The Web as a Means of Communication[1]

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Abstract. The radial structure of the orb web with the spider in the center, and the
tightly stretched polypeptide material with its specific chemical and physical properties, are
discussed as efficient transmitters of various signals to a number of specialized sense organs
on the spider's body. An animal's behavior in response to a signal is dependent on the nature
of the signal and on age, sex and species of the receiver. An overview of the research
literature endeavors to separate a small amount of evidence from a large array of speculation
and surmise, in regard to the orb web as a means of communication, mainly in the cross-
spider, *Araneus diadematus* Cl.

Introduction

Communication has been defined as the act of imparting or transmitting
information, the facts or information communicated, or the access between
persons or places (*Webster,* 1965). This paper is limited to discussion of the orb
web as a means of communication in spiders. If one observes the spider turning
toward a fly which has just struck the web, in contrast to the same spider sitting
unresponsive on the surface of a table while a fly walks by (*Baltzer,* 1923) — or
if one observes the elaborate approach and retreat ritual elicited by the male
spider's drumming on the female's web — one can hardly have doubts about the

important role which the web plays in imparting or transmitting information; it constitutes an essential route of access to the spider's perceptual systems.

There is much less certainty about the nature of the signal. It may be asked whether the web transmits and the animal receives just one signal which puts it on alert, or whether there are specific frequencies which are recognized as signals of danger, and others as challenges for attack. Do the eight legs lying on different threads provide the means for establishing the direction and distance of the prey? And how much is actually transmitted by the web, how much by other means such as airborne sound? As one looks at the results of experiments and observations, one finds an abundance of predominantly circumstantial evidence, much of which is in my judgment quite convincing for the designation of the web as a means of communication. However, there is an absence of reports on the investigation of the whole chain of events, starting with the origin of the signal, its transmission, its reception, and final analysis by the receiver. If the animal has an organ particularly sensitive to vibrations of the substrate, and if the strands of the web will transmit the struggles of the prey, and the animal's behavior indicates that it reacts to the movements of the prey, one could assume that vibrations transmitted through silk strands of the web are signals containing information for the spider about prey. Although investigations may alter details, it will be shown in the following, on the basis of circumstantial evidence only, that it has to be assumed that the web forms a substantial means of communication between spider and spider, between spider and prey, and between spiders and their environment[2].

The Web as a Substrate for Communication

Web Architecture

A look at an orb web photograph (fig. 1) shows specific components of the structure as most suitable candidates for reception and transmission of information to the centrally located spider. All orb webs are variations on the same theme, with a slightly larger or smaller central area, or with more or less oval shape (*Witt et al.*, 1972). The signal thread, which in some webs connects the centrally located hub with the legs of a peripherally hidden spider (fig. 2), appears to make the function of the radial structure even more obvious. The radii function as extensions of the sensitive eight legs of the spider, and so for a nearly blind animal enlarge the perceptual space. The communication advantages

2 Most observations have been made on *Araneus diadematus;* where not specifically mentioned, this species was observed.
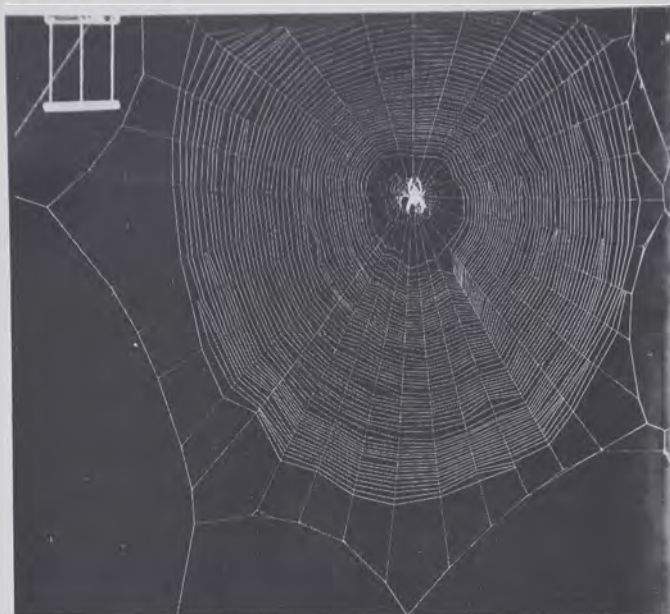
Fig. 1. This web of an adult female *Araneus diadematus* or cross spider is one of many which the animal built in the laboratory in the early morning hours during a period of about 30 min. The three parallel lines of the scale in the upper corner indicate the direction of gravity and 20-mm distance between each two of the three threads. Observe the radial structure of the orb, with the spider in the hub, and the suspension of the frame in the environment.

of radial construction can be appreciated if one contrasts it with the inefficiency of signal transmission to one point in a web which consisted of a rectangular grid, in which the threads formed small squares.

If we touch a vibrating tuning fork to one radius of the web (*Boys,* 1880), a centrally located spider will immediately turn in the direction of the fork. It will run out toward the fork, and it may even wrap some swathing silk around its prongs. If less hungry, the animal may apply only short pulls to the radius while it stays in the hub. It has been shown (*Peters,* 1931, 1933; *Bays,* 1962; *Robinson,* 1969), that a weighty object like a glass bead, when properly vibrated, bears sufficient resemblance to a struggling prey to bring a hesitant spider out to the object. The radii put the spider virtually 'in touch' with the fly.

Such observations leave hardly a doubt that the web architecture plays a role in communication between prey and predator and, as will be seen later, between mature male and female of the same species.

Fig. 2. Another species of spider, *Zygiella-x-notata,* leaves one sector of the orb web free of spiral threads. A signal thread connects the hub with the retreat. During most of the day the spider sits in the retreat, front legs on the signal thread, and waits for prey to get entangled in the web. Vibrations are presumably transmitted from any part of the web through the radii to the hub and from there through the signal thread to the spider's legs.

Other parts of the orb web, i.e., the frame and the sticky spiral, probably play a supportive or at least a non-inhibitory role in communication. The frame suspends the whole cartwheel pattern under balanced tension in the air and quite effectively buffers against shifts in the supporting structures. Observations of frame construction show an animal's efforts to revise the structure repeatedly through shortening of frame threads (*Salzmann and Witt,* 1973). An *Argiope aurantia* web, anchored only in grass, survives a heavy breeze showing that frame threads are good mediators between a shifting environmental structure and a relatively rigidly, fine-meshed net.

The sticky or catching spiral, which crosses the radii at angles close to $90°$, is thinner and more elastic than the radial thread, and provides minimal inhibition to the transmission of vibratory signals along the radii. That the thinness of a strand is important is stressed by *Jackson*'s (1971) close-up photographs of radius-spiral crossings: a thickened sleeve gives strength to the connection and adds only a little rigidity to the transmitting radial threads (fig. 3).
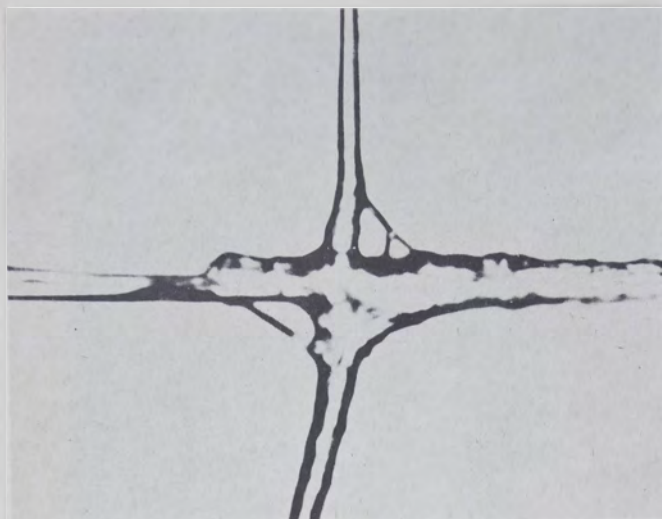
Fig. 3. In this close-up photograph by *Jackson* (1971) the radius runs from right to left, the spiral vertical, the periphery of the web is toward the right. Note how a relatively thick sleeve of protein material reinforces the crossing of the threads, while the silk in between is thin and has an even surface.

The spider's practice of tightening the web, after prey has been cut out, points to the importance of maintaining an even tension. It preserves the structure's function as a transmitter; for prey-catching alone, a loose web would be just as effective as a tight one. Often no effort is made to close the hole which results from detaching the prey; but as figure 4 shows, the periphery of the hole is reinforced so that sagging of the residual structure is prevented. This peripheral reinforcing is only done for small repairs; more extensive destruction results in partial replacement of the missing web part.

The idea had been proposed (*Finck*, personal communication) that the web may provide an early warning system for the approach of flying prey. It could hypothetically amplify the air disturbances produced by a slowly approaching fly, and transmit them to the waiting spider. As far as I know, no such function has up to this time been established (*Walcott*, 1969; *Finck*, 1972), and the existence of a variety of hairs on the spider's legs which are highly sensitive to air currents makes such a function for the web unnecessary. If a vibrating tuning fork is moved through the air toward a spider, it raises the front legs in the direction of the fork as if probing for air-transmitted waves, rather than receiving
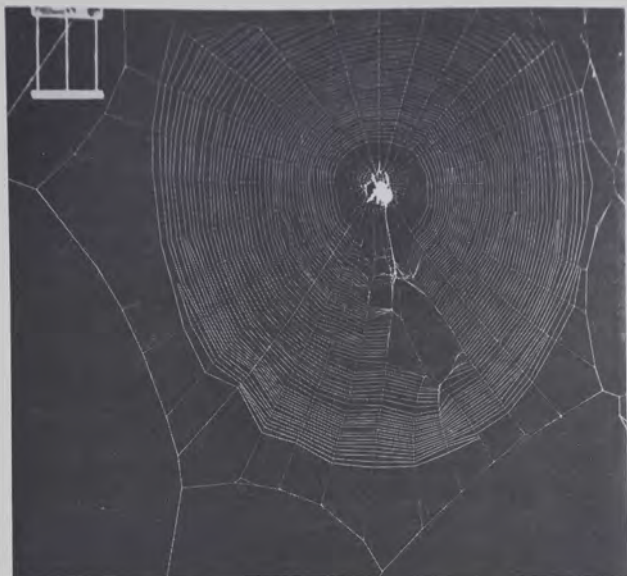
Fig. 4. The same web as in figure 1 was photographed after the spider had caught one house-fly. Note the big hole in the net and the reinforcements which the spider has applied to the sides of the hole: the undamaged part of the web is as tight and functional as before.

vibrations from the web. At our present state of knowledge there is no good reason for assuming that the web acts as a receptor for airborne waves, and that it provides an early warning system for the spider.

Some Relevant Information on Silk Chemistry and Physics

Only one type of gland, the ampullate gland, produces the dry silk for hub, radii, and frame of the orb web (*Peakall,* 1964, 1968); other glands provide the cover and/or the core of the viscid spiral thread, others the silk for the egg sac, and others again the attachment discs and swathing bands. The product of the ampullate glands should provide thread suitable for transmitting signals as well as permit the spiders to run along the radii to any part of the web.

For amino acid analysis, *Peakall* either rolled out ampullate silk onto a machine-turned glass rod and dissolved the product, or he collected web silk just before the sticky spiral had been started. He was able to establish the amino acid composition of structural silk, confirming earlier analyses of *Lucas and Shaw* (1961). A predominance of amino acids with small side-chains (glycine, alanine, serine) was found, with variations in ratio according to species. Such composi-

tion appears to be dictated by structural requirements of the silk; it does not seem to reflect phylogenetic relationships of the builders. It can be deduced from these data that the function of the structural silk strands is of prime importance for the survival of the animal. One such important function is communication.

Somewhere between the lumen of the ampullate gland and the emergence from the spinneret a transformation takes place: the fluid silk is made into an insoluble and strong thread. The process is not completely understood. *Warwicker* (1960, 1961) concludes from X-ray diffraction photographs that his data are best fitted by 'random packing of antiparallel pleated sheets of polypeptide chains'. The high tenacity of the structural silk (7.8 g/denier) and its considerable elasticity (extension of 31 at break) (*Lucas,* 1964), can be explained as a result of the macromolecular structure. If one considers the relatively large bulk of an adult female *Araneus diadematus* spider with a weight of about 500 mg dangling at the end of or pulling with full strength at a silk strand of $1-2\,\mu$ diameter without breaking it, one gets an impression of the high strength and elasticity required of the thread.

Of special interest are the calculations of *Langer* (1969) who finds that the 'material properties of the silks are related to the structure and functions of the spider webs'. He considers gravity and wind forces, but finds localized forces of particular interest. He treats mathematically two signal velocities on a silk filament, a longitudinal velocity of about 2 km/sec and a transverse velocity which is much slower. *Langer* concludes that a tug in one web element results in a proportional response in every other element of the web, with a time delay of the faster signal in the order of $10\,\mu$sec. The separate circulation of the two signals through the web to the spider's leg could quickly provide information on the nature, location, and sort of disturbance in the web.

While there can be hardly any doubt that the orb web qualifies as a good transmitter of vibrations and tension changes, its part in providing chemical signals has hardly been explored. *Millot* (1946) describes observations of *Kaston* (1936) and experiments of his own which make it likely that a spider receives chemical signals when it touches the web. According to *Millot,* a thread secreted by a female excited the male of the same species on touch, even in the absence of the female. If the silk was left in air for 2 days, or if it was dipped for 15 min into ether, it no longer excited the male. After evaporation of the ether, the glass still elicited a reaction from the male. *Millot*'s conclusion, that sexual behavior of male spiders is released by a volatile chemical on the silk (and integument) of the female, may not apply to all web-builders. It would be important to repeat the experiment with several orb-web builders and carefully exclude all other cues; increasing experience with pheromones (*Blum and Brand,* 1973) should make it worthwhile to try to identify messenger substances. Organs which could receive *Millot*'s chemical signals from the thread will be described below.

The Spider as a Receiver of Communication through the Web

Vision

It has been stated earlier that vibratory signals play the main role in information gathering for a spider in the orb web. Several lines of evidence support the view that vision is unimportant.

As far as can be established, the histological substrate for high visual activity is lacking in web-builders. *Hanström* (1934) points out that web-building spiders, in contrast to hunters, show a relatively poorly developed nerve mass for receiving and processing visual signals. On the other hand, web-builders, in contrast to hunting spiders, have a relatively well developed central body in the central nervous system, which apparently coordinates leg placement in web construction. Destruction of the central body by a laser beam was followed by a severe distintegration of the pattern for all webs built afterwards (*Witt,* 1969).

Most spiders construct their webs in the dark and can use them for prey catching during the night. In order to make sure that no residual light was needed in web construction, the author compared 27 parameters in the geometry of orb webs built by spiders in the lighted laboratory with orb webs built by the same spiders after they had been sealed into an opaque box: no differences were found. *Peters* (1931) eliminated the eyes of web-builders and obtained similar results: the orbs built thereafter appeared unchanged.

Lyriform Organs (Slit Sense Organs)

In a brief, comprehensive review, *Barth* (1973) discusses the structures of these organs and deduces their function from structural principles. The receptors consist of either one or several slits which are covered with a flexible skin in which a nerve fiber terminates. The slits lie between rigid pieces of spider cuticle. The skin is deformed as a result of pressure on the cuticle, and even small forces applied to the cuticle provide deformation of the sensillum. Mechano-electrical transduction is most likely caused by non-uniform compressional deformation of the dendritic end of the receptor nerve, and the signal is analyzed in the central nervous system.

An interesting feature is the distribution of the slit sense organs: over 100 have been counted, mainly along the eight legs of the spider, close to each joint and near the pedicel. *Seyfarth and Barth* (1972) ascribe the kinesthetic orientation of their spider (*Cupiennius salei* Keys.) to these organs. They are able to show, in selective destruction experiments, that spiders are impaired in their ability to find their way back if specific slit sense organs are destroyed. The same organs could play an important role in web construction and orientation in the web. Consider the nearly blind animal (in the dark) apparently using information on the position of all eight legs to probe the width of angles between threads and thread distances. It is interesting to speculate that the input from more than

100 slit sense organs from all parts of the body could be integrated and analyzed in the central nervous system in such a manner that the animal has an inner 'picture' of the position of all parts of its body at all times. Such function could be compared to that of the human secondary visual centers, which integrate information received from many points on the retina. It is difficult to explain in any other way the number of slit sense organs and the well-oriented behavior of the spider on the web.

The lyriform organs consist of a row of several slits. They are located on the distal end of the metatarsus and appear to be sensitive vibration receptors (*Liesenfeld*, 1961; *Walcott*, 1969). All investigators find a discrepancy between the behavior of the animals and the electrophysiological records: while the prey vibrates the web at relatively low frequencies, and while the spider reacts quickly to frequencies well under 50 Hz, the electrophysiological reaction is definitely most sensitive at frequencies over 100 Hz. It is even more puzzling when *Bays* (1962) states that he could train his spiders to distinguish between the vibration of two low frequency tuning forks, and *Markl* (1973) finds the electrical sensitivity of spider-leg nerves nearly independent of frequencies below 100 Hz. One may have to consider the complexity of the signal of varying amplitude and with possible overtones which the fly elicits, together with input from other organs which perceive, for example, airborne vibrations, to understand the behavioral reaction of the spider to low frequency signals.

Trichobothria

Most hairs covering the legs of spiders lie closely along the surface; interposed single bristles $100-700\,\mu$ long stand at right angles to the cuticle. The latter are called trichobothria; under a microscope it can be seen that they vibrate slightly in the faintest breeze. *Görner and Andrews* (1969) have shown, in non-orb web builders, that trichobothria react to airborne vibrations of low frequency over short distances. *Markl* (1973) discusses the difficulties which are encountered when one tries to distinguish between airborne and surface-transmitted vibrations. For this discussion we can regard trichobothria as auxiliary perceptual organs for airborne waves which add to the information which the spider received through the web.

Chemosensitive Hairs

It was considered above that the male spider responds to a possible chemical transmitter on threads of the webs of mature females. Observation of prey-handling by spiders leaves no doubt that the animals can distinguish between bitter tasting (quinine), and sweet tasting (sugar), and many other solutions. But until recently it remained an open question whether the spider had to swallow the chemical in order to identify it.

W. Holden (unpublished film) took moving pictures in the author's labora-

Fig. 5. A spider had been enticed to leave the hub and run down toward a fly in the periphery of the web while movie pictures were being taken at 18 frames per sec; the fly was covered with quinine solution of very bitter taste. In this picture the spider just touches the fly with a leg; in the next it has already started to withdraw. Repetition of such procedures of movie-taking, with bitter or untreated flies, indicates that contact with one leg is sufficient to transmit a chemical signal to the animal. Photograph by *W. Holden.*

tory of spiders rushing out to a fly in the periphery of the orb web: in several instances the fly had been covered with quinine solution, a non-volatile substance. The pictures show clearly (fig. 5) that after barely touching the prey with the tip of one front leg, the spider turned away if quinine was present; by contrast it approached further and bit the prey which was untreated.

Curved, blunt-tipped hairs were found by *Foelix* (1970), among other places, on the tips of the legs of web-building spiders. The tip of each hair is open, and the lumen is innervated, so that a striking similarity exists with contact chemoreceptors in insects. Such hairs would permit a spider running along a

thread to identify chemicals on the surface of the silk. While electrophysiological proof is lacking, it is likely that the web serves also for chemical communication between spiders.

Types of Communication in Orb Webs

Communication between Conspecifics in Early Life

In the lifetime of a spider, several striking changes can be observed in the reaction of one animal to the presence of another animal of the same species in one web. Maturation of the web-builder may cause the changes, alteration in web pattern with age of the builder may be the instrument. It will be shown that our knowledge is quite fragmentary, and that the field is wide open for experimental investigations.

Several hundred young spiders emerge nearly simultaneously from an egg cocoon. They look like small editions of adults and already at this early age, begin to lay threads as they run. A few days after the first animals have hatched, one can observe a sheet-like silk structure which lacks apparent geometry: it is usually called a communal web, and is the result of all the babies' joint efforts. The spiderlings run restlessly around on the sheet, touch each other, and lay down additional threads. Very little is known about factors which influence the activity of the animals during this time. There exists a definite tendency to move upward on consecutive days, and the animals appear to be attracted to each other. If sufficient space is available, one can see, after 2–3 weeks, single spiders in the hub of individual geometric orb webs near the communal web. Measurements reveal (*Witt et al.*, 1972) that the early orb webs look narrow-meshed, small and very regular, and the pattern bears a striking resemblance to the adult web.

Peters (1969) argues that the presence of a suitable frame promotes early orb-web construction. There are some indications that lack of space postpones construction of the first orb webs. If sufficient space is not provided in time, we find smaller spiders falling prey to their littermates.

Spiders like *Araneus diadematus* radically alter their behavior toward their siblings between the communal web stage and solitary life on the orb: they live peacefully together on the communal web, but they attack, bite, wrap and eat each other in the orb. The usual explanation for this change (see for example *Bristowe*, 1941) goes as follows: the spiderling hatches with a yolk supply in its abdomen. After the yolk has been exhausted, the animal feels hungry, which releases the performed orb-web building behavior, together with the corresponding behavior of trapping prey in the web. The more one thinks about such an argument, and the closer one observes the animals during the transitional period, the less convincing the simplicity of the causal chain becomes.

There is motion-picture evidence in the author's laboratory that a spiderling from the communal web attacks, bites, and wraps a *Drosophila* fly at a time when it is still living in peace with its littermates. Even during the communal web period it appears to be able to distinguish between a fly and other spiders. It also looks to the observer as if in the orb-web period the violence with which a littermate is attacked increases with time. An abrupt change in aggressiveness does not coincide with life on the new structure. I rather believe that a change in internal readiness, be it neural or chemical, makes a spider kill its littermate one day, and tolerate it a day earlier. In other words, it is not the signal from one spider to the other which determines the behavior — assuming that the signal is different in a geometric orb and in a sheet — but rather the 'mood' of the receiving animal which causes it to attack once and tolerate another time.

After the initial orb web has been built by a spider, the structural details change in a systematic fashion from childhood to maturity. *Witt et al.* (1972) have shown that in *Araneus diadematus* the number of radii decreases, the mesh size and irregularity of spacing increases, and the thread length and catching-area size increase first, and later decrease statistically significantly, during the life of an individual. There exists an age-characteristic web at all times. The obvious question is whether the changing pattern can be simply explained by the changing body proportions of the builder, or whether we have to look for other variables.

Two observations speak against the first argument:

(1) if the web fine-structure were well adjusted to the body proportions of the builder, a spider should have difficulty in using another spider's web, if the other individual were of different weight and size; no such difference in prey-catching efficiency was found by *LeGuelte* (1969) and *Richardson* (1973) on webs of spiders of different size and species.

(2) According to an extensive statistical analysis by *Rawlings* (*Witt et al.*, 1972) spiders of two species *Argiope aurantia* and *Araneus diadematus*, at a time when they showed similar body weight and leg length, built orb webs so significantly different in several structural details, that the measures permitted classification of the builder as to its species. Body weight and leg length apparently did not determine web fine structure.

At the present stage of our knowledge one is lead to conclude that a gradual change in the information-receiving spider rather than a change in the transmitting web structure determines alterations in behavior between conspecifics.

Communication through the Web in Mid-Life

From around the time a female builds its first orb to a few weeks after the last molt, the spider seems to lead a lonely life in the hub of its web. It turns in the direction in which the web is touched and shows a number of different behaviors, obviously as a consequence of the signal it receives. As far as can be

established, the response to the signal also depends on the state of the animal, and evidence shows that hunger as well as experience play a role in the regulation of a spider's reaction to web-transmitted signals. Again, the observed behavior is the composite result of sensory input and the inner state of the animal.

In their extensive analysis of predatory behavior in an orb-weaving spider, *Robinson and Olazarri* (1971) called the first two stages prey location and prey discrimination. Their thorough analysis of behavior units is mainly concerned with sequences after the spider has touched the prey, and they discuss problems of communication only marginally.

According to *Robinson and Olazarri* the spider is being alerted by the impact of an object striking the web. Next it turns in the direction of the impact, frequently plucking the radii with one or two sharp jerks of the front legs. Plucking can continue during approach. The spider may then either bite the prey at once, wrap it first, return to the hub, or cut and drop the prey out of the web. Toward very large prey the spider may approach slowly, sometimes with anterior legs raised off the web and flexed back. Little is known about the kind of signals transmitted from prey to predator during all this time.

The alert reaction of the spider to a vibrating tuning fork touching the web (*Boys,* 1880) provides evidence that low-frequency vibrations transmitted along radii are frequently among the first signals which reach the spider. By turning around and plucking, the animal appears to search for further information. Plucking may induce an immobile prey to struggle, it may serve exact location of the object in the web, and it may provide preliminary information on the size and weight of the potential prey. The question must be asked whether a spider can identify an object through the web (or the air) before it touches it. I believe that it can.

The experiments of *Bays* (1962) support this belief: he paired one frequency tuning fork with a bitter tasting fly and another frequency with a sugar-coated animal. After a training period he could replace the flies with glass beads of similar weights and could randomize the sequence with which he offered the taste-frequency combination. His spiders would learn to approach, bite and wrap one set of tasteless beads, and cut out the other set, apparently without touching them. If confirmed, this would show that spiders can distinguish between different tuning forks, and that they can avoid adverse objects in the web from a distance. The signal transmitted by the web would provide sufficient information to determine the subsequent type of behavior.

There is also a substantial amount of anecdotal evidence that spiders cut dangerous bees from the web without ever touching them. They would have to 'know', or have learned, which signals warn of danger, and which incite approach and attack. It is conceivable, but has never been proven, that spiders can learn from one adverse experience about danger of certain prey. *Reed et al.* (1970) found that prey-catching behavior, in contrast to web building, showed signs of

plasticity: adult spiders who had never been allowed to catch prey on the web
built normal patterns, but disregarded flies in their webs.

As far as can be established from the literature and our own observations
there is no evidence that spiders in mid-life discriminate between their conspe-
cifics and other prey items in the web.

Approach of Male to Female

The mature female permits the mature male to approach through the orb
web for copulation. The elaborate ritual which precedes copulation looks to an
observer as if it has become difficult for the female web-builder to accept any-
thing but prey in its trap. There are characteristic differences from species to
species. My own observations with *Araneus diadematus* will be mainly men-
tioned, and some of the interesting descriptions of *Grasshoff* (1964) will help in
the identification of species specificity underlying communication in the web by
mating spiders.

Many weeks before maturity, males stop web building; they move around
over relatively great distances, laying drag-lines of silk as they run. In the labora-
tory, it is nearly impossible during that time to induce them to take food, and
they stop growing. The female of the species, in contrast, builds large webs daily
and feeds voraciously. The female webs just before and after the last molt reach
the largest size and are built with the longest thread, if compared to webs built
at any other time in the spider's life. At mating time the female may weigh
5–10 times as much as the male.

Frings and Frings (1968) write that the male generally finds the female by
chemical signals: 'Her web is usually scented with a specific odor. The male
wanders about until he blunders upon the web. He is capable of determining the
species and sex, but generally not the sexual readiness of the female. If she is,
the male generally uses vibrations of the web as signals.' The authors do not
present the evidence on which these statements are based. When the male gets to
the female web, it shows two characteristic behaviors: it fastens a 'safety thread'
outside the female's web which lets it swing away, and return to the web, at any
time; it plucks the thread on which the female's front legs lie in a characteristic
rhythm. Recordings of the signals which pass through the web are to my knowl-
edge lacking, and *Grasshoff*'s description is detailed enough to show what we
know about the communication between male and female at that time.

The male plucks a radius eight to nine times in quick succession and then
applies a strong jerk, which shakes the female visibly. After an interval of a few
seconds the process is repeated. About 5 min after the male has begun its ap-
proach, the female responds by moving toward the male, turning the abdominal
surface toward the male and shaking the two pairs of anterior legs. The male
answers with further approach, plucking with increasing speed, slowly beginning
to vibrate its whole body, interrupted by periods of immobility. Finally the male

jumps toward the female, holds her legs, and copulation occurs. The preliminary approach may be repeated many times, interrupted by the swinging of the male out of the female's web on its security thread.

As in all other instances discussed earlier, there can be no doubt that the web is an important substrate for the communication between the sexes. It seems likely that chemical and vibratory signals are used, the latter being transmitted through silk as well as through the air.

One interesting question addresses itself to the role of the female in the early phases of mating; does she actively participate, sending signals back to the courting male? I believe this to be most likely. *Scarboro* (personal communication) has observed in this laboratory that a web without a female is much less attractive to a male, though some drumming and searching takes place. And even a web with an inert weight in the hub appears to present an insufficient stimulus for the male to continue courtship behavior. *Grasshoff* describes an *Araneus pallidus* male on an *Araneus diadematus* web. It appears unable to arouse the female to cooperation. Interestingly enough it took 5 h for the male to cease approaching the wrong female; and only a few minutes later, after the male had been removed and the proper male brought to the web, the female mated with the male of its species.

From such a description it appears doubtful that there is a species specific early recognition system through the web between male and female. It looks as if, beyond a general alertness caused by the male's drumming on the web, the female 'waits and sees'; the male apparently takes a long time and has to approach quite close to the female in order to be sure that it is dealing with the proper species. The question of the function of the species-specific form of the orb web is left wide open. Investigations have not been detailed enough, in my opinion, to discard the hypothesis that the variation in web architecture according to age and species has some survival value, like aiding in species isolation or helping the male to recognize the mature female web builder. One must hope that questions like these will be investigated in the near future.

Epilogue

There must be a difference in communication through webs between the builders of single orbs, the subsocial spiders with groups of interconnected webs, and the social spiders with mile-long sheet-webs (*Kullmann,* 1972). How do social spiders perceive the difference between members of their species and potential prey? *Krafft* (1971) has identified several signals in *Agelena consociata,* mainly of a chemical nature, which support interindividual tolerance and even cooperation. Little is known about the role which the web plays in communication of these spiders. To discuss this further would require too much speculation for which too little knowledge exists at the present time.

The whole discussion of the web as a means of communication has suffered from lack of exact data. Many authors have observed the phenomenon and reported it marginally in papers which address themselves mainly to other subjects. It has been difficult, sometimes impossible, to decide who should be credited with having thought of and contributed to any of the aspects of communication which were discussed here. Sometimes I have selected the earliest known author, at another time a sentence from a recent review in order to have one paper of each author in the reference list. This review in no way provides a complete list of references.

Maybe the discussion of communication requires the presentation of many different approaches, in order to lead to a final understanding of the process. The web architecture and the chemical and physical properties of silk appeared as important as the perceptual equipment and behavioral record of web-building and use. At a future date it may become clear to what extent the change in web pattern and to what extent the maturation of an animal contribute to the extensive changes in behavior which a spider shows in reaction to signals transmitted through its web.

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