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# ORB WEBS: FORM AND FUNCTION

by

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This report reviews results of investigations, which were performed over a long period of time, namely for more than 25 years. However, only results of those experiments are summarized, which are based on a single method, the measurement and evaluation of web geometry of spiders. Most observations (many thousands) have been made on webs of *Araneus diadematus* Clerck, less on webs of *Zygiella x-notata* Clerck, or *Argiope aurantia* Lucas, and even less on five other species; this permits limited generalization of conclusions to other orb-web builders, and results are least applicable to those spiders which build horizontal webs and therefore use another set of cues.

My introduction to web photography and its measurement came through Prof. H. M. Peters in 1947. In the following years the method was further developed, leading to the use of a highly controlled laboratory environment, quick, simple photographic methods, and computer evaluation of measurements. Progress was made with the help of laboratory technicians, students and research fellows. While improved methodology permitted evaluation of hundreds of webs in a few weeks, statistical procedures were extensively applied to reduce measurements per web to a manageable minimum without loss of accuracy. About 50 research reports, resulting from measuring of webs, have been published over the years in scientific journals.

The human visual system is able to extract from a complex structure like the orb-web a great amount of information, and it may take many measurements and a long time to provide objective proof for an observation which an observer has made casually. Everybody who keeps orb-web building spiders around for some time can recognize each individual's web: i.e. an animal has escaped from its labelled cage and has spun a web in the corner of the laboratory; it is immediately identified by a look at the web. But it required the measurement and statistical evaluation (univariate analysis of variance and multiple discriminant analysis) of several webs of many individuals to show, that there are individual, litter (animals from one cocoon), and species web characteristics (Witt, Rawlings & Reed, 1972).

The differences just mentioned lie mainly in a combination of various size measures like thread length, number of radii and spiral turns, and the expanse of the center-, catching- and frame-areas. Size measures provide also information on many other interesting aspects of a spider's life. A large web covers a wider area in which flying prey can get caught; it also needs a larger open space in which it can be built. Such data permit speculation on the ecological significance of various web sizes. A large web built with a long thread requires more silk than a smaller web built with less silk; measures of thread length and thickness have led to the discovery of a humoral regulation of silk synthesis in the epithelium of the ampullate gland of *Araneus*; silk production can be slowed down by anticholinergic drugs like atropine (4 mg/kg in 16 hours); on the other hand, cholinergic drugs like physostigmine speed up silk synthesis: the relatively large webs built with more

than the normal amount of silk 36 hours after 1 mg/kg physostigmine stimulated speculation on regulatory mechanisms. Such regulations are probably located in the spider's central nervous system; and they would be responsible for adjusting thread spacing during web construction to the available silk supply.

Relatively reduced thread length is found in webs built by spiders who carry about 30% added weight and consequently build a thicker shorter thread. And a shorter thread is measured in webs built by spiders 36 hours after they have received 100 mg/kg of the tranquilizing drug diazepam (Valium); here the animal terminates web construction before the silk supply in the glands is exhausted; it has laid out a smaller structure, probably to save effort. In each such instance the insect-catching function of an orb web is preserved through adjustment of its form. One can speculate that only such flexibility in form accompanied by preservation of function has permitted web-building spiders to survive so long.

It is even more surprising to find that functional spider webs are built under extraterrestrial conditions, to which man adjusts mainly through a careful process of planning and environmental manipulation. Though to my knowledge the data obtained in the Skylab III experiment have not been given by the National Aeronautics and Space Administration to any scientist for evaluation, the scrutiny of newspaper reports and television pictures permitted preliminary conclusions. Two adult female *Araneus diadematus* Clerck, had built "control webs" on earth under conditions which simulated much of the environmental stress produced in space, leaving out only weightlessness. When these animals, which had been accustomed to construct orb webs by using their body weight to pull thread from the spinnerets and hang suspended from it, were successively released in the space laboratory, they appeared first (according to CBS television news pictures) to float helplessly through space, threads wafting in loose loops from their spinnerets. As far as can be ascertained, it took each animal only two days after it had been released from its tube, to construct an orb web; this first web appears to me in size (small) and regularity (slightly irregular spiral spacing) similar to the webs we recorded as first webs built by spiders which had been raised in narrow tubes (Reed, Witt & Peakall, 1970). From the little information we have so far it is apparent that the spacelab spiders, like their tube-released counterparts on earth, were able to build larger and more regular webs after only a few days. Better photographs than those obtained from newspapers are required to find out whether the usual oval web shape has been changed through lack of gravity. We can summarize that a web has been built — presumably after several trials and errors — under highly adverse environmental conditions. The building behavior, which looks to the observer of web-building as rigidly programmed as the works of a clock, proves to be adaptable to contingencies which can hardly be expected ever to arise on earth.

There is additional evidence that the orb web is so essential for the builder's survival, that a structure of some kind is built, even under highly adverse circumstances. Drugs can disturb the web-builder's behavior in many ways, from sluggishness after a sedative all the way to overstimulation by caffeine. In looking at the web measures from structures built by heavily drugged spiders, it appears that high doses of many drugs like caffeine, d-amphetamine, phenobarbital, or nitrous oxide cause highly irregular webs. The web form has been so severely altered that the definition of web geometry in polar coordinates is no longer helpful. One can hardly distinguish a hub and radii from spiral turns and frame threads. This has made it so far impossible to define severe web alterations in terms of drug specificity, — or as a definable disturbance of the central nervous system. Smaller

doses of the same drugs alter web-building behavior, as measured in the regularity of thread spacing, in various measurable, drug-specific ways.

Returning to our ability to distinguish between various web forms, we find that little training is necessary before one can guess the age of an orb-web builder reasonably accurately from looking at its webs. Again it required measurements of many hundred webs, and the correlation of web measures to age, sex, and body weight, to establish the complex growth pattern which the web follows throughout the life-time of the builder. Of webs built by orb-web spiders of different ages least is at present known about the form or function of the communal web which is constructed by hatching spiderlings. One can interpret it from the phylogenetic point of view; and other speakers here are more qualified than I to do that. Our laboratory pursues at present a line of investigation which tries to isolate and define the physiological and behavioral role which the communal web plays in the life of the animal. After the first orb web has been constructed, and after the spider has become solitary in its habit, the changes in pattern have been well defined in several species. The measure which we call "mesh width" permits to assess the fineness of the fabric; it constitutes a composite of area size and thread distance in the ring-shaped catching zone of the orb web; it determines the kind of prey which the web will hold. Mesh width changes most uniformly throughout the life-time of the web-builder: the young animal builds the densest catching structure, the just adult female web has significantly wider meshes, and the old female builds the catching area with a comparatively large mesh. Area size changes simultaneously from small in spiderlings to large in adults, and back to small in old animals. One can try to relate such changing form to the changing function of the web in prey catching; to communication, especially before mating; and to the web as substrate for the moving animal of changing size and proportions.

This last set of observations provides only one more example for our finding, that by measuring the form of the orb web one can gain valuable insight into its various functions (Witt, Reed, Peakall, 1968). This paper is the result of diligent measuring of many thousand webs performed by many scientists; we acknowledge much private and public support, most notably from the National Science Foundation.

## References

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