code. This code is passed on from generation to generation and, although subject to mutation and natural selection in individuals, for the species overall it is largely unchanged for long periods of time.

To explore the extent of previous coding, investigations have been made to determine whether spiders reflect individual experience in the web pattern: following earlier efforts, Reed, *et al.* (1970) measured web patterns of growing *Arnaeus diadematus* littermates, half of which had caught flies in their web daily, while the other half had been exclusively fed by mouth. One could speculate that non-use of the orb web as trap for prey would result in decreased attention to detail in construction, perhaps giving rise to less regular, wider-meshed webs. However, no difference could be found between the webs of fly-catching and those of mouth-fed spiders, indicating the minimal influence of experience on fine structural design. Other experiments with spiders raised under different conditions confirm this conclusion. One can infer that non-use of structural elements in spiders will lead to their disappearance even more slowly than in human building.

On the other hand, we have made pictures to show that some novel environmental contingencies are reflected in design (Fig. 3). These photographs were made when spiders were confined to cages in which they could not select an appropriate site; such a condition may never occur in nature, where they can change web site according to available open space. Under these somewhat artificial building conditions, mechanisms exist which adjust to immediate requirements in web-building spiders.

Partially in an effort to test the effects of extreme environmental changes on web pattern, and partially to find out whether behavior of an invertebrate animal can adjust to weightless conditions which have never been experienced by the species before, web-building spiders were sent into space to Skylab II as it circled the earth. Two animals were carried to the lab in small vials in the astronauts' pockets; they were released into cages, and were monitored photographically. Four days after release from the vials the first animal started to build a web which was about as large and the silk as regularly spaced as if it had been made on Earth.

The webs were distinctly different from earth webs only in radial angle distribution, thickness of thread and number of turning points in the spiral, all indicators of orientation to gravity (Witt, *et al.*, 1976). One can compare the activities the spiders and astronauts performed under weightless conditions: the latter went through extensive training, read and thought about how to adjust to the expected new conditions, while the spiders had to cope with everything completely unprepared. Both solved the problem of moving around and structuring their environment in the usual way, compensating efficiently for the absence of gravity. This indicates that comparable results can be achieved by the two different organisms, each approaching the problem in his own way.

There are no fossil webs preserved, so we do not know how the selection process has affected web design in phylogenetic spider history. The surprising observation is that only a few basic structural designs, like the orb, the sheet and the space pattern, are repeated time and again in various combinations by thousands of web-building spider species. It has given rise to speculation that they are so good and unique a solution to the functional problem, that they have been discovered several times independently by different species (see Kullmann, 1972).

Another way to explain the many appearances of few designs in various species would be to assume the existence of an ancestral web-builder which was a subsocial animal with a composite web complex, similar to that now found in *Metepeira*. With development through the millennia, increasing specialization occurred: some species developed into single hunters with very large, regularly and quickly constructed orbs, others into social beings where communal asymmetric continuous webs satisfied their needs best, and others again into semisocial animals with mixed web structures. Robinson and Robinson (1975) call such a phenomenon 'web development with progressive reduction in complexity'. In contrast to men, who preserved the flexibility to live alone in family or communal groups, housed in single or multifamily dwellings, present spiders are largely born into their social and web patterns, which are species-specific, coded in their genes.

Pattern changes throughout the lifetime of an animal are another indirect piece of evidence that the various designs of spider webs have a common origin. Newly hatched *Araneus diadematus* spiders construct and live communally on a space web. As long as they stay on this structure, they show mutual tolerance, even though they already have the ability to catch and wrap small prey. After one to two weeks, single animals will leave and build a first, perfect orb web of their own; on this new web all signs of tolerance disappear, and littermates are attacked and killed if they stray onto the orb.

One has to conclude that here the ability to construct space webs and geometric orbs are both genetically transmitted to every *Araneus diadematus* individual, becoming manifest at different periods in their lives. If the animals build two different types of web in their lifetimes, this implies a change in the web-building 'program' contained in the central nervous system. It is important to remember at this point that many other factors, such as body shape, are considered when a phylogenetic family tree of spiders is constructed: our interest at present is only to look at the web design as one component for identification of relationships.

The choice of material influences design. As steel beams or prefabricated units of reinforced concrete become available, new possibilities are opened in the construction of building spaces. Spiders, in contrast, have apparently kept to one material in all their structures, a polypeptide: silk. Silks of very similar composition have been used widely, even by animals as remotely related to spiders as insects, mainly moths and butterflies, the most widely known being the larvae of the moth *Bombyx mori*, the silk worm. Lucas and Rudall (1968), reviewing studies of the silk of the orb-weaving spiders *Argiopidae*, have compared silks from various glands in the same species with silks produced by other species.

The thread which bears the weight of the spider and maintains the tension of the web contains a high percentage of short side-chain amino acids: Peakall (Witt *et al.*, 1968) gives for alanine figures between 32.7 and 33.4 g/100g silk, for glycine 24.3 g/100 g silk, and serine 6.3 to 6.4 g/100 g silk. 10 or 11 other amino acids with longer side-chains make up the rest of the silk. A comparison shows that the strength of dragline silk with 7.8 g/denier tenacity is almost as high as that of nylon with 8.7 g/denier: but at the same time the extensibility of spider silk is considerably higher. To accomplish similar ends, both spiders and humans have developed comparable processes. With the building of the Brooklyn Bridge, a suspension bridge completed in 1883, the Roeblings, father and son, developed a device for spinning steel strands on the job into great cables and used these in crossing vast distances with majestic grace. Steel thus was used in tension, consistent with its inherent nature' (Lloyd Wright, 1962).

Comparing drag-line silk, which has to bear the weight of the animal, with cocoon silk, which has more protective-isolating functions, Lucas and Rudall (1968) conclude that the mechanical properties of these two silks made by the same animal are appropriate for their function in that the drag-line has a very high tensile strength, while that of the cocoon is only moderate. After developing such optimal materials, genetic inertia insured that spiders would use them for many generations. Or looking at it in another way, the development of strong and elastic silk has made it possible to produce the current web designs; but the inherited pattern of silk synthesis has thereafter restricted the possible variety of web structures.

Under human conditions, material restraints can be observed in Greek temples. The stone structures followed post and beam construction, which was developed with the older material, wood. Spaces became limited by the length of stone beams, and columns had to be spaced close together, resulting in massive buildings. Only generations later were the arch and vault developed, making it possible to build greater spans out of stones; and the light Gothic cathedrals could be constructed by using the 'new' material in an adequate way. Stone was eventually superceded by steel and reinforced concrete, which again led to new developments in human building design.

CONCLUSIONS

We have analyzed a small sample of spider webs, deliberately selected for its great variety. We have tried to explain the characteristic design of each structure by the functional requirements. Parallels were drawn between the design of human and spider structures, and in many instances it was possible to compare structural details with each other and find similar underlying engineering principles.

Like humans, spiders build temporary as well as permanent structures, the former requiring a plan which can be executed quickly, the latter being built more slowly, with options for later additions. The embracing modular design has been found economical in both living beings for certain building requirements; the repetitious design for others.

Individuals have to communicate and require a certain amount of privacy. Both needs can be traced in the buildings constructed by spiders and by men. There are walls to separate individuals, as well as pathways for access to each other; and communication over distances is achieved in both kinds of structures through specialized elements, like vibrating silk lines or electric wires.

Designs reflect clearly the degree of social behavior which the inhabitants exhibit. Single living beings are housed differently from families and fraternal groups. Offspring can be raised in the parents' structures, or can occupy their own shelter, designed to serve only the babies' functions.

Spiders' space, orb, and sheet webs have been shown to be distinctly different in design as well as function. They represent different adaptive strategies, and have their parallels in human construction. We have seen that they can occur by themselves, or in combination. Thus many functions can be served in one building through the integration of designs.

Even the obvious differences between arachnid and human structures, like building material and coding of design, can be seen as showing some similarities in underlying system principles. The natural selection process for the most efficient spider web is comparable to economical considerations which enter an architect's mind when he designs a building. Materials, though more uniform in spider structures than in human buildings, have been selected in both examples for efficiency, and have consequently dictated structural layouts.

One of the most interesting features of spider webs is their interaction with the environment. The surroundings influence web structures, but, in return, web structures alter the area in which they occur. We have only just started to investigate such questions. The understanding of this interaction between building, builder, and the environment may be the area in which we human habitat builders can learn most in the future from observing spider web designs more closely.

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