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Photo by M. Scarboro

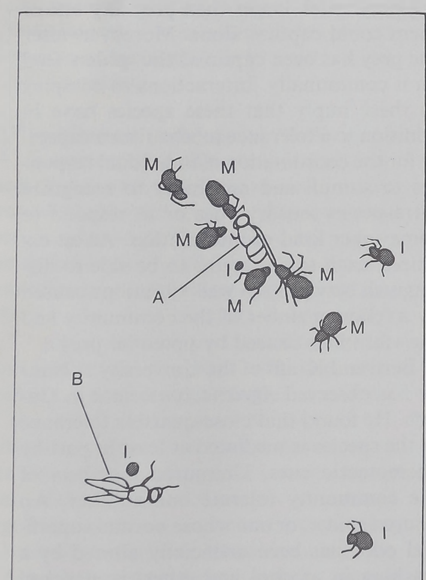
Social Spiders

Most adult spiders lead solitary lives. A few species, however, are gregarious and others even build large communal webs. Both degrees of spider sociality can be observed among species native to Mexico

by J. Wesley Burgess

Among insects—notably bees, ants and termites—social behavior is common. Among spiders it is rare. All spiders are predatory carnivores; among many of them even the male of the species cannot approach the female without risk of being attacked and killed. It is therefore paradoxical that there are any social spiders at all. How, then, can such spiders exist?

The number of social spiders is small; only in 12 genera distributed among nine families of spiders is any kind of sociality known. The 12 genera are, however, widely distributed, with representatives in both the Old World and the New. Two of the New World species are found in Mexico. I recently visited areas near Guadalajara where both species are present, observed the social spiders in their natural habitat and brought home to North Carolina a number of specimens for rearing and further observation in the laboratory.



COOPERATIVE CAPTURE of a fly (*A*) by several spiders is seen in the photograph on the opposite page. The diagram above identifies prey and predators. Spiders labeled *M* are mature; those labeled *I* are immature. Only two of the many flies on the web (*A, and B at bottom left*) are new catches. The spiders are of the social species *Mallos gregalis*. The cluster of mature spiders is feeding or preparing to feed. One immature spider has been drawn to the scene; another is approaching. The photograph was made in the author's laboratory; spiders were collected in Mexico.

The two Mexican species lead distinctively different lives. *Mallos* (formerly *Coenothele*) *gregalis* is a small spider, with a body that rarely exceeds five millimeters in length. It builds a large colonial web, surrounding the branches of a tree with a continuous sheet of silk. Its aggregations may be socially the most complex spider colonies in North America. *Oecobius civitas* is an even smaller spider; few have bodies more than two and a half millimeters long. It lives gregariously, spinning its silk shelter and alarm-system web in a dark and narrow microhabitat: the underside of a rock.

Spider societies are different from the societies found among the higher social insects both in kind and in degree. One reason is that a spider's web extends its range of sensory perception in a way that has no analogy among insects. Another is that the structure of a spider's mouthparts is such that it can feed only on other animal life. Any animal of appropriate size that a spider encounters, including a spider of another species or even the same species, is potential prey. It will nonetheless be useful in describing the sociality of the social spiders to sketch the probable evolution of different degrees of sociality among insects.

As Edward O. Wilson of Harvard University has pointed out, the eusocial insects, or higher social insects, have three traits in common: cooperative care of the young, a division of labor whereby more or less sterile individuals attend to the needs of fertile individuals, and a life cycle long enough for the offspring at some point to share the activities of the parental generation. The evolutionary routes that may have led from nonsocial to eusocial behavior appear to be traceable in terms of the less than eusocial behavior found among various insect relatives of the eusocial species. Charles D. Michener of the University of Kansas has outlined two such possible routes.

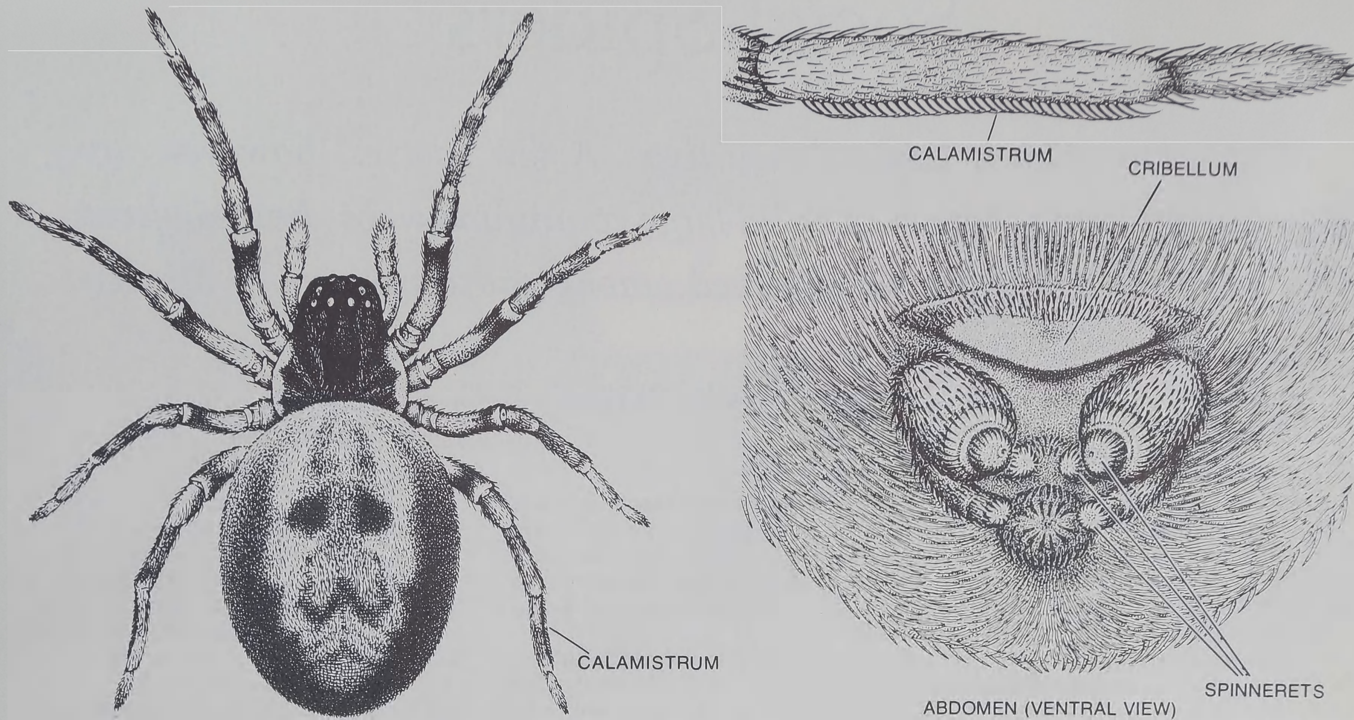
The first route Michener calls parasocial; on it there are three levels of increasingly complex behavior on the way to eusociality. The lowest level, communal behavior, is characterized by an aggregation of female insects, all belonging to the same generation; once the females have aggregated they build a communal nest for their young. The next level, quasi-social behavior, is characterized by cooperative care of the young. The third level, semisocial behavior, is characterized by the appearance of different castes that serve different roles. Thereafter eusociality is achieved when the life cycle is extended so that parents and mature offspring coexist in the same colony.

Michener's second evolutionary route he calls subsocial. On this route only one level of behavior precedes eusociality; it is characterized by solitary rather than communal nest building. The solitary female remains at the nest, however, and cares for her young. Eusociality is achieved in one step when the nest builder lives long enough to have the assistance of its first daughter generation in caring for subsequent, caste-differentiated daughter generations.

Looked at in these terms no social spider is eusocial. We must define the common base of spider sociality in much more restricted terms: the existence of various degrees of communality and of characteristic interactions among the members of communal aggregations.

Here it should be noted that with few exceptions even spiders that are solitary in habit go through a semicommunal stage early in their life cycle. Unlike insects, spiders do not have a larval stage. Each emerges from the egg as a functioning miniature adult, although it retains a yolk sac that supplies it with nutrients for several days. It grows in size and develops its sexual characteristics through a series of successive molts, the earliest of which takes place within the shelter of the parental egg sac. It leaves the egg sac fully prepared to spin silk and disable prey.

One might therefore expect that the spiderlings of the solitary species would scatter as soon as they leave the egg sac. Instead for the duration of a period known as the tolerant phase the spiderlings aggregate, and many of them join in the labor of building a small sheet web. They may even attack any small prey animal that blunders into the



COMMUNAL SPIDER *Mallos gregalis* has an average body length of five millimeters. Its complex flytrap web incorporates many sticky bands of silk that entangle intruders. The sticky silk is drawn from hundreds of microscopic pores in an abdominal plate (*right*), the cribellum. The spider combs out the silk with its calamistrum, an array of bristles that grows on the metatarsal of each of its hind legs.

web and wrap the intruder in silk. At this early stage, however, they never feed on the prey. After several days of the tolerant phase have passed the spiderlings disperse, build individual webs and feed on the prey they capture. All the spiderlings appear to adopt the solitary behavioral pattern simultaneously.

It is also noteworthy that in certain solitary-spider species (including representatives of the families Eresidae, Theridiidae and Agelenidae) the adult female does not abandon the egg sac after constructing it but remains with it, or carries it with her, until the spiderlings emerge. The female may then allow them to share her captured prey or may nourish them with regurgitated food or special secretions. Such parental care of the offspring bears a certain resemblance to the lower level of Michener's subsocial route to higher sociality. Thus even among the spider species that are recognized as being solitary, transient episodes of sociality may be observed.

When spiders live in groups, a number of additional interaction patterns are evident. Spider groups form in a variety of ways. For example, adult spiders of some species in the families Uloboridae and Araneidae will aggregate without regard to whether they are the offspring of the same parents or different ones. Each individual in these aggregations spins its own web. Among some species the individual may also contribute silk to a communal web area. Some of these groups may be made up of as many as 1,000 adults. In general each individual lives independently. All, however, share the benefits of a large aggregate web surface and of monopolizing a habitat that might otherwise have been shared by competitive species.

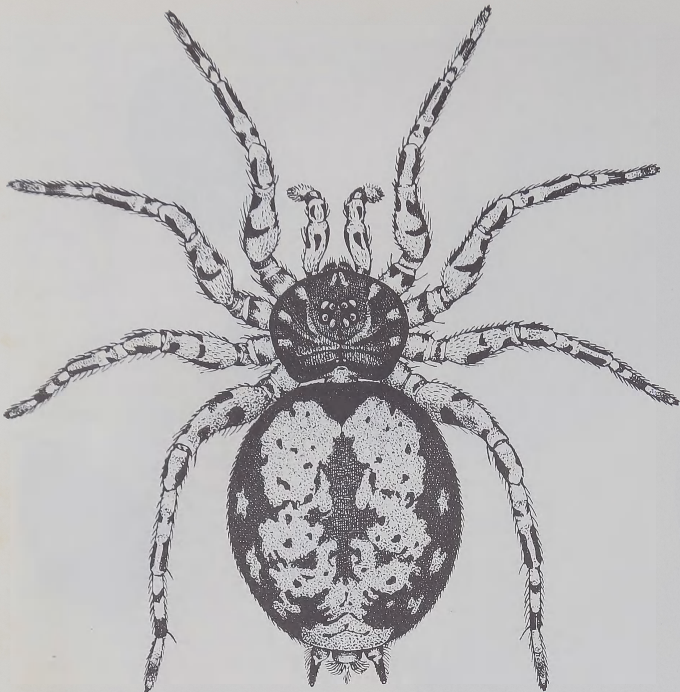
The viability of simple aggregations such as these demonstrates the existence of a tolerance mechanism in the individual adult spiders. At the very least the mechanism must be strong enough to keep the spiders from eating one another when prey are scarce. Evidently the mechanism is also species-specific; it is not limited to simply ensuring that the spiders are tolerant of all the other spiders in the aggregation. They are also tolerant of any spider of their own species. This has been demonstrated as follows. Individuals of the species *Metepeira spinipes,* a member of the family Araneidae, have been taken from populations living hundreds of miles away and introduced into local aggregations of *M. spinipes.* The presence of strangers did not disrupt the tolerance mechanism within the local aggregation, nor was any difference noted in the behavior of the two groups.

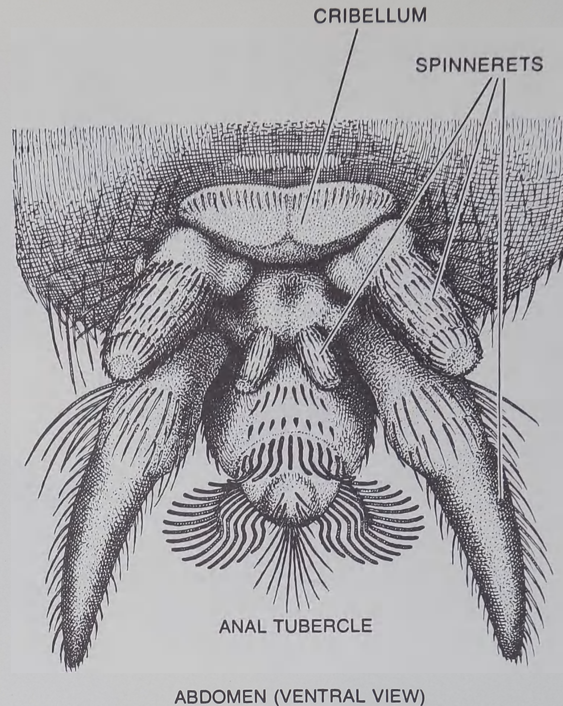
The most dramatic examples of spider sociality involve interactions substantially more complex than those I have been describing so far. These interactions are known only for four (possibly five) spider species. Two of the species are African: *Agelena consociata* and *Stegodyphus sarsinorum.* The others are New World spiders: *Anelosimus eximus* (and possibly a second species of the genus, *A. studiosus*) in South America and one of the species I have collected in Mexico, *Mallos gregalis.* All have in common the habit of constructing a large central web that is occupied by all the spiders in the aggregation. By combining their labors the spiders are able to construct a web that is much larger and far more elaborate in architecture than the web of any single spider; the structure is occupied by successive generations.

These spiders also collaborate in capturing prey much larger than prey any one of them could capture alone. Moreover, after the prey has been captured the spiders feed on it communally. Interactions as complex as these imply that these species have in addition to a tolerance mechanism a capacity for the coordination of individual responses to stimuli and an ability to recognize intraspecies sensory cues or to respond to some other kind of information. As an example, each spider seems to be able to distinguish between the web vibrations caused by a fellow member of the community and the vibrations caused by potential prey.

Bertrand Krafft of the University of Nancy has observed *Agelena consociata* in Gabon. He found that close-quarters tolerance in the species is mediated at least in part by chemotactic cues. Uninjured members of the community tolerate one another. An injured spider, or one whose normal superficial odor has been artificially altered by a washing in alcohol and ether, is attacked immediately. Neither the chemotactic cues nor other possible but still unidentified components of the spiders' tolerance mechanism are confined to local populations of the species. As with *Metepeira spinipes,* individual spiders of the same species can be moved from one colony to another without disrupting the communal activity pattern.

There is no evidence that any of these spider species has evolved a caste system such that the adults differ in form in accordance with any division of labor. Some difference in behavioral roles may exist as a result





GREGARIOUS SPIDER *Oecobius civitas* **has a body averaging two and a half millimeters in length. Like** *Mallos gregalis* **it has a cribellum, but it uses its sticky silk actively, wrapping its prey rather than waiting for it to become entangled. The spider combs out a thread of the silk with its anal tubercle (*right*) and winds silk around the prey by circling it, abdomen foremost (*see middle illustration on page 106*).**

of age or variations in biological rhythms, but just how cooperation is cued remains unknown. The pattern of behavior is nonetheless an example of sociality that is not easily equated with any pattern of sociality among insects. These spiders' behavior may well deserve a category of its own: communal-cooperative.

The Mexican social spider *Mallos gregalis* traps mostly flies on the sticky surface of the communal sheet web it spins around the branch of a tree. The spider has long been known to Mexicans as *el mosquero,* the fly-killer, and in the rainy season, when houseflies are particularly oppressive, those who live in the Guadalajara countryside will bring a web-covered branch into their house in much the same way that other people might string up flypaper. A member of the family Dictynidae, *M. gregalis* is a cribellate spider. Such spiders have a sievelike plate, the cribellum, on the underside of their abdomen [*see illustration on opposite page*]. Sticky silk emerges from fine holes in the cribellum and is combed away with the two hind legs that bear a special row of bristles known as the calamistrum. This is the silk that forms the sticky prey-trapping areas on the outside of the spider's web. The web as a whole is an elaborate structure that includes supporting lines running between the surface sheet and the twigs and leaves of the branch, sheltered retreats for the spiders and special chambers where the female spiders live with their egg sacs. The sacs, thin wrappers of silk, contain from 10 to 20 eggs. The surface sheet is perforated in places with holes that provide access to the interior of the web.

The communal web of *M. gregalis* can be very large. One I saw near Guadalajara covered the limbs and branches in the upper three-quarters of a 60-foot tree of the mimosa family. Where the limbs met the trunk the silk of the sheet web was gray, but near the tips of the branches the silk was new and white. Evidently construction was continuing outward along the limbs. The spiders were not confined to the newer portions but were active in all parts of the web.

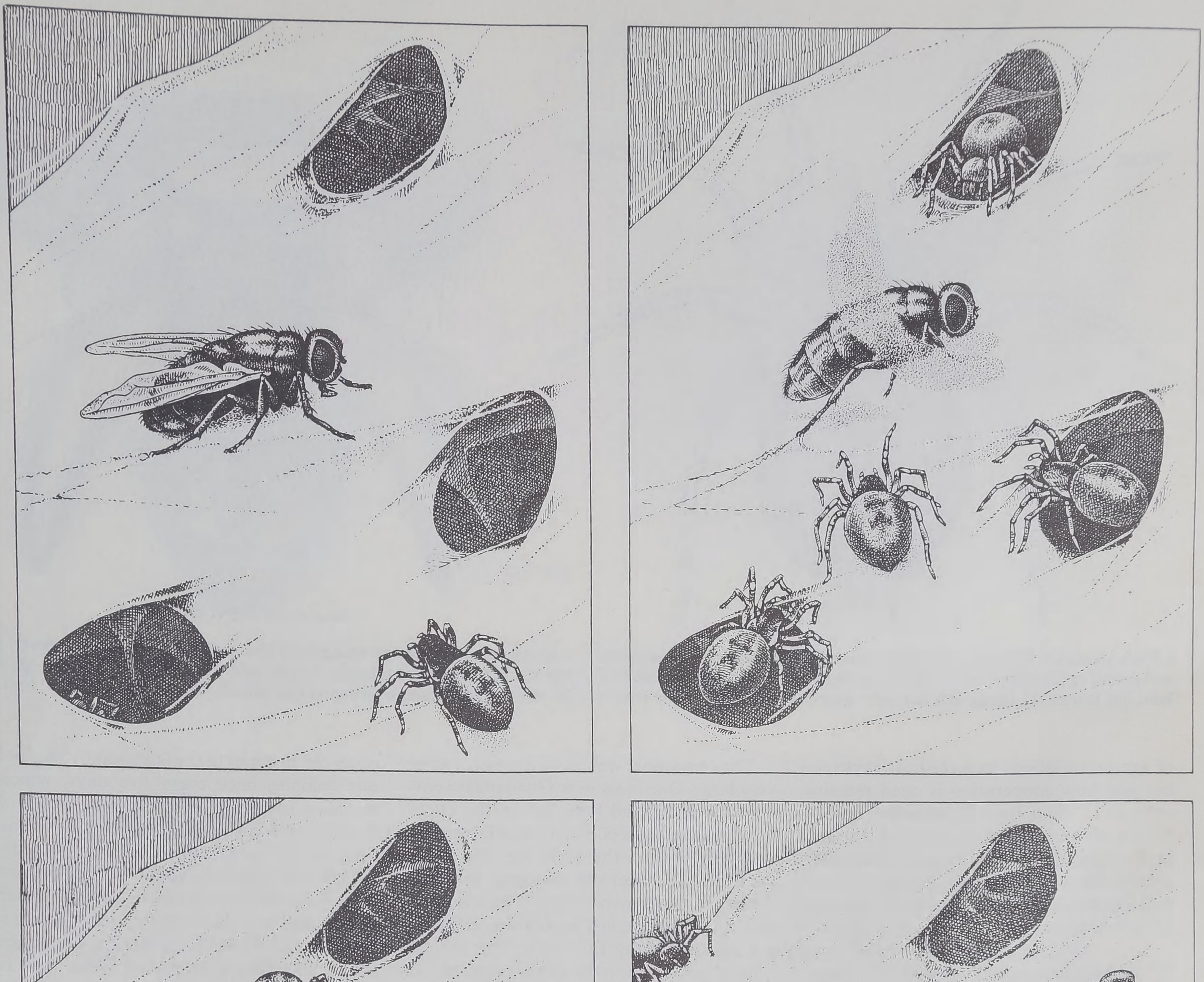
Both field and laboratory observations confirm that the construction of the *M. gregalis* web is a mutual effort. If a laboratory colony of the spiders has some treelike support available, such as an upright stick, the spiders will build their characteristic enveloping sheet web. In the absence of such a support they will build the kind of three-dimensional web that is typical of other dictynid species. Although this web looks different from the natural one, it too includes retreats and egg-sac chambers. In the laboratory web a task begun by one spider may be finished by another. I have also seen one spider of the colony lay down strands of ordinary silk, after which other spiders added bands of the sticky cribellate silk.

Observed in nature, the spiders seem to move around at random and without haste, emerging from and disappearing into the holes in the surface of the web. Their fly prey are trapped by the sticky web when they alight on it. When a fly gets stuck, two or three spiders approach the buzzing insect, immobilize it with their venomous bites and then feed on it. On occasion the spiders can be seen carrying flies down the holes into the interior of the web.

The spiders' predatory behavior can be observed in detail in the laboratory. We feed our colonies once every five days, which increases the probability that a majority of the spiders will be ready to feed at the same time. At any given moment one or two individuals in a colony of about 100 spiders are usually on the surface of the web; the other spiders will be in the web's interior. When a housefly is put into the spider cage and flies about, it makes a humming noise that is audible to the experimenter but causes no apparent change in the random activity of the spiders.

A fly that lands on a nonsticky part of the web and walks around stimulates a localized response; some of the spiders will turn to face in the direction of the fly, but that is all. If the fly gets entangled in a sticky part of the web and begins to buzz loudly, the behavior of the spiders changes abruptly. Throughout the web spiders that have been at rest turn toward the trapped fly and begin to approach it in short jumps. The fly continues to buzz even after the first spiders to reach it start their attack, usually by biting a leg or a wing. The buzzing draws more attackers; they move directly toward the fly over the web surface until eventually the prey almost disappears under the feeding spiders. Both male and female spiders attack. Even immature spiders take part, swarming over the adults in search of a place to feed.

Even though the attacking spiders in the caged colony are quite aggressive, we have never observed one spider attacking another. As we canvass the behavioral repertory that differentiates social spiders from solitary ones, this aspect of feeding in aggregations is significant. For example, young soli-



RESPONSE TO AN INTRUDER by a colony of communal spiders is reconstructed in these drawings on the basis of laboratory observation. Unlike the members of a wild colony all the spiders in the laboratory colony have fasted the same length of time. The sound of a passing fly is audible to a human observer but attracts no attention from the spiders. Even when a fly lands on the surface of the web (*top left*), only the nearby spiders reorient themselves. The buzzing of a fly entangled in sticky silk (*top right*) stimulates a response throughout the colony, and the spiders advance on the prey in quick jumps. The bites of the first spiders to reach the fly (*bottom left*) give rise to a louder buzzing that further stimulates spiders to approach the prey. As feeding begins (*bottom right*) immature spiders join the adults.

tary spiders such as those of the species *Araneus diadematus,* when they are artificially confined in close quarters, will also feed communally. Among the artificially confined solitary spiderlings, however, a tolerance mechanism, if it exists at all, operates only imperfectly; they will feed communally both on captured flies and on one another. This suggests that it is a strong tolerance mechanism that accounts for communal feeding in *Mallos gregalis* just as coordination mechanisms account for communal capture of prey.

The tolerance mechanism at work in *M. gregalis* colonies is being studied in our laboratory. It is evident from our observations that the mechanism is strong and that it operates both at close quarters and over considerable distances. Indeed, several separate mechanisms may be at work, perhaps mediated by cuing systems that allow discrimination between, say, the web vibrations caused by trapped prey and those caused by members of the colony. To test this hypothesis we are subjecting the colonies to the stimuli of various web vibrations in the hope of isolating such cues.

WEB-COVERED BRANCHES of a species of mimosa near Guadalajara support part of the communal web of a *Mallos gregalis* colony. Scattered holes allow the spiders to move freely from areas inside the web to the sticky outer surface where intruders become trapped. In the fly season local people often bring such branches indoors to serve as a kind of natural flypaper.

The social behavior of the second Mexican spider, *Oecobius civitas,* at first seems to be principally aggregative, like the behavior of other spiders that build their nests in close proximity. The darkness of this spider's microhabitat makes observation of its behavior difficult, but its unusual method of prey capture has been recorded. *O. civitas* has a finger-shaped organ, the anal tubercle, on the abdomen near its silk-extruding spinnerets. With this appendage it can comb sticky silk out of its cribellum in a rope that it winds around its prey [*see illustration on page 103*].

A closer study of the sociality of *O. civitas* proves that it is more than merely aggregative. The spiders' behavior features a curious combination of tolerance and avoidance. On the underside of the rock that shelters the spiders each individual weaves a small open-ended tube of silk that is its hiding place; around this retreat the spider constructs a thin, encircling alarm-system net close to the surface of the rock. The pair of structures makes up the spider's web, which is generally found in a hollow or a crevice of the rock. If a spider is disturbed and driven out of its retreat, it darts across the rock and, in the absence of a vacant crevice to hide in, may seek refuge in the hiding place of another spider of the same species. If the other spider is in residence when the intruder enters, it does not attack but darts out and seeks a new refuge of its own. Thus once the first spider is disturbed the process of sequential displacement from web to web may continue for several seconds, often causing a majority of the spiders in the aggregation to shift from their home refuge to an alien one.

Field observations and experiments indicate that, as with *Metepeira* and *Mallos,* the mechanisms responsible for the combination of tolerance and avoidance extend beyond the local population to include other spiders of the same species. Moreover, within the local population the shift to another spider's shelter may be a semipermanent move. The reason is that when the spiders are undisturbed, they occupy a fixed web position for long periods. In any event the behavioral pattern of the species benefits the individual spider by providing more than one available retreat in an emergency.

The group behavior of *Oecobius civitas* is far simpler than that of *Mallos gregalis.* It is nonetheless effective in enabling the spiders to live together under crowded conditions. No doubt the avoidance mechanism makes a major contribution toward the spiders' ability to maintain a high population density in their restricted microhabitat. Other contributing factors probably include the spider's unusual predatory technique and the spacing of individual webs. In any case, although we remain largely ignorant of the mechanisms underlying avoidance and tolerance, they appear to be the basic building blocks that provide a foundation for more complex group behavior.

It has been suggested that *Oecobius civitas* displays an even more remarkable kind of sociality: construction of a communal egg sac by the females in the aggregation. The possibility of such a behavioral advance, unknown among spiders, came to light recently when William A. Shear of Hampton-Sydney College undertook a taxonomic review of the oecobiid spiders. He was assisted by a number of colleagues who donated specimens to the project. Among the donors was Willis J. Gertsch, curator emeritus of spiders at the American Museum of Natural History, who had collected specimens of *O. civitas,* its web and its egg sacs in the Guadalajara area.

The usual oecobiid egg sac contains from five to 10 eggs. In the preserved material donated by Gertsch, however, Shear found two groups of more than 200 immature spiders. Each group was contained in what gave every appearance of being a single egg sac. Shear published his observation in 1970, suggesting that *O. civitas* might be a communal egg layer.

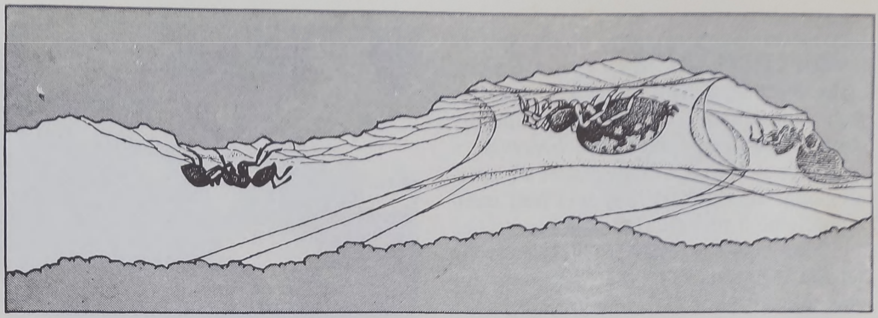
When I collected specimens of *O. civitas* and its egg sacs in the area near the shores of Lake Sayula, where Gertsch had done his collecting, I found that several other species of spiders shared the rocky habitat with the oecobiids. As a result a variety of egg sacs could be collected. This I did, sealing individual egg sacs in individual tubes. I was disappointed to find that only the small sacs, averaging seven eggs to a sac and mainly collected in or near *O. civitas* web retreats, hatched oecobiids.

After rearing this spider in the laboratory for three generations and observing only individual egg sacs containing from five to 10 eggs, I consider that to be the normal pattern of reproductive behavior in *O. ci-*

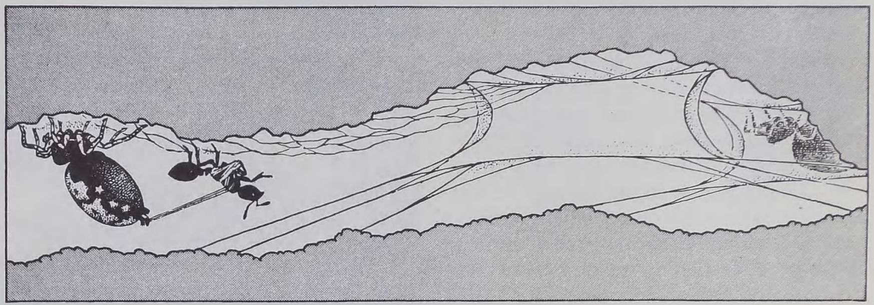
vitas. To resolve the question beyond all doubt other single *O. civitas* egg sacs containing eggs or immature spiders in large numbers will have to be collected in the field.

Mating behavior has not yet been observed in our laboratory populations of either *Mallos gregalis* or *Oecobius civitas*. Solitary male spiders go through elaborate pre-mating maneuvers, so-called courtship patterns that supposedly inhibit predation in the female at the time of copulation. Among social spiders, which live in tolerant aggregations, such maneuvers would not seem necessary. Indeed, if differences in copulatory patterns between solitary and social spiders do exist, they may even provide clues to the evolutionary background of spider sociality. In this connection we have made one possibly significant observation concerning fertility. Solitary spiders raised in the laboratory retain the cyclical breeding rhythms characteristic of their wild state, but when our *M. gregalis* colonies are provided with a uniform environment and controlled periods of darkness and light, they produce fertile eggs throughout the year.

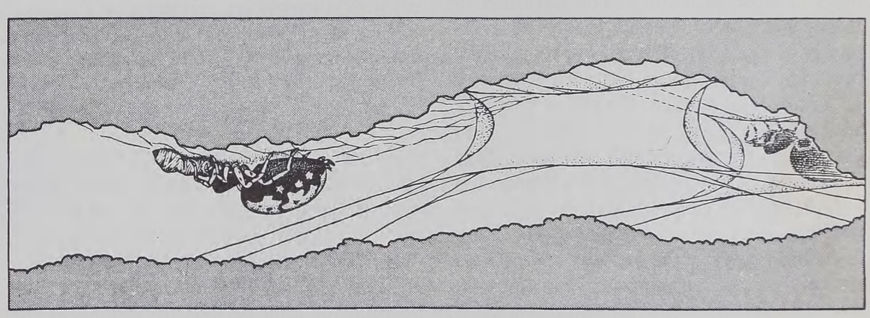
Observation of the two Mexican spiders has uncovered a substantial amount of information about their sociality, but that information more often than not merely defines the extent of our ignorance. For example, we do not know what conditions favor the development of spider sociality or even what mechanisms are involved in tolerance, avoidance, the formation of groups or the coordination of activity. Moreover, it is not known how different forms of spider sociality are related to one another or how, in complex interactions, intragroup information is transferred. The search for answers nonetheless seems to offer one certainty: The more we learn about the sociality of comparatively simple animals, the better we shall be able to understand the sociality of more complex species, including our own.



CAPTURE OF PREY, usually a foraging ant, by a spider of the gregarious species *Oecobius civitas* follows a complex pattern that begins when the intruder disturbs the spider's alarm web.



ALARMED SPIDER leaves its shelter and moves in circles around its prey, its abdomen foremost and raised clear of its legs, while it combs out a strand of sticky silk with anal tubercle.



WRAPPED IN SILK, the ant is immobilized. The spider may rest for a time or may turn (*left*) to bite and disable its prey. Only the captor feeds on the prey; nearby spiders do not approach.