BRITISH ARACHNOLOGICAL SOCIETY

(formerly The British Spider Study Group)

VOL. 1 No. 5 BULLETIN January, 1970

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THE EVOLUTION OF SOCIAL PHENOMENA IN SPIDERS[1]

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> "I might just here mention that I found, near St.Fe Bajada, many large black spiders... having gregarious habits... . This gregarious habit, in so typical a genus as Epeira, among insects which are so bloodthirsty and solitary that even the two sexes attack each other, is a very singular fact."
>
> Charles Darwin, Voyage of the Beagle, p.37.

The spiders that Darwin remarked on are almost certainly a species of *Cyrtophora*, a widespread genus of orb weaving spiders known for their habits of forming large communities. Both before and after Darwin's observations, other writers have commented in the same anecdotal style on numerous examples of so-called social spiders, and all have found it equally remarkable that the "bloodthirsty" spiders could exist together in close contact without feeding on one another.

Such phenomena are now known from more than a dozen spider genera in eight families. No attempt has ever been made to survey the available information, or to offer an evolutionary explanation for what has been superficially considered social behavior among spiders. The importance of evolutionary explanations of behavior has been stressed by Lorenz (1956) among others. The problems inherent in such speculations (to use the proper term) fall into the categories of real problems and those that have arisen as artifacts of our incomplete knowledge. Certainly a lack of detailed field observations and carefully planned experimentation is the greatest barrier to further understanding. We do know enough about these cases, however, to state some of the real problems: (1) does the behavior of these spiders fit a meaningful definition of sociality, as it is applied in other arthropods? (2) what is the adaptive significance of such behavior? (3) do other related spiders show any preadaptations that might enhance the selective pressures leading to sociality? Since the mode of life of these spiders is not general knowledge, there follows a brief review of what is now known.

[1] While this paper was in press, a short review of sociality in spiders by Kullman (1968), written in German, appeared. Dr. Kullman's bibliography made me aware of two publications by Brignoli (1966, 1967) which deal with possible social relationships between different species of spiders, and with myrmecophilous and termitophilous spiders. I must point out that future research on sociality in spiders should concentrate on discovering how new colonies of truly social species are founded, and on the breeding structure of these species. The articles mentioned above have been inserted in the bibliography at the end of this paper.

I would like to express my appreciation to Dr. Mary Jane West, Dr. H.W.Levi, Dr. Ernst Mayr, Mr. William Eberhard and Mr. Fred Coyle for their helpful suggestions, but they should in no way be held accountable for any errors, or for the conclusions.

SURVEY OF SOCIAL BEHAVIOR IN SPIDERS

The majority of so-called social spiders belong to the cribellate families of araneomorph, or labidognath, spiders. No social Mygalomorpha are known, although there are some indications that subsocial phenomena are not uncommon (Coyle, verbal, 1968). Most non-cribellate social species belong to the Araneidae and Theridiidae, two of the most specialized families. Agelena consociata Denis (Chauvin and Denis, 1965) belongs to the Agelenidae, a rather generalized family, and is the most thoroughly studied species.

Family Dictynidae: Coenothele gregaria Simon has been reported on by Diguet (1909a, 1909b, 1915) in its native habitat in tropical Mexico, and by Semichon (1910) in France, where it was accidentally transported. The webs are woven over bushes and are usually about a cubic meter in volume. There are nearly a thousand individuals in a single large web; the natives carry such webs indoors for use against flies. Little else is known about this species.

Family Amaurobiidae: Amaurobius socialis Rainbow is known from the Jenolan Caves of New South Wales, Australia. The shawl-like webs are said to be stretched among stalactites and the largest measure nearly 12 by 4 feet (Rainbow, 1905). Each web contains numerous individual retreats in which the spiders are found while inactive. Egg sacs are constructed by individual females; they are papery and 7-8 mm. across. Simon (1908) set up a new genus, Phryganoporus, for three new species of amaurobiid from Australia "...said to be social (Simon,1908)..." but there is no further published information about these species.

Family Oecobiidae: A new species of Oecobius (Shear, in MS), a small one, native to the region of Lake Sayula, Jalisco, Mexico, was originally studied by me for taxonomic purposes. Stretched out, whole, preserved webs were only about 10" square, but each contained from 110-180 spiders in individual retreats. This species is unique among social spiders in that the females apparently deposit their eggs in a common egg sac (inferred from the observation that solitary species of the same genus lay from 2-10 eggs; the sacs in these social webs contained more than 200). Nothing is known of the life history.

Family Uloboridae: Simon (1891, 1892) described Uloborus republicanus from Venezuela and U.raffrayi from Singapore. U.republicanus weaves a large tangle supported by long lines to surrounding vegetation. Between these lines, individual females and juveniles weave typical uloborid orb webs, though all retreat to the central tangle when disturbed or inactive. After maturity, males stay in the central retreat, where mating takes place. Individual females construct egg sacs and guard them until hatching; the sacs are stellate in form and contain up to 163 eggs (Gertsch, 1949). A web of this species observed in the West Indies (Schwarz, 1904) was 7-9 feet wide, 5-7 feet high and 3 feet deep, and contained nearly a thousand individuals. Other smaller webs were inhabited by around 300 spiders. U.raffrayi has similar habits (Simon, 1892). In southwestern North America, U.arizonica and U.oweni occur in colonies of 20 to 200 individuals; the inference is that their habits are like those of U.republicanus (Muma and Gertsch, 1964), but since no central retreat is constructed, it seems unlikely that there is a real correspondence. Hatching and colony foundation has not been observed, nor have the spiders been observed to feed communally on captured prey.

Family Eresidae: Social species of Stegodyphus occur in Africa and in tropical Asia. The most complete published observations to date are those of Jambuthan (1905; the recent paper of Subrahmanyan, published in 1953, adds nothing to this), who observed S.sarsinorum in Madras. A photograph published in this paper showed a spongy mass of webbing 12-14 feet long and 2-5 feet wide, on a hedge. The main body of the web is honey-combed with tunnels and retreats; separate sheet webs surround the periphery, but these are each built by several spiders. When prey falls on one of these webs, it is attacked by a number of spiders and dragged to the interior where communal feeding takes place.

Males remain in the central web after maturity, and often interrupt the work of the females in order to mate. Egg sacs are constructed by individual females and are woven into the central mass. After hatching, the young are fed prey captured by adults and are even carried around on the backs of the females, but it is not known if each female limits her actions to her own brood. As the young mature, the previous generation dies off. The founding of new colonies was not observed, but Jambuthan (1905) speculated that pregnant females may be carried off by the wind; this is unlikely in view of their size.

In South Africa, an unidentified social Stegodyphus increases the size of the web by letting draglines out to the wind and strengthening them if they become attached. Eggs of this species are found in the fall (February-March), and after the young hatch the adults die off by early winter. The colonies were observed to move en masse to a new location when the webs were taken over by Mashona doormice (Marshall, 1898). Distant (1898) reported similar behavior in yet another species. Giltay (1927a, 1927b) found S.simoni to occupy a much smaller web lacking capture sheets.

For comparative purposes, it might be useful to refer to a study of the solitary S.lineatus carried out by Millot and Bourgin (1945). The web of this species resembles a funnel, with the large end pointing away from a tubular retreat occupied by the spider. The side walls are filled in irregularly, and much insect debris is incorporated in them. The female shows a certain degree of parental care, bringing the egg sac out of the tube each day to expose it to the sun. The female sometimes feeds small prey to the newly hatched young, but more commonly they attack prey communally and feed on it as a group. Millot and Bourgin (1945) found that under crowded conditions, the young could be induced to remain in the parental web long after the death of the mother, eventually elaborating it into a colony similar to that described for S.sarsinorum. It was emphasized, however, that this elaboration has not been observed in nature.

Family Araneidae: On the island of Teneriffe, Wheeler (1926a) observed a single nest of Cyrtophora citricola Simon extending for more than 100 feet along an Opuntia hedge, though more commonly the colonies were 12 by 4 feet. The web consists of an irregular network with numerous horizontal orbs suspended in it. Prey capture is usually carried out by individuals, and communal feeding has been observed (Wheeler, 1926a). Darchen (1965) published a photograph of a colony of Cyrtophora sp. in Gabon, and made the observation that the spiders compete for prey, often intruding into one another's orbs to steal captured insects. No cannibalism was observed, however. Egg sacs are not communal; each female makes a string of sausage-like sacs along the center of her own orb (Wheeler, 1926a).

Araneus bandeleiri was described by Simon (1891) from Venezuela. He found it to be not at all gregarious until the time came for the females to lay eggs, when they all aggregated and constructed a large, closed papery bag within which each female constructed and guarded her own egg sac. Hatching and other interactions were not observed.

Other members of this family, more or less closely related, to Araneus, have been characterized as "gregarious", but most reports are old, superficial, or are on spiders that are not readily identifiable from the data given (Ricard, 1855; Masterman, 1869; Myers, 1927; Schoutenden, 1932). Cyclosa trilobata of New Zealand is gregarious, according to Myers (1927). It is a common observation in the tropics and subtropics that the webs of Nephila spp. often adjoin, or share support lines. However, nothing more than this mere tendency to "clump" has been observed. The same "clumping" has been noted for other members of the family (Kajak and Luczak, 1961).

Family Theridiidae: Anelosimus eximius was studied by Simon (1891) in Venezuela. His excellent account and illustration show a large tangled web with a central retreat made from dead leaves. Around 1000 spiders occupied each web, and the communal retreat was compartmentalized. The spiders felt one another continuously with their first legs and palpi. Prey was attacked simultaneously by numbers of individuals and dragged to the interior, where communal feeding took place. Individual egg sacs were constructed in the retreat, and are spherical. A. studiosus, which ranges farther north, exhibits similar behavior, but the colonies are much smaller (Gertsch, 1949; Levi, 1956).

Parental care of the young is rather common among theridiids, and the pertinent literature has been summarized by Kaston (1965). For example, Theridion sisyphium not only feeds the young by regurgitation, but allows them to share her prey. Other Theridion species behave similarly. More typically, Achearanea tepidariorum spiderlings live together in the maternal web for some time, but eventually cannibalism begins and only two or three out of 50 hatchlings reach adulthood (Bonnet, 1935).

Family Agelenidae: The remarkable Agelena consociata of Gabon has been the most thoroughly studied of all known social spiders. Preliminary field observations and a few experiments were carried out by Pain (1964), and amplified by Darchen (1965), Chauvin and Denis (1965), and especially Krafft (1965, 1966a, 1966b, 1967).

In their natural habitat the spiders occur along forest margins, under conditions of partial sunlight and high humidity. The largest webs are 2-3 meters long, and consist of numerous interconnected sheets at various levels, as shown in a photograph by Pain (1964, p.48). The web is constructed by the spiders in a more or less haphazard manner; there is no cooperation between individuals (Darchen, 1965). Groups of individuals captured from webs in the field can be induced to construct new webs in the laboratory, provided the conditions of Gabon are approximated (Krafft, 1966, 1967). The number of sheets constructed seems to depend on the number of individuals present: 150-230 spiders wove a single sheet, about 400 spiders built two sheets, 500 constructed four (Pain, 1964). Darchen (1965) isolated small groups of spiders in containers, where they built miniature communal webs. The colonies fused into a larger nest when the barriers between containers were removed.

Over a period of three months, a large nest in the laboratory gave rise to four new ones by what Darchen (1965) called "swarming". A group of individuals from the main web would move from a portion of the nest and build a new sheet and retreat. At least initially, these new sheets were connected with the old one. Spiders from the new nest were readily accepted by those in the old web. Forty-five individuals placed in a box together first wove webs in groups of 15, but when the edges of the sheets came in contact, the whole population became integrated into one community.

Prey-capture and feeding were closely observed by Darchen (1965) and Pain (1964). Large prey was attacked by a number of individuals and subdued both by swathing and by biting. Since the threads of the sheet are not sticky, the prey often ran across the sheet, pursued by a group of spiders. The stimulus, releasing prey-chasing behavior, is obviously the vibration of the web, which is effective in bringing spiders to the epicenter from about 60 cm. away (Chauvin and Denis, 1965). After the prey has been subdued, as many as 30 spiders of all ages and both sexes may feed on it communally.

In contrast, if the prey is small, individuals may capture and kill it alone, then return to their retreat to feed on it (Pain, 1964). Frequently another spider will attempt to secure the prey from the first individual, though all this competition takes place only as a "tug-of-war", and no combats have ever been seen (Pain, 1964; Darchen, 1965; Krafft, 1966b). The individual feeding on small prey may be joined by others, which does not invoke any competitive acts (Krafft, 1966b).

The age composition of a given nest is not even (Chauvin and Denis, 1965) and the proportion of males:females varied in several webs from 1:1 to 1:28 (Pain, 1964); this may be a function of the time of observation. Pain also suggested that the sex ratio must be biased towards females in order for egg sacs to appear, and that the more males present per female, the fewer egg sacs were constructed. An experiment combining males and females in tubes in various proportions seemed to support this idea (for example, a 1:1 ratio gave no egg sacs; 82 females with 4 males constructed 17 sacs 9-10 days after mating). Estimates of the numbers of egg sacs per web vary from 100 (Chauvin and Denis, 1965) to 20-30 (Pain, 1964). The sacs are made by individual females and contain 20-30 eggs, as compared to 50-100 for solitary congeners of a similar size, However, some of the sacs may not be viable. Of 100 sacs collected in early April, Darchen (1965) found that only four contained egg shells or spiderling exuvii; Krafft (1966b) found 78 sacs divided thus: 24 with viable eggs, 57 with dead eggs, 3 with young. The spiders pay no attention to inviable or empty sacs, but are "strongly attracted" to full or viable sacs (Krafft, 1966b).

Hatching occurs about 30 days after oviposition. Isolated young behave like the adults, but on a smaller scale. However, when adults are present, the young almost never participate in hunting, but cluster in the retreats in groups of around 50 individuals. Adults bring prey to these groups, which feed communally on it, sometimes along with the adult that brought it in (Krafft, 1966b). Krafft (1965) demonstrated an exchange of materials among individuals during feeding by labelling some of the spiders with a radioactive isotope of phosphorus. But this is not surprising, since spiders feed only on liquid food and regurgitate digestive fluids into the prey; during communal feeding some exchange is inevitable. There is no evidence to indicate that true trophallaxy is taking place. Rather, the main medium of communication between individuals seems to be touch. Individuals frequently feel one another (but also probably sticks, leaves, etc., that make a disturbance near them).

Spiders from another nest far removed are not recognised as strangers. In fact, individuals of Agelena labyrinthica (a solitary European species) were not treated differently from nest-mates when placed in A. consociata webs (Krafft, 1966b).

Some solitary agelenids have developed parental care. Tretzel (1961) has observed that Coelotes terrestris, a solitary European species, feeds its young, which live in the parental web for some time after hatching. The young stroke the mother's chelicerae with their palps and elicit a feeding response; after the death of the mother, the young feed on her body (Tretzel, 1961).

DISCUSSION

A meaningful definition of sociality must avoid being too broad; Thompson's (1958) definition of social behavior as "...(a) a process of some kind occurring between individuals that (b) has certain results (Thompson, 1958)" is so broad as to take in virtually all behavior involving more than one animal. Emerson (1958) has defined a society as "...a group that manifests systematic division of labor among individuals of the same sex (Emerson, 1958)". Still a third definition by West (1967) has the advantage of including forms where a systematic division of labor is not in evidence, but excluding aggregation due to summation of individual behavior: "Social ["altruistic"] behavior may be defined as the activity of an individual benefiting the young of another of the same species (West, 1967)."

Obviously, such definitions could be the source of endless controversy, but making a choice between them need not be arbitrary -- I prefer West's concept because it has the advantages of extending the term social to numerous forms in which the usually competitive interactions between individuals are suppressed, yet which do not have a systematic division of labor. As with any definition, there are a number of cases which cannot be satisfactorily placed. Perhaps two additional classes postulated by Michener (1953) would prove useful. Michener calls insects, in which individuals of the same age aggregate show a weak division of labor or cooperation, semisocial. An example:

> "...in such species as Pseudagapostemon divaricatus... two to forty females usually use a single entrance burrow... In every such semisocial nest there was always or almost always a female blocking the entrance with her head... Thus bees in the common nest have the advantage of only having to dig one main burrow...(and) have the advantage of protection against intruders (Michener, 1958)."

Subsocial species were defined by Michener (1958) as those in which one or both parents survive to feed and care for the young, but die before the young mature. West and Alexander (1963) have discussed a recent case of this in a cricket, Anurogryllus muticus. The female digs a burrow, feeds the young on cut grass stems, and defecates in a special side chamber.

It is perhaps difficult to separate these three types of behavior from feeding and defensive aggregations; but a discussion by Williams (1966, p.212) of the origin of primitive schooling in fishes helps. Such schools are advantageous for individuals near the centers, since predators are more likely to seize fish at the school's margins. The compactness of the school is thus a summation of the tendency of individuals to stay away from the periphery; in this type of school there is no division of labor of even the weakest kind, no leadership or dominance hierarchy, and no interaction with the young of another individual (or, indeed, with an individual's own young).[2] This type of gregarious behavior is common in animals.

Clearly, there are parallels to all these behavioral groups in the species of spiders described in the review section above. Agelena consociata must be considered social by any definition. The young cluster in groups of 50 or more in the retreats to be fed, and since there are no more than 30 eggs per sac, it seems possible that any given individual feeding them may not be the parent of all. It is not known for sure if Stegodyphus sarsinorum females limit their attentions to their own young. In Cyrtophora citricola, on the other hand, any benefit to the young of another by a single spider's activities would be at best indirect; this species might be described as semisocial, along with the other "social" members of its family. The numerous cases in which the young are fed and cared for by the mother fit neatly into the subsocial category.

Michener (1958) and Evans (1958) have postulated two different ways in which sociality might have arisen among the Hymenoptera. In bees (Michener, 1958), sociality could have developed through a tendency on the part of the adults to form semisocial groups. In wasps (Evans, 1958), social behavior developed at several different times, through a series

[2] Williams does not infer that more specialized kinds of social behavior do not occur in fish; rather, that this is a plausible explanation for some fish schooling behavior.

of steps in which females became more and more closely associated with their young in a subsocial relationship. Thus the resemblance between these two forms of insect society is the result of convergence from a series of different intermediate steps.

It seems likely that this also holds true in spiders, to a limited degree. Araneus bandelieri and the aggregations of Nephila spp. and other araneids in which common constructions are built qualify as semisocial, but it is a moot point as to whether any true social species passed through these stages. On the other hand, Agelena consociata and Stegodyphus spp. are probably social because of the development of an extended period of subsociality on the part of some ancestor. Subsocial species occur in both of their families.

The selection pressures responded to by an increase in the cohesiveness of the group are, as Hamilton (1964a, 1964b) and others have established, directed at the individual. It can be demonstrated that individual spiders benefit in numerous ways from being a part of the group in a social web. In A. consociata social webs, prey much larger than individual agelenids of the same size are capable of handling, is subdued and devoured, and the species is allowed to enter a niche not occupied by other agelenids. The young benefit by being hidden deep in the recesses of a huge mass of silk, and a risky inference might be made that the reduced number of eggs per sac in this species, is a response to the greater number of young that reach adulthood under these conditions.[3] A certain amount of protection against parasites and predators might also influence the density of semisocial aggregations. Like fish in a primitive school, the spiders occupying webs near the center of a large mass would be less likely to be attacked; hiding in a dense central retreat would further protect the individuals. However, as Williams (1966) points out for fish schools, these dense aggregations could prove tempting to predators or parasites that adapt to the high population density they provide.

Semisocial and especially subsocial phenomena occur in several other families of spiders in which nothing approaching true sociality is known. The Lycosidae carry first the egg sac, then the young, about with them. Some Pisauridae, normally without webs, build a large nursery nest in which the young are guarded by the female; and in the Salticidae, dense hibernating aggregations form. Why has some form of sociality not developed in these families? Perhaps the answer lies in the wandering hunting habits of the adults and in the fact that even if the young are tightly clustered, they can only be in communication with a few of their sibs at any given time. On the other hand, the close communication between the young of web weaving forms can easily be demonstrated by tweaking a single thread of a cluster of newly hatched Araneus: nearly all the young react immediately. The same observation can be made for the semisocial or gregarious groups of the same family. Communication between individuals is extremely important in forming and holding together societies (Thompson, 1958), and a web provides this vital factor.

Thus the two most important preadaptations to sociality among spiders

[3] Such a response to parental care has been described for birds (Cody, 1965).

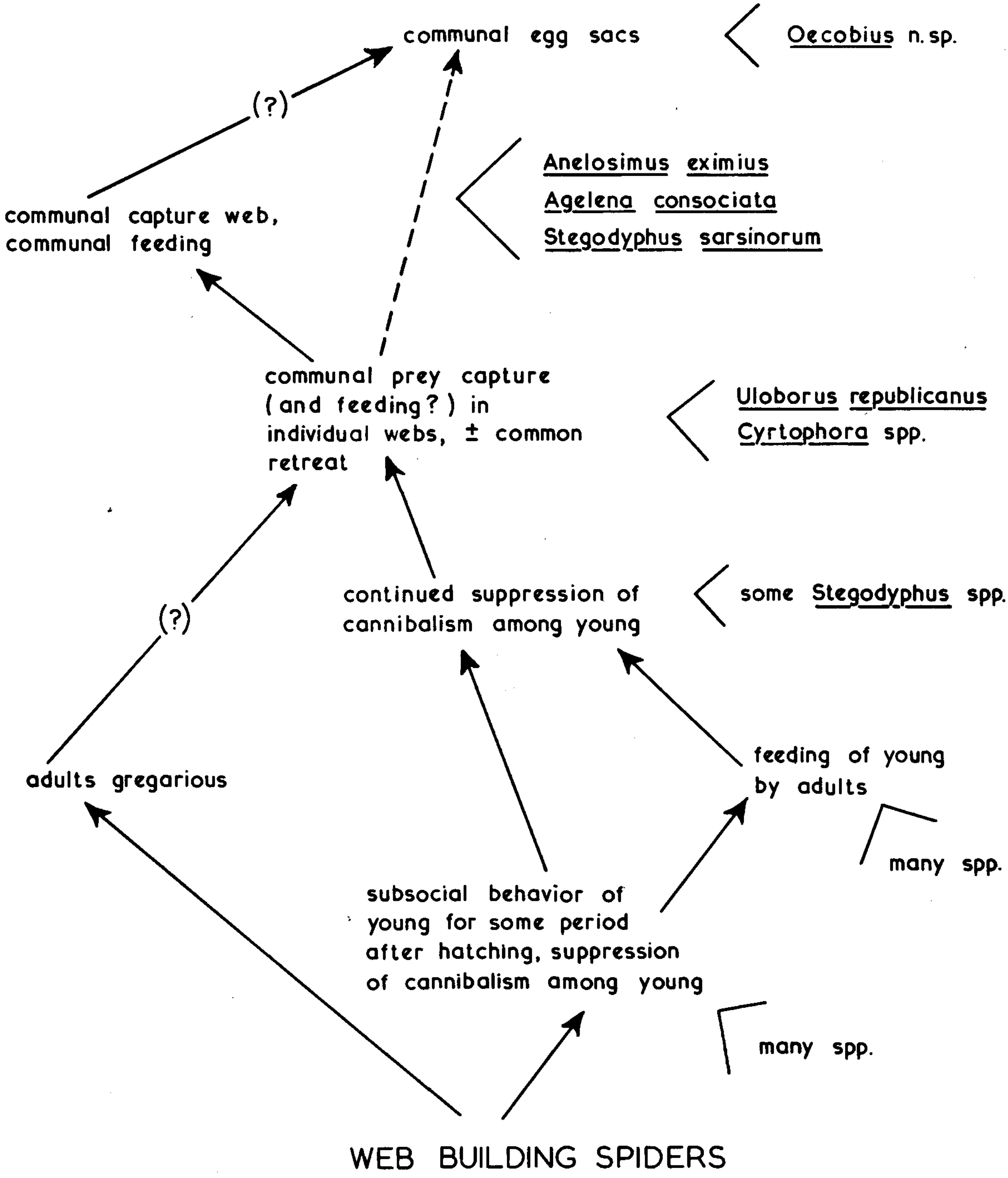

Fig. 1. Hypothetical phyletic sequence of events on pathway to sociality in spiders.

are the occurrence of subsocial or semisocial phenomena and the presence of a web.

A hypothetical sequence of phyletic steps based on this discussion is given in Figure 1. It must be emphasized that the list of species on the right side of the chart does not infer relationships between the species, but merely which level each species presumably occupies.

SUMMARY

1. Some of the so-called social spiders are to be considered truly social. Others are best thought of as subsocial and semisocial.
2. The selection pressures that move species towards sociality are directed at the individual through more efficient food capture, care of the young, and protection from parasites and predators.
3. The two most important preadaptations to social life in spiders are the web, which keeps all members of the group in contact with one another, and subsocial or semisocial phenomena, which form the group in the first place.

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