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Spider Solidarity Forever

Social spiders create the communes of the arachnid world

By LAURA HELMUTH

Most spiders have beastly social skills. They're aggressive, territorial loners that would just as soon eat a sibling as look at one.

Of the 35,000-odd spider species that have been described, however, a few dozen flout tradition. These social spiders live in groups. They cooperate while hunting and building their communal homes. They even care for their own—and sometimes each other's—young, whereas typical spiders lay their eggs and creep away.

Nineteenth-century biologists, including Charles Darwin when he voyaged to South America, discovered a few spider species that gathered in huge colonies. In the past 20 years, researchers have found more examples of gregarious spiders. Now, scientists are exploring the social webs that bind together these infamous individualists.

By looking at the social world from a spider's-eye view, biologists are gaining insights into the evolution of sociality, the costs and benefits of group living, and the ways that creatures relate to their kin.

Entomologists have long studied the social worlds of a variety of insects—ants, bees, and termites—that live in large, cooperative networks. Like the six-legged social species, many cooperating spiders hunt together and share food.

Although arachnid societies bear a superficial resemblance to these insect communities, they operate by markedly different reproductive rules. In insect groups, workers are sterile and only the queen lays eggs, whereas all spiders in a colony are able to reproduce.

In that regard, social spider species interact more like a herd of wildebeests than like a hive of bees, says George W. Uetz of the University of Cincinnati.

Deborah R. Smith of the University of Kansas at Lawrence compares social spiders to a pride of lions. "It's always interesting to see an organism one usually thinks of as asocial, predatory, and cannibalistic, forming large cooperative societies," says Smith.

The most social of the social spiders live in multigenerational colonies in the rain forests of South America. *Anelosimus eximius,* one of the best studied of these cooperative species, builds a hammock-shaped web suspended from the lush vegetation by long threads. Their mahogany bodies are about the size of pencil erasers. They band together in colonies of hundreds to tens of thousands of individuals, spinning their collective web above rivers and roads and where light filters in through the tree canopy.

Several generations of spiders live together in the community, and with constant repairs, the meter-long nest can last several years. Adult spiders care for the young, but they don't distinguish between their own progeny and those of others. They guard eggs against predators, move egg sacks to the web areas with the most comfortable temperatures, and feed hatchlings.

When a colony grows too large, the nest starts to break up of its own weight, Smith says. The spiders split into two or three groups, or the young adult females crawl away on bridges of silk to spawn their own colonies.

Group living has its benefits, says Leticia Avilés of the University of Arizona in Tucson, who studies cooperative spiders in Ecuador. Working together, social spiders can capture prey as large as 10 times their size, whereas an individual spider is lucky to bag a bug twice as big as itself.

Cooperative spiders also save on the cost of silk. Frequent tropical rains pelt the sheetlike webs. By working together, the cooperative spiders conserve on energy and protein as they repair the damage from a web-ripping storm.

As the colony expands, however, parasites are more likely to find it and infest its egg sacks.

Field studies show that females living in an intermediate-size colony raise the largest numbers of offspring, Avilés reported in the September 1998 AMERICAN NATURALIST.

Cooperative behavior evolved in eight unrelated spider genera in different families, says Smith. She has gleaned clues to the evolution of this behavior by looking at some modern species that are related to social spiders. They have some social traits but haven't fully committed to group living.

In such species, the mothers care for the young well after they have hatched but do not establish colonies. Each generation of young goes off and makes its own single-family web. These species, Smith speculates, resemble forerunners to the fully social spiders. After some point in evolution, she says, "the babies just never leave home."

All this togetherness over many generations inevitably leads to inbreeding, normally considered an evolutionary no-no. "We had to ask, Were they really doing this?" says Smith.

They were indeed, according to recent research on the genetics of spider societies. Smith finds genetic variation between colonies of one cooperative species, but within one nest, the individuals are virtually identical.

When the living is easy, it's fine to be a clone, Smith says, but without genetic variation, an entire population could be wiped out by an epidemic. For instance, a mysterious spider plague swept through Panama in 1983, killing entire nests of cooperative spiders.

The cooperative spiders' evolutionary history may have prepared them somewhat for inbreeding, says Smith. The immediate ancestors of cooperative spiders probably didn't disperse far from their birthplaces. Adults therefore likely mated with their cousins, and perhaps this early stage of inbreeding purged some of the harmful genetic traits that could overwhelm an inbred social group, she speculates.

As biologists have started teasing apart the web of relationships inside spider societies, they have helped rehabilitate a concept called group selection. Once shunned by evolutionary biologists, the idea may be one of the best ways to understand how cooperative social spiders have evolved, says Theo Evans of the University of Melbourne in Parkville, Australia, who studies social spiders in eucalyptus forests.

In classical Darwinian evolution, the most fit individuals of a species survive and reproduce. In the 1960s, theorists suggested group selection as a communal corollary. According to this concept, certain behaviors benefit entire species of animals rather than individuals.

Male deer, for example, compete with each other through nonlethal displays. This type of behavior may have evolved because it led to fewer deaths for the species as a whole rather than to breeding advantages for the individual, suggested adherents of group selection theory.

Although the concept made a certain amount of intuitive sense, it doesn't generally hold up to evolutionary scrutiny, according to today's biologists. Groups don't reproduce, after all. Only individuals do, and individuals compete with their neighbors for food and mates. Moreover, groups are fluid, with individuals moving in and out of them at a rate that would dilute any benefit accrued by temporary team work.

Today, biologists are focusing on evolution at the level of whatever carries a gene, says Evans. In most cases, genes confer advantages on the individual who carries them. In social spiders, however, an entire, inbred group may be the vehicle that carries a gene, proposes Avilés.

The sex ratio among cooperative social spiders supports this theory. Ninety percent of a cooperative spider population is female. This sex ratio benefits colonies in their competition with other colonies, says Avilés.

The more fertile females there are in a nest, the faster the colony grows to a safe, productive size, and the more daughter colonies the group can spin off. However, any individual in a

colony could pass its own genes along faster by bearing many males, who could inseminate many females. Thus, the sex ratio appears to be a trait selected at the group level.

High in the canopies of Australia's eucalyptus forests, another sort of social spider builds its nests, which are wonders of arachnid architecture. The crab spider species *Diaea ergandros* constructs its homes out of long, flexible eucalyptus leaves, says Evans.

Unlike cooperative spiders, thumbnail-size social crab spiders live together for just one generation and then disperse to form the next season's nests, says Evans. Each year, the female constructs the foundation for her nest with five or six leaves, then lays her egg sack in the inner chamber. She sits on the egg sack, like a mother hen incubating her eggs, and guards it against predators and parasites.

When her 40 to 80 offspring grow strong enough, they tie more leaf layers around the nest. The spiders first fold one leaf over and tie its ends together with silk. Then, they wrap another leaf around the first, and another, and another, making the layered nest look like a head of cabbage. They work until the nest reaches the size of a softball.

The group also gangs up to ambush bees, moths, and butterflies that alight on or near the nest.

For a spider, the mother crab spider invests heavily in each of her progeny. Nonsocial crab spiders may lay 10 egg sacks per year, each containing as many as 1,000 eggs, and then leave them on their own. The social crab spider lays just one egg sack, and she feeds the young throughout the year. When autumn comes and food supplies grow scarce, she serves up her last meal to her young: herself.

Evans brought colonies of social crab spiders into the lab and provided them with long, leaf-shaped, flexible pieces of transparent plastic, which they constructed into nests. He could see into the heart of the nest and watch how the social crab spiders defend themselves against predators.

The nest serves as a labyrinth, in which the crab spiders can avoid invaders, Evans observed in the lab. He introduced a predatory spider, which gnawed the silk threads holding together the plastic that formed the nest's narrow passageways. The crab spiders sensed the source of the vibration and shrunk from that part of the nest. When the predator finally gave up, the crab spiders repaired the damage.

In the wild, the nests protect the spiders from insects, birds, and small mammals, as well as other spiders. "It's a very scary world out there," says Evans.

Without the large, protective nests, crab spiders would be easy prey in the Australian forests. Under such conditions, a lone individual can't survive as well as one who gives up some autonomy and shares food with the group, he says.

The spirit of "all for one and one for all" succeeds better, evolutionarily, if the "all" being served share most of their genes. In social crab spiders, scientists were surprised to find that the family group will accept nonrelative but same-species crab spiders. The colony hunts with these outsiders and offers them asylum in the nest, a seeming violation of evolutionary rules.

The apparent altruism turns out to serve a purpose, however. When food is scarce, crab spiders eat these immigrants rather than their own siblings, Evans reported in the Feb. 7 Proceedings of the Royal Society of London B.

Other social spiders show a little more respect for each other's personal space. The colonial orb-weaving spiders of Mexico and the southwestern United States build interconnected webs, but they defend their own turf, says Uetz. The longest continuous colony that has been observed was built of orbs knitted together by hundreds of thousands of 1-centimeter-long spiders. It measured 4 m across and 2 m high and stretched nearly two football fields long.

The spiders cooperatively erect the long silk lines to which individuals anchor their orbs.

Each spider fends for itself within the scaffolding, however, ejecting other spider intruders and parasites, hiding from predators, and catching insects that land on its own orb.

Insects that fly into the long quilt of webs may bounce out of the first orb they hit, but they are likely to ricochet right into a neighbor's lair, says Uetz. Each spider captures about as much prey as its neighbors, he says.

In flush times, it behooves a colonial orb spider to live in large groups, because the big net that the spiders collectively create provides each individual with plenty to eat. When times are tight, however, this modified group-hunting system breaks down. Each individual still captures about the average amount of prey, but that smaller amount isn't enough to sustain it.

In such conditions, says Uetz, a spider's best chance would be to fend for itself. Theoretically, some would still starve, but others would survive.

Uetz started studying social spiders 20 years ago in Mexico, where orb-weaving species anchor their orbs to cactus spikes. Uetz wondered whether the sparse desert vegetation concentrated the orb weavers, their proximity only giving the appearance of communal behavior. To test this, he picked spiders up and introduced them to new locations with more abundant sites. He found that the orb weavers do seek each other out and build their colonies together.

No one knows yet whether the social orb weavers always live in colonies. In different environments, says Uetz, the spiders may try different strategies for survival. He is following a species of colonial orb weavers that he found just below the cliffs of Pebble Beach in California. During last year's bug-rich El Niño spring, the orb weavers lived together in a large colony. He plans to return when food is sparser to see whether the spiders are still living socially.

Social spiders have evolved independently in Africa, the Middle East, the Americas, and Australia. The repeated appearance of social behavior has puzzled spider experts. "We're all trying to figure that out," says Evans. "And we all disagree."

It may be that communal living offers some spiders their only chance in a harsh world. When leaving a nest is too dangerous, rebuilding a web each day is too demanding, or finding mates is too difficult, sociality can win out over solitude.

Living together and sharing resources "may not be a good option," Evans says, but in certain circumstances, "it's the best of all available options." □