

# Social Behavior in Group-Living Spider Species

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## SYNOPSIS

Gregariousness in spiders can range from apparently fortuitous aggregations to highly integrated social systems employing communication, interaction and co-operation among members. About 33 species are known which reportedly conform to these group-living criteria: they are found consistently distributed in species-characteristic clumps, and they interact or transfer information between individuals. Using new reports and original, unpublished observations, species' societal and behavioral strategies are compared to determine patterns in spider social organization. The 20 best-known species are from different taxa and distant geographical areas; they are found to make up four distinct lifestyles which are similar across many dimensions. This supports the hypothesis that there exist some predominant patterns of social lifestyle into which species may have settled, according to their behavioral pre-adaptations.

## INTRODUCTION

In spiders, there are few enough group-living species to make it possible to study social trends in the entire order. What patterns exist in group-living spiders? Are there certain basic ways in which spiders are likely to be social, i.e. interrelated complexes of behaviors which make up general strategies favored by behavioral pre-adaptations and the survival requirements of available niches? Some alternative hypotheses might predict that social patterns are centered in certain taxonomic lines or are correlated with geographic areas. To begin to answer these questions, this paper will compile known group-living species and compare their lifestyles along many dimensions, concentrating on predation, young-caring, and web-building behaviors. Sources include previously unreviewed studies, as well as personal communications to and observations by the author.

Out of 30 000 known spider species (Kaestner, 1969), there is clear evidence for group-living behavior in only about 33 species. I use the following criteria to identify group-living, possibly social species: (1) the species must be found in statistically demonstrable clumps and (2) individuals must exhibit some communication or interaction beyond that seen in male/female mating pairs. Much information presented in previous reviews (Kullmann, 1968; Krafft, 1970; Shear, 1970; Wilson, 1971) will not be repeated here.

## GROUP-LIVING SPECIES

Listed here is a glossary of terms. Web: web component terms taken from Burgess & Witt (1976). Orb-webs are temporary structures unless noted. Tangled or loose space web may be different from tensioned space web. Sheets consist of planar threads, with few strong connections. Individual: behaviors performed by a single spider; catching prey, feeding; staying near, touching or manipulating the egg sac. Communal: behaviors performed in a group; predation, feeding, attending egg sacs. Cohabitation is temporary sharing of web components. Juveniles: care and behavior of early immatures. Size: reported size of colony, web complex or maternal group. Spacing: spatial relationships in group. Contact species are close and touch without aggression. Uniform species maintain a minimum nearest neighbor distance.

### Dictynidae

*Mallos gregalis* (Diguët, 1909; Burgess, 1976; Burgess & Witt, 1976) Mexico. Web: sheet, tunnel, chambers. Communal: building, predation, feeding, egg sac care. Vibration predation cue (Burgess, 1975). Juveniles: share adult's prey. Size: thousands. Spacing: contact.

*M. trivittatus* (Jackson, this volume, p. 79 Southwest USA. Web: retreats, sheets connected by tangled interstitial webs. Individual: sheet-building, predation, feeding. Communal: interstitial web-building, cohabitation in retreats (female/male or female/juvenile) or interstitial web (juveniles); feeding with cohabitant (rare). Size: 1-10 200. Spacing: nearest occupied retreat, 6.1 cm (s.e. 0.68, 27 aggregations).

*Dictyna calcarata*, *D. albopilosa* (R. R. Jackson, pers. comm.) Mexico. Like *M. trivittatus*. *D. coloradensis*, *D. tridentata*, *D. annexa*, *D. phylax*. West USA. Web: sheets, retreats. Individual: building, predation, feeding. Communal: cohabitation.

### Amaurobiidae

*Amaurobius socialis* (Rainbow, 1905; Gertsch, 1949) Australia. Web: sheet, tunnel, chamber. Communal: living? Many individuals build together.

*Ixeuticus candidus* (McKeown, 1952) (= *Phrygenoparus gausapata*, *P. tubicola*, *P. nigrinus*; Main, 1971) Australia. Web: sheet, tunnel. Juveniles: build individually around female's web.

### Oecobiidae

*Oecobius civitas* (Shear, 1970; Burgess, 1976) Mexico. Web: connected sheets, peripheral lines. Individual: building, predation, feeding. Communal: web-stealing, prey-stealing. Size: 1-100. Spacing: nearest neighbors 0.52 cm (0.04 s.e., 6 complexes; author's observations).

*O. annulipes* (Gertsch, 1949) and other oecobiids. Sometimes aggregated.

## Uloboridae

*Uloborus republicanus* (Simon, 1891; Wilson, 1971) South America, West Indies. Web: orbs connected by space web. Individual: orb-building, predation, feeding, egg sac care. Communal: space web-building, cohabitation on space web. Size: hundreds–thousands. Spacing: females apart on orbs and space web.

*U. mundior* (Struthsaker, 1969) Panama. Individual: predation, feeding. Communal: spiders move throughout colony. Size: 14–21 (mean 24.7, 4 colonies).

*U. raffrayi* (Simon, 1891) Singapore. Web: orbs, tangled (space?) web.

*U. arizonicus*, *U. oweni* (Muma & Gertsch, 1964) Southwest USA. Web: orbs, space web. Size: 20–200. *U. americanus* (Comstock, 1971) North America. Sometimes found aggregated.

## Pholcidae

*Physocyclus dugesi* (author's observations; determined by W. J. Gertsch) Mexico, southwest USA. Web: loose space web (up to 10 m long). Individual: predation, egg sac care. Communal: building, web sharing. Size: clusters of 1–10. Spacing: nearest neighbors 2.07 cm (s.e. 0.33, 15 clusters).

## Eresidae

*Stegodyphus sarisinorum* (Kullmann, Nawabi & Zimmermann, 1972; Jacson & Joseph, 1973) Africa, Afghanistan, India. Web: sheet, tunnels, chambers. Individual: egg sacs opened. Communal: building, predation, feeding, egg sac care. Juveniles: regurgitation-fed, share adult's prey. Size: 3–518 (mean 91, s.e. 35.1, 15 colonies). Spacing: contact.

*S. mimosarum* (= *S. hildebranti*, *S. gregarius*, *S. africanus*; Kullmann *et al.*, 1972) Ethiopia, Tanzania. Web: sheet, tunnels, chambers. Individual: egg sacs opened. Communal: building, predation, feeding, egg sac care. Juveniles: regurgitation-fed, share adult's prey. Spacing: contact.

*S. pacificus* (Kullmann *et al.*, 1972) Afghanistan. Web: sheet, tunnel, chamber. Individual: as adults, egg sac opened. Juveniles: stay with female, regurgitation-fed, eat mother, catch prey together. Disperse, seen in groups of 4–5. Size: female + 260–600 young. Spacing: contact (mother and offspring).

*S. lineatus* (Kullmann *et al.*, 1972) Palestine, Afghanistan. Web: sheet, tunnel, retreat. Individual: as adults. Juveniles: stay with female, regurgitation-fed, eat mother. Spacing: females touch offspring.

## Araneidae

*Metepeira spinipes* (Burgess & Witt, 1976; author's observations; determined by W. J. Gertsch) Mexico. Web: orbs and retreats connected by space web. Individual: orb-, retreat-building, predation, feeding, egg sac

care. Communal: space web-building, cohabitation on space web, in retreats (female/male). Size: 1-31 (mean 11, s.e. 1.4, 42 colonies). Spacing: nearest neighbors 15.63 cm (s.e. 2.38, 11 colonies). Leg-jerking toward orb intruders.

*M. labyrinthea* (McCook, 1889) North America. Sometimes aggregated.

*Metabus gravidus* (Buskirk, 1975a) Costa Rica. Web: orbs connected by lines. Individual: orb-building, predation, feeding. Communal: web-stealing, prey-stealing (rare), aggregate under rock or log (at night). Juveniles: disperse, may later join colony. Size: 5-70. Spacing: nearest neighbors in orbs, about 16-22 cm; hierarchy of displays defend individual's web and feeding spaces (Buskirk, 1975b).

*Cyrtophora citricola* (Kullmann, 1958; Blanke, 1972) Africa, Afghanistan. Web: permanent orbs, surrounded by space web, connected. Individual: building, predation, feeding, egg sac care. Communal: web-stealing, prey-stealing, some cannibalism, space web repair. Size: 1-200. Spacing: minimum hub distance, 15 cm (Blanke, 1972).

*C. moluccensis* (Lubin, 1974) New Guinea. Like *C. citricola*. Leg-jerking, tensioning, shaking defences of web space.

*C. monulfi* (Lubin, 1974) New Guinea. Sometimes aggregated.

*Araneus bandeleri* (Simon, 1891) Venezuela. Communal: otherwise solitary females observed in a sac with egg sacs. Single observation, not corroborated.

### Theridiidae

*Anelosimus eximius* (Gertsch, 1949; Brach, 1975) South and Central America. Web: sheet, tangled interior. Communal: building, predation, feeding. Juveniles: share adult's prey. Size: thousands. Spacing: contact.

*A. studiosus* (Brach, 1977; D. Gowan, pers. comm.) Southeast USA. Web: sheet, retreat, space web above. Individual: adult females, egg sac care. Communal: females, males, offspring. Juveniles: regurgitation-fed, catch prey together. Size: female, males + 30-50 young. Spacing: females contact offspring, drive away conspecific females.

*A. jucundus* (author's observations; determined by N. I. Platnick) Mexico. Web: sheet, leaf retreat, tangle above. Webs contained either female carrying egg sac or young. Juveniles: stayed in retreat, caught prey on web.

*Achaearanea disparata* (Darchen, 1965, 1968) Africa. Web: sheet, leaf retreat, space web above. Communal: building, predation, feeding, share retreat, egg sac care. Spacing: contact.

*A. tepidariorum* (Gertsch, 1949). Juveniles: briefly share female's web.

*A. riparia* (= *Theridion saxatile*) (Nørgaard, 1956) Europe, USSR. Web: space web, retreat. Individual: as adults, egg sac care. Juveniles: share female's retreat, web, prey. Vibratory signals. Spacing: females touch offspring, adults sometimes aggregated.

*Theridion sisyphium* (Bristowe, 1958; Kaston, 1965) Europe. Web: space web, retreat. Individual: as adults. Juveniles: share female's retreat, web, prey-catching; regurgitation-fed. Spacing: females touch offspring.

*T. impressum* (Kullmann, 1970). Web: space. Individual: as adults. Juveniles: regurgitation-fed, eat mother. *T. pictum* (Nielsen, 1932). Juveniles: share female's web, prey. *T. zelotypum* (Gertsch, 1949). Juveniles: briefly share female's web.

### Agelenidae

*Agelena consociata* (Darchen, 1965; Krafft, 1970) Africa. Web: vertical, horizontal sheets, tunnels, chambers. Communal: building, predation, feeding, egg sac care. Juveniles: share adult's prey. Size: 1-330 (mean 49.7, s.e. 15.3, 29 colonies; Darchen, 1976). Spacing: contact.

*A. republicana* (Darchen, 1976). Similar to *A. consociata*. Size: 5-515 (mean 66.6, s.e. 13.0, 50 colonies)

*Coelotes terrestris* (Tretzel, 1961). Juveniles: share female's web, prey-catching, regurgitation-fed. Vibration discrimination.

### Dipluridae

*Macrothele darcheni* (Darchen, 1965) Africa. One colony of 20 members. Communal: space web-building, predation, feeding. Spacing: contact.

### Lycosidae

*Sasippus floridanus* (Brach, 1976) Southeast USA. Web: funnel sheet, space web above. Individual: as adults, egg sac care. Juveniles: carried by female; share her web, prey, prey-catching. Size: female+20-70 offspring. Spacing: females touch offspring.

## DISCUSSION: PATTERNS OF SOCIALITY

There are behaviors which are conspicuously absent from any of the species here reviewed. For example, no species is without some sort of web, including a representative from a family which contains few web-building species (*S. floridanus*). This evidence supports Shear's (1970) hypothesis that web was an important pre-adaptation to sociality and, indeed, web has been shown to be important for communication (Witt, 1975), tolerance (Burgess, 1975), and even the aggregation (Krafft, 1970; R. R. Jackson, pers. comm.) of spiders.

There is no present evidence that any of these species have developed morphologically distinct castes or insects' eusociality (Wilson, 1971). This could be explained by some differences between spiders and hymenopterous insects, e.g. spiders are not known to be haplodiploid, they have no larval brood that demands great care and their co-operative behavior appears to emphasize simultaneous co-ordination of

individuals' efforts on a task instead of division of labor. Even the building of a common, central egg sac is doubtful, although egg sacs may be stored or tied closely together.

Within several taxonomic genera there are some possible continua of colonial development, from species that are loosely affiliative, to those that are more distinctly social. In both of the genera *Mallos* and *Anelosimus* there are species which build loose clusters of aggressively defended individual webs and species which share a large group web and have co-ordinated communal behavior. Species in the genera *Stegodyphus*, *Anelosimus* and *Theridion* show a range of maternal care from brief passive tolerance to elaborate feeding behavior. In each of the genera *Uloborus*, *Metepeira*, *Cyrtophora* and *Oecobius* are found both a species which forms fortuitous, non-social aggregations of touching webs and at least one species forming regular aggregations, where characteristic interactions are observed. It is possible that the different behaviors within genera represent steps along one or more evolutionary roads to sociality. In genera like *Mallos*, *Theridion*, *Anelosimus*, *Stegodyphus* and *Agelena* which have close-spaced communal web species, the first step in evolutionary development to sociality could be neoteny: the retention of the tolerant behavior of juveniles which remain peacefully in their maternal web. Prolonged living on the female's web is seen in *Anelosimus studiosus* and a generalized juvenile tolerance (retained in a web-complex organization) is retained in *Mallos trivittatus*. In genera like *Cyrtophora*, *Metepeira*, *Uloborus*, *Oecobius* and *Metabus* which include regularly spaced web-complex builders, the first step toward group-living could be the tendency of mature individuals to build webs close together in fortuitous aggregations as is seen in *Cyrtophora monulfi*, *Metepeira labyrinthica*, *Uloborus americanus*, *Oecobius annulipes* and other species. After these initial steps resulting in predictable aggregated habits, selection for sets of interrelated social behaviors could begin. Such hypotheses could be tested by comparing various other attributes (e.g. morphology, protein chemistry or additional behaviors) of the species in a transformation series to see if they predict the same order of development (N. I. Platnick, pers. comm.).

In close-spaced, communal web genera like *Mallos*, *Agelena*, *Anelosimus*, *Theridion* and *Stegodyphus*, the first step in evolutionary development may have been neoteny; the retention of behaviors of the juveniles who remain close together in the web, tolerantly building and feeding (seen in many species). Selection for social advantages of increased investment in offspring and social facilitation in prey-catching and the building of catching and sheltering web components would operate on both young and old individuals. *M. trivittatus* and *D. calcarata*, where juveniles and males can remain in individuals' webs temporarily, may retain this intermediate behavior which has become stable through the presence of separate communally-used web structures. In regularly-spaced web complex builders like *Cyrtophora*, *Metepeira*, *Uloborus* and *Oecobius*, the first step toward group living may be the tendency of mature individuals

to build webs close together in fortuitous aggregations as is seen in *C. monulfi*, *M. labyrinthea*, *U. americanus* and *O. annulipes*. After these initial steps resulting in predictable group habits, gene selection for sets of interrelated social behaviors could begin.

Surely the most striking behavioral trend here is that similar behavioral strategies are seen among groups of spiders which are from widely different taxonomic groups and from distant geographical areas. Diverse species not only share similar feeding (Kullmann, 1970), maternal care and adult aggregative behaviors (Wilson, 1971), but groups of species' lifestyles are similar along many dimensions. This conclusion was suggested and supported by a multifactorial cluster analysis of behavior traits of the 20 best-known species, which will be published elsewhere. The groups generated form the patterns discussed below.

Several highly aggregative species which share many facets of their lifestyle are *M. gregalis*, *Agelena consociata*, *Anelosimus eximius*, *S. sarasinorum* and possibly *Amaurobius socialis*. A large sheet web is built communally to catch prey, with accessory tunnels and chambers which house spiders, egg sacs and young together. Egg sacs are hung in groups and are attended by several females. Predation and feeding is communal and cannibalism is not seen. The major food for young spiders is prey caught by adults. Webs are permanent and spiders on them are close together and touch each other frequently. The webs offer a large catching area for individuals plus protection from the elements and from the eyes of spider predators. Prey caught together is often large compared to the size of the individual spiders. All age/sex classes are found together. Colony population can be very large (200–1000+), but clutch size is quite small (10–30). These species have access not only to a larger web and closer mates but also share the tasks of prey capture and care of young with other group members. This lifestyle strategy could be called "communal-co-operative".

Another group of species loosely conform to Kullman's "maternal-social" category and also share many other behaviors: *A. riparia*, *T. sisyphium*, *Stegodyphus pacificus*, *A. studiosus*, *Sosippus floridanus* and possibly *C. terrestris*. None of these species is found consistently aggregated as adults, but immature spiders remain in their mother's web for some time. Females remain close to their young and touch them, but do not prey on them. The young eat regurgitated fluid and/or prey caught by the mother, and may catch prey together on the female's web. Webs all possess a retreat area inhabited by the mother and young spiderlings. Webs are permanent, and may be repaired but are not usually replaced. As the young grow older, they become more aggressive toward each other until they finally disperse. Young have access to the protection of the web and food obtained from the mother or caught communally. Clutch size (36–450) is lower in this group than in most solitary web builders, supporting the notion that brood survival is increased by maternal care (Kullman *et al.*, 1972).

Still another set of shared behaviors are seen in *M. spinipes*, *U. republicanus*, *M. trivittatus* and *D. calcarata*. Well-defined communal and individual activities are present, facilitated by the existence of both individually-built webs, where prey is caught, and centrally located, communally-built structures, where many individuals can stay. *M. spinipes* and *U. republicanus* are strikingly similar orb/space web builders, while *M. trivittatus* and *D. calcarata* construct sheet webs connected with tangled interstitial silk. Prey-catching webs are usually spaced apart, but cohabitation of webs is commonly observed and spiders may stay quite close to one another without aggression. Intruders onto an individual web may be met with aggression, however, especially if they are the same age and sex as the web occupant. Many webs in the colony are built by adults, but younger spiders are also seen. Prey-catching and feeding are performed individually. Young are not cared for; they are tolerated and allowed to remain close to their parent's web. The aggregated webs provide little additional cover and the cost of individual prey-catching is probably not much different from that in solitary species. By locating their webs together, additional "knock-down" area is available to entangle and slow down prey. Communal web creates a firmer foundation on which to build individual webs, as well as allowing vibration signals and other colony members to move between webs. Males' ease in locating females is certainly improved over solitary species and spiders can benefit from access to web area or prey caught while in cohabitation without having to build a web. Colonies can also monopolize large attractive habitat areas (such as sites over flowing streams).

A somewhat similar pattern is seen in the behaviors shared by *M. gravidus*, *C. citricola*, *C. moluccensis* and *O. civitas*. Webs are built together, but no communal or specialized connecting components are constructed. This means that if an animal ventures from her web, she can easily be in the web of a neighbor, and considerable aggression is observed when spiders defend web space. Cannibalism occurs but is probably not frequent. Feeding and prey-catching are individual, and spiderlings receive no maternal care. Young disperse, but some also join the web colony. There is generally a minimum distance between web centers in these colonies. The extra knock-down area of neighbors' webs may increase prey caught by individuals (Buskirk, 1975a) as well as providing support. Because of the rather high incidence of prey and/or web stealing, individuals benefit from access to the webs of all their neighbors. For this reason this group could be considered "web-complex builders".

The conclusion from this compilation is exciting; species have independently developed social strategies that are demonstrably similar along many dimensions. Species which share behavior are not concentrated in the same genera nor even live on the same continents. The results are consistent with the notion that certain behavioral traits are *more beneficial* for an individual when they are present along with other

behaviors. Certainly there is growing evidence that behaviors in colonial spiders are rather flexible and interrelated. For example, in a species which builds orb-webs and is found in spatial aggregations, the behaviors which result in building a communal web, aggressive defense of web space and tolerance to cohabitants may be selected for more than behaviors leading to maternal care or co-operative prey-catching. This thesis could be supported or refuted by examining more species and looking at additional behaviors which are thought to be interrelated. It is hypothesized that there are certain predominant patterns of social life-style seen, into which a spider species may fall, according to its behavioral pre-adaptations. And that, in specializing within a given behavioral pattern, many behavioral traits work together and complement each other to form an integrated system of group living which is unique, yet predictable for each species.

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