

# ECO-ETHOLOGY AND EVOLUTION OF SOCIAL SPIDERS

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## SUMMARY

The various ways of social organization of spiders can be subdivided into four categories — territorial subsocial, non-territorial subsocial, territorial social, and non-territorial social. Familial behaviour seems to lie at the origin of these societies, at least in the species that weave irregular webs. The social spiders are distinguished from insect societies mainly by the spiders' use of their silk as a means of communication. The silk transmits various vibratory information enabling the individuals to coordinate their activities. Territoriality can be attributed to the geometrical structure of certain traps or to the necessity of maintaining a minimum capture area per individual. The evolution of spider societies can be attributed not only to minor ethological changes, such as the development of mutual tolerance, but also to particular ecological conditions.

## RÉSUMÉ

### Eco-éthologie et évolution des araignées sociales

Les différentes organisations sociales des Araignées se subdivisent en 4 catégories : les Araignées subsociales territoriales et non territoriales et les Araignées sociales territoriales ou non territoriales. Le comportement familial semble être à l'origine de ces sociétés, au moins chez les espèces qui tissent des toiles irrégulières. Les Araignées sociales se distinguent essentiellement des sociétés d'insectes par l'utilisation qu'elles font de la soie en tant que moyen de communication. Celle-ci transmet diverses informations vibratoires permettant la coordination des activités des individus. La territorialité peut s'expliquer par

la structure géométrique de certains pièges ou par la nécessité de maintenir une surface de toile de capture minimum par individu. L'évolution des sociétés d'Araignées s'expliquerait non seulement par des modifications éthologiques mineures, telles que le développement de la tolérance réciproque, mais également par des conditions écologiques particulières.

## INTRODUCTION

The spiders, which are exclusively predatory arthropods, generally manifest strong intolerance towards their congeners. However, of the 30 000 species now known, about thirty show a more or less complex social organization (Burgess, 1978), by Wilson's definition of a society (1971) : «It is a group of individuals that belong to the same species and are organized in a cooperative manner». The organization of monospecific groups of spiders shows a gradation from solitary to social that makes it difficult to draw a clear and objective dividing line between these two ways of life (Krafft, 1979). Socialization has not produced morphological and physiological changes comparable with those in social insects. There are no castes, nor any obvious division of labour. The transition from solitary life to social life is made with a small number of behavioural modifications, such as the appearance of mutual tolerance and the exploitation of silky structures to transmit vibratory information (Krafft and Leborgne, 1979 ; Krafft, 1980). But «a small evolutionary change in the behavior pattern of individuals can be amplified into a major social effect by the expanding upward distribution of the effect into multiple facets of social life» (Wilson, 1975). The appearance of mutual tolerance, combined with favourable ecological conditions, has made possible the transition from a solitary status to a social one.

## THE VARIOUS TYPES OF SOCIAL ORGANIZATION

The spiders that manifest a social organization can be subdivided, by reference to the structure of their groups and the nature of their webs, into four categories : territorial subsocial, non-territorial subsocial, territorial social, and non-territorial social.

### Subsocial spiders

The species whose young cooperate, without intervention by the mother, for some time during the construction and maintenance of the nest or the capture of prey, but disperse before reaching adulthood, are known as

subsocial. This term suggests an evolution of the social phenomenon in accord with the most probable hypothesis on the origin of spider societies.

*Territorial subsocial spiders* : in this type of organization, still little studied, each individual exploits a portion of the web more or less exclusively. *Ixeuticus candidus* (Dictynidae, from Australia) weaves irregular webs. During the gregarious phase, the young construct their individual retreats in contact with the nest of the female (Main, 1971). *Eriophora bistrata* (Araneidae, from Paraguay) weaves orb webs. By day all the spiders cluster tightly against one another. At dusk, each spider weaves an individual web hung from the long, common frame threads. In such a colony, hunting is normally an individual matter, but when the size of the prey exceeds that of the spider, two or three individuals sometimes cooperate to overcome the prey. The spiders disperse when they become adults (Fowler and Diehl, 1978).

*Non-territorial subsocial spiders* : this type of organization is observed only among the spiders that weave irregular webs. Among many species showing maternal behaviour, the gregarious life of the young continues after the death of the mother. Some tasks are carried out in common, such as the construction of the trap and the capture of prey. The interactions necessary for this cooperation imply the existence of mutual tolerance and of a mechanism temporarily preventing the dispersal of the individuals, with effects resembling those observed in social spiders. This subsocial organization persists for different times among different species of the same family. Among the Theridiidae. *Theridion impressum* shows a non-territorial subsocial organization that is very fleeting : the young disperse after the second moult that takes place outside the cocoon ; in *Theridion sisyphium* the dispersal happens only after the fourth moult (Kullmann, 1972) ; and the individuals of *Anelosimus studiosus* remain grouped and cooperate up to the subadult instar (Brach, 1977). The same pattern is observed in the Eresidae : the dispersal of the young appears after the fourth or fifth moult in *Stegodyphus pacificus*, after the fifth in *Stegodyphus lineatus*, and after the sixth in *Eresus niger* (Kullmann et al., 1972 ; Kullmann and Zimmermann, 1975).

### Social spiders

The species whose adults stay grouped and cooperate in the capture of prey or the construction of the silky structure of the colony are known as social spiders. In some cases the adults cooperate in the care of the young, but these young are always less developed than among the highly evolved social insects.

*Territorial social spiders* : these spiders live in colonies made up of individual webs linked to one another by the frame threads. These frame

threads, which are established in common, constitute a tie between the individuals and permit an exchange of vibratory information. The individual webs hold either a single spider or a group made up of one adult female, several young of various ages, and perhaps a male. Each web can be likened to a territory according to the definition of Wilson (1975), since it is «an area occupied more or less exclusively by an animal or a group of animals by means of repulsions through overt defense or advertisement». The territorial social spiders that weave irregular webs, which are the best known, are *Dictyna calcarata* and *Dictyna albopilosa*, from Mexico, and *Mallos trivittatus*, of the southwestern United States, belonging to the Dictynidae (Jackson, 1978a). *Mallos trivittatus* shows both a territorial social structure and to some extent a non-territorial subsocial structure. Each web holds one adult female and perhaps several young and a male. The same social organization has been seen in a theridiid spider from Gabon, *Achaearanea disparata* (Darchen and Ledoux, 1978 ; Darchen, personal communication).

All orb-weaving social spiders are territorial. The colonies, which can hold up to 350 individuals, consist of orb webs linked to one another by frame threads and each holding only one spider. Territorial behaviour is well developed and hunting is an individual matter. Spiders without webs cling to the frame threads. This type of organization is observed in *Cyrtophora citricola* (Araneidae, from Africa), *Cyrtophora moluccensis* (Araneidae, from New Guinea), *Metabus gravidus* (Araneidae, from Costa Rica), and *Uloborus republicanus* (Uloboridae, from South America). The territoriality of these species limits their social interactions, but this type of organization implies a certain form of cooperation during the establishment of the frame threads, frequent interchanges of information between the individuals, and a certain development of mutual tolerance (Krafft, 1979).

*Non-territorial social spiders* : all the non-territorial social spiders belong to families weaving irregular webs. This type of silky structure facilitates the inter-individual relations to the extent that one web can be exploited simultaneously by several individuals. It is in this group that one finds the most elaborate social organization (Krafft, 1979). Most activities are carried out in common. The spiders cooperate during the construction of the silky structure, combine their efforts when prey is captured, and may cooperate in the feeding of the young. The colonies of some species can contain more than a thousand individuals of both sexes and all ages. The spiders of this type belong to families including also species that show parental behaviour or sub-social organization. The best-known species are *Mallos gregalis*, from Mexico (Dictynidae) (Jackson, 1979 ; Burgess and Witt, 1976), *Stegodyphus sarasinorum*, from Afghanistan and India (Eresidae) (Kullmann et al., 1972) ; *Anelosimus eximius*, from Central America (Theridiidae) (Brach, 1975) ; and

*Agelena consociata* and *Agelena republicana*, from Gabon (Agelenidae) (Darchen, 1967). *Agelena consociata* displays interattraction and mutual tolerance ; cooperates in the construction of the trap, the capture of prey, and the feeding of the young ; and also shows a group effect (Krafft, 1971, 1975).

The classification of the various types of social organization in the spiders is different from that generally adopted for insects (Michener, 1969). In insects, the classification is mainly based on the appearance of castes and the development of brood care. In spiders, whose young are less strictly dependent on the adults, owing to their mode of development, the functioning of the society is more oriented towards the elaboration of a trap that permits the capture of prey. The silky structures assure the transmission of the information necessary for the coordination of the activities of the individuals. All members of the society, including the young, benefit directly or indirectly from the consequences of this coordination. The care of the young is no more developed among the social spiders than among the solitary spiders that show maternal behaviour.

## CONSEQUENCES OF GROUP LIFE AMONG SPIDERS

It is often difficult to evaluate objectively the adaptive value of ethological characters. Such an analysis very often amounts to hypotheses, but in the case of spiders some of them are strengthened by facts.

### **Adaptative aspect of non-territorial social organization**

All the individuals, adults and young, benefit from the nest's protection against bad weather and possible predators. In web-spinning spiders, the harvest of food is closely related to the efficiency of the silky trap. Owing to the cooperation of a large number of individuals, this trap can be remade rapidly after being destroyed. The coordination of the activities of the individuals allows social spiders to capture much larger prey than they would be likely to overcome as isolated individuals. The effects of this is to enlarge the range of prey.

Captured prey are consumed communally. Individuals that did not participate in the capture also take part in the meal. Since spiders' digestion is partly external, it is not impossible that the participation of several individuals in the meal helps to better digest the prey. In certain species, the adult females feed the young of the first instars by regurgitation (Kullmann, 1972). The females may also feed young that do not belong to their own brood. In all cases, the young can benefit from prey captured by any individual of the

colony. Their development therefore becomes independent of the survival of their mother. This eliminates the hazards of harvesting food that are faced by the young of solitary species.

Lastly, the simultaneous presence of males and females in one nest facilitates encounters between the sexes. It would be useless to try to rank the various characteristics according to their adaptive value. Overall, their effects become evident in two ways. Firstly, the social spiders constitute high concentrations of individuals in a limited space. A nest of *Agelena consociata* extending over 5 m<sup>2</sup> can hold 500 to 1000 individuals. Such a concentration is never observed among solitary spiders. Secondly, the social spiders survive even though they have much less reproductive potential than most solitary species. This relative lack of reproductive potential is proportional to the development of maternal, subsocial, and social behaviours. *Agelena labyrinthica*, a solitary species, lays about 150 eggs per cocoon; *Coelotes terrestris* (Agelenidae), which shows maternal behaviour, lays only 50; and *Agelena consociata* lays only 10. In the Theridiidae, *Theridion impressum* lays 100 eggs per cocoon, *T. sisyphium* lays 50, *Anelosimus studiosus* 35 to 50, and *Anelosimus eximius* 20 to 25. In the Eresidae, *Stegodyphus pacificus* lays 450 eggs, *St. lineatus*, which is also a subsocial species, lays 110, and *St. sarasinorum* lays about 40. While the artificial aspect of such a comparison must be emphasized, since the differences between species could be not only ethological but also ecological, this nevertheless suggests a reduction of egg-laying that parallels the development of social organization. These results should be considered in relation to the protection from which the young benefit and their nutrition by the adults, which reduce mortality.

#### Adaptative aspect of territorial social organizations

Several observations indicate that territorial social organization also has several advantages. The presence of frame threads bearing the whole of the colony facilitates the construction of the individual webs of *Metabus gravidus*. On average, one spider needs 23 minutes to construct an orb web at the periphery of the colony, whereas at the center of the colony spiders have an adequate network of frame threads and take only 19 minutes to construct their webs (Buskirk, 1975a). The construction of large colonies increases overall the efficiency of capture in *Cyrtophora citricola* (Rypstra, 1979). On average, 30 % of the prey that strike the silky structure are captured by the spiders. But this efficiency varies from 10 % for small colonies, with 17 individuals, to 40 % for large colonies, with 350 individuals. In a large colony, a prey that escapes from one individual web has more chance of falling into a neighbouring web. The construction of vast colonies also allows

spiders to exploit very open sites through which flying insects pass (Lubin, 1974 ; Buskirk, 1975a ; Rypstra, 1979).

This increased efficiency of capture of prey can be related to the fact that the colonies of territorial social spiders constitute a substantial concentration of individuals in a limited space. In one biotope it has been observed that *Mallos niveus*, a solitary spider, was present at a concentration of 12 individuals per 100 m<sup>2</sup>, whereas in a comparable area up to 10 000 individuals of *Mallos trivittatus* can be found (Jackson and Smith, 1978). The young are not fed by the adults, but they generally establish themselves in their colony of origin, taking advantage of the frame threads put up by the adults.

It is difficult to evaluate the protection against possible parasites that territorial social life affords. However, when a hymenopteran parasite flies through a colony of *Cyrtophora moluccensis*, some females grip their cocoons and shake them vigorously. They are then imitated by other spiders, behaviour which suggests that this may be an alarm system (Lubin, 1974). Finally as for the non-territorial social spiders, the presence of males and females in the colony decreases the risks run in the search for sexual partners.

### Disadvantages of social life

The social life of spiders does not produce only advantages. By day, certain prey can detect and thereby avoid the imposing silky structures of the colonies. On average, 40 % of insects avoid the colonies of *Cyrtophora citricola* (Lubin, 1974). Owing to the high concentration of individuals in a limited space, the volume of hunting web per individual is smaller for social spiders than for solitary spiders. The capture web of *Mallos niveus* has an area of about 35 cm<sup>2</sup>. It is 5 cm<sup>2</sup> per individual for *Mallos trivittatus* and about 2 à 3 cm<sup>2</sup> for *Mallos gregalis* (Jackson and Smith, 1978). This reduction of the capture area per individual can be partially compensated for by an increase in the capture rate, that is, the percentage of prey touching the web that is captured. But such a balance can be reached only in favourable ecological conditions. Indeed, non-territorial social species are found only in the tropical regions. It seems that the social spiders have been able to develop only in biotopes that permanently contain a high enough density of prey.

## TERRITORIALITY AND SOCIAL ORGANIZATION

The amount of prey captured depends on many factors, including the area of the trap and the web-site selected by the spider. Because insects are

distributed heterogeneously in the biotope, not all web-sites are equivalent (Pasquet and Krafft, 1980). Selection of the most favourable sites involves intra-specific competition (Riechert, 1976). In the solitary spider *Agelenopsis aperta*, each individual occupies a hunting space whose dimensions, which greatly exceed the area of the web, are inversely proportional to the density of prey. This hunting space can range from 0.10 to 10 m<sup>2</sup>. When, in any given biotope, two spiders exploit an area equivalent to one individual hunting space, the capture rate for each individual is reduced by 40 % (Riechert, 1978a, 1978b). The agonistic behaviour of these spiders therefore has the effect of balancing their energy budgets. The young of *Tegenaria domestica*, which are raised in groups, show in the laboratory a cannibalism that is inversely proportional to the amount of prey given to them (Mielle, 1978). Solitary *Amaurobius* or *Stegodyphus* species can be kept so close together in one enclosure that their webs touch, on condition that enough prey is distributed to them. In the colonies of *Metabus gravidus*, the individuals that have orb webs manifest agonistic behaviour when a congener approaches. These displays of aggressiveness are no longer observed when the spiders are situated on the frame threads (Buskirk, 1975). The colonies of *Cyrtophora citricola* are made up of several concentric layers of individual webs. The intermediate layers have the highest rates of capture – and it is in these most efficient layers that the spiders most often manifest agonistic interactions (Rypstra, 1979).

These various observations suggest that the territorial behaviour of the spiders corresponds to the defense of a hunting space big enough to ensure that each individual's energy budget is balanced, in accord with the ecological conditions, that is, the density of prey. Finally, it must be emphasized that the orb web of the orb-weaving spiders, because of its structure, cannot be exploited efficiently by several individuals simultaneously. These facts undoubtedly explain the existence of territorial social spiders and the dispersal of subsocial spiders. As they develop, the young of subsocial species have increasing energy needs. The web gradually becomes unable to provide for the needs of all the individuals, resulting in the appearance of agonistic behaviours, which are responsible for the dispersal. This hypothesis seems to be confirmed by the fact that in the laboratory the disappearance of mutual tolerance and of the grouping tendency in *Coelotes terrestris* can be delayed by feeding the young generously (Horel et al., 1979). Theoretically, the spiders would be able to choose to increase the dimensions of their trap. But such an extension is rapidly limited by the damping of the vibratory phenomena transmitted by the web. At too great a distance a prey might not be detected. The dispersal can be total, or, on the contrary, limited, as is the case for *Mallos trivittatus* or *Achaearanea disparata*. The territoriality of the territorial social species would



have the effect of ensuring a minimum capture area per individual compatible with their energy needs, while preserving a high efficiency for the trap which the colony represents. In biotopes rich in prey, territoriality has disappeared in certain species, thus giving rise to the non-territorial social spiders. Certainly it is possible to find in one biotope non-territorial social, territorial social, and solitary species. They may be species belonging to different families, exploiting different microhabitats, with capture techniques that are not necessarily equally efficient. But on the other hand territoriality must be considered an adaptive factor that has undergone strong selective pressure among the solitary spiders. Such characters are liable to be maintained, even in ecological conditions that could conceivably allow them to disappear.

This hypothesis is also reinforced by the existence of temporary aggregations of solitary spiders in favourable ecological conditions. In *Leucauge* species from Costa Rica, 50 % of the adults are gregarious. These aggregations hold from two to eleven individuals, whose webs are linked to one another (Valerio and Herrero, 1977). Depending on the ecological conditions, the individuals of *Philoponella semiplumosa* (Uloboridae, from Costa Rica) are gregarious or isolated. The associations are temporary and facultative (Lahmann and Eberhard, 1979). The same is true for *Nephila clavipes* (Farr, 1977). Therefore there is a possibility of temporary, facultative gregariousness among adult spiders according to the conditions of the biotope. The presence of many prey would produce a reduction of the territoriality, allowing the webs to be close together.

## CONCLUSION

The comparison of these different types of social organization makes it possible to give a picture of the stages that have led from the solitary to the social spiders.

In the non-territorial social spiders, which all weave irregular webs, association seems to have originated from species displaying maternal behaviour. The appearance of cooperation among the young led to the subsocial species. Favourable ecological conditions made possible the transition to the social type of organization, since the young no longer found it necessary to disperse in order to satisfy their energy needs. In all the families concerned, in fact, there are solitary species, species that display maternal behaviour, subsocial species in which the dispersal of the young comes more or less late, even as late as the subadult instar, and finally social species (Krafft, 1979). This evolution has apparently been able to occur only in regions with ecologically favourable conditions.

To be clearly established, the evolution of territorial social species still requires further investigation. For the spiders that have irregular webs, however, it may be assumed that the young which disperse, either immediately or after staying for some time in their mother's web, stay in the immediate vicinity, exploiting in part the pre-existing frame threads. This partial dispersal might be the consequence of ecological conditions that have not induced a complete disappearance of territorial behaviour. Unfortunately, we have no data about the maternal behaviour in these species.

The path towards socialization has been blocked among the orbweaving spiders by the geometrical structure of their webs. The species do not display any elaborate maternal behaviour. Because the young do not systematically disperse they weave their webs in contact with that of their mother, or within the colony when this already exists. The hypothesis of the assembly of adults under the influence of favourable ecological conditions, combined with the absence of dispersal of the young, must still not be set aside. But regardless of the ecological conditions, none of these species has reached the stage of adopting a non-territorial social organization. The important role that ecological factors seem to have played in the appearance of spider societies can be explained by the fact that socialization in these animals has not necessitated morphological changes and depends on a very few ethological changes, such as the absence of dispersal and the appearance of mutual tolerance. The presence of silky structures has doubtless been a determining factor, constituting a particularly efficient means of communication between individuals (Witt, 1975).

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