Elusive Form of Evolution Seen in Spiders

A study of spider colonies supports a controversial idea in evolution — that natural selection can act on communities as well as on individuals.

By Emily Singer

Social spiders work together to capture a grasshopper.

As a rule, spiders are antisocial. They hunt alone, zealously defend their webs from other spiders, and sometimes even eat their mates. "Cannibalism and territoriality comes naturally to Arachnida, even during sex," said [Jonathan Pruitt](), a behavioral ecologist at the University of Pittsburgh. But a handful of the more than 40,000 known arachnid species on the planet have learned to rein in that aggression. Like ants or bees, they cooperate for the good of the group.

For example, so-called tangle-web spiders form bands of 1,000 or more to spin webs that stretch for hundreds of yards, entrapping flies, small birds and "virtually any invertebrate imaginable," Pruitt

said. Smaller groups of a few dozen work together "like a pride of lions," he said; some of the spiders hunt for prey, while others rear the colony's young.

Female Anelosimus studiosus spiders can have either aggressive or docile personalities.

The spiders present a puzzle to evolutionary biologists. According to ordinary Darwinian natural selection, only the fittest individuals will pass on their genes. But if that's the case, why do tangle-web spiders act in ways that might conflict with an individual's drive to outcompete its neighbors? A spider that defends the nest might put itself at personal risk, jeopardizing its chances of producing offspring. And a spider that rears the young might have to wait to eat until the hunters are sated, so it might go hungry. These are not behaviors that would be expected to enhance an individual's fitness.

Biologists have long argued over the question of how natural selection can promote the evolution of traits that are good for the group, but not necessarily for the individual. Scientists have developed a number of mathematical models to attempt to explain the phenomenon. According to one model, known as kin selection, highly related organisms such as bees and ants can develop altruistic behavior — for example, many females forgo reproduction in order to raise the queen's brood — because they will still pass down their genes indirectly, through the queen.

The Hen Gangs

The product of the most famous — and profitable — experiment in group selection gets served on millions of breakfast plates every day. Commercial chickens kept for egg production are typically housed in group pens, an efficient arrangement that also presents a problem for farmers: The most productive birds tend to be the most aggressive. They can lay lots of eggs because they terrorize and sometimes kill their cage mates, hogging all of the group's food. If you breed chickens from individuals with a high egg-laying capacity, "you get hens that produce the most eggs or meat, but at the expense of their neighbors," said Michael Wade, an evolutionary biologist at Indiana University in Bloomington.In the 1980s, William Muir, an animal scientist at Purdue University in West Lafayette, Ind., came up with a better plan. Rather than selecting the best individual egg layers for breeding, he picked the groups that produced the most eggs. Egg output improved dramatically, because group selection produced kinder, gentler birds better suited to living in a group.The peaceful chickens have become a classic example of group selection. But they are also the result of a distinctly human force. Biologists don't yet understand how often natural environmental forces drive adaptation of the group. "That's where the controversy is nowadays, not so much whether group selection can work but how often it produces a trait," said Peter Nonacs, an evolutionary biologist at the University of California, Los Angeles. "Now we are transitioning from an argument among mathematical biologists to something experimentalists are trying to parse out."

But despite its altruistic appearance, kin selection is selfish — it helps an individual's genes to survive. Can natural selection promote truly unselfish traits, behaviors that are good for the group, but not necessarily to the benefit of individuals (or their immediate kin)? Some evolutionary models predict that it can, but while these models have been successfully tested in the lab, they have been studied only indirectly in nature.

Now, however, a new study of Anelosimus studiosus, a species of tangle-web spiders, published this week in Nature, suggests that evolution does indeed work at the level of the group. If certain groups of animals are more productive than others — that is, if they produce more progeny — then evolution will tend to favor the traits that make such fecundity possible. According to Pruitt, the findings are the first to provide direct evidence that natural selection can drive the evolution of a group trait in the wild.

Social Spiders

Female tangle-web spiders possess two basic personalities: aggressive "warriors" and docile "nannies." The warriors spend their time capturing prey and defending the group from predators and parasites, while nannies raise the colony's young. (To figure out an individual's personality, scientists put it in a box with other spiders — aggressive arachnids fight for space while docile ones cuddle, Pruitt said.)

The balance of warriors and nannies in any particular Anelosimus studiosus colony appears to be tuned to fit the colony's habitat. In large colonies with an ample food supply, warriors tend to abound, while colonies in sparser regions are dominated by nannies.

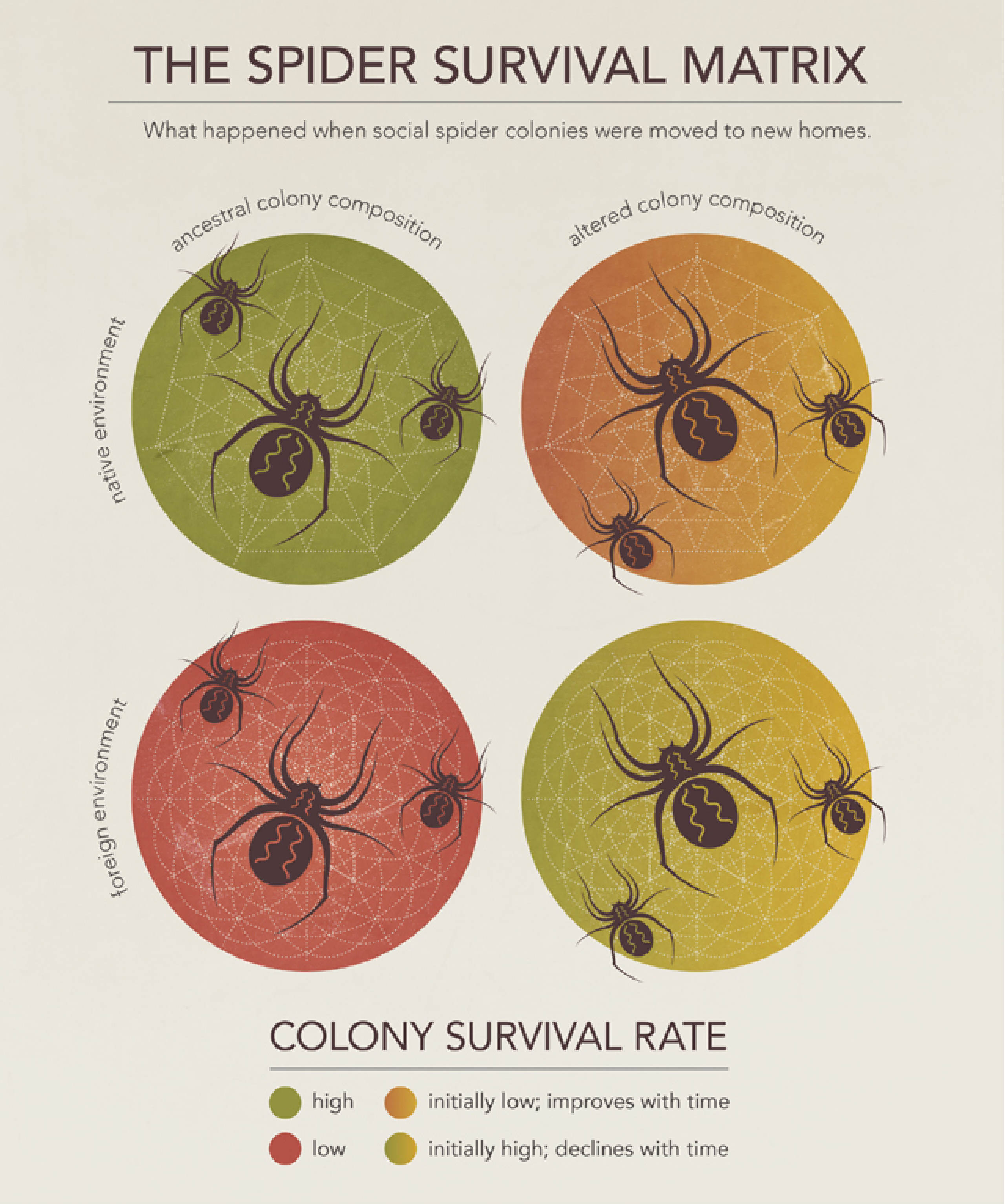
How does nature maintain this balance? One possibility is that it's the result of evolution at the individual level. In this scenario, warriors might do better in prey-rich areas because there's simply more prey for them to eat, while nurses might thrive in prey-poor areas because they may not require as much food as the warriors do.

However, there may be a different explanation. If the group, not the individual, is the most important basic evolutionary unit, then the group as a whole will evolve characteristics that are best suited to the environment, such as an intrinsic ratio of warriors to nannies. Colonies with the ratio best suited to the environment will be most likely to survive. Others will be more likely to die off.

To figure out which of these two possibilities is correct, Pruitt put together an array of custom-made spider colonies in the lab, creating different blends of personalities. He took spiders from warrior-heavy colonies and used them to assemble new groups that were heavy on the nannies. He also used spiders from mostly docile colonies to create warrior-laden groups. In addition, he assembled control groups that matched the composition of their original groups. He then transferred each colony to a tangle of chicken wire and transplanted the nests into various locations in Tennessee, where the spiders rapidly abandoned the wire to weave treetop webs. Some of the colonies were returned to their ancestral homes. Others went to new, foreign terrain.

After a year, 60 percent of the colonies were extinct. Control groups that returned to their ancestral homes tended to do well, and those that were transplanted into a new environment generally died. Neither of these outcomes was much of a surprise.

The most interesting results came from colonies made up of spiders that had been forced into a composition different from the one they grew up in — warrior-majority colonies containing spiders from mostly docile groups, for example. The colonies whose composition fit the new environment tended to survive. But over time, surviving colonies reverted to their members' original group composition. The warrior-majority colonies went back to having more nannies, for example. On the face of it, this is bizarre behavior; if the colonies are well-suited to their environment, why not maintain that ratio? It seems that some innate sense, perhaps encoded in the spiders' genes, pulled the colony back to its original configuration, even though this change meant the colony would perish.



Social-spider colonies are made up of “warrior” and “nanny” spiders. Different colonies have different ratios of warriors to nannies, depending on the environment. Researchers engineered new colonies, some of which retained their ancestral ratio, and some of which were altered so that spiders from warrior-heavy colonies were used to create nanny-heavy colonies, and vice versa. The new colonies were then placed in native and foreign environments. After a couple of generations, the altered colonies began to revert to their ancestral compositions, suggesting that natural selection shaped the composition of the group to be best suited to its native environment.

Pruitt and his co-author, [Charles Goodnight](), a biologist at the University of Vermont in Burlington, report that the experiment provides ample evidence for group selection. Other scientists agree. “No

other explanation fits the observed data as well as group selection," said Peter Nonacs, an evolutionary biologist at the University of California, Los Angeles, who was not involved in the research. "Having the right proportion is the main determinant of success in both groups and individuals."

The findings are particularly significant because the researchers watched the spider colonies revert to their ancestral composition over generations. "It's really good experimental work," said Michael Wade, an evolutionary biologist at Indiana University in Bloomington. "If the characteristics of groups stay the same from one generation to the next, it's evidence there is a genetic basis for the trait."

Pruitt and Goodnight don't propose a mechanism by which the colonies boomeranged back to their original state. And without such a mechanism, some researchers argue that the results could be due to ordinary selection acting on individuals. "I think they over-interpret [the results] as evidence of group-level adaptation," said Andy Gardner, a biologist at the University of St Andrews. "Natural selection may factor in the needs of the group, to some extent, when it hones the adaptations of individuals. But group fitness is not the whole story."

Family Ties

A combination of group selection and individual selection could be the key to resolving this tension. Historically, researchers have thought of the two as extremes, always at odds, but "sometimes group selection and individual selection are not necessarily conflicting," Nonacs said. Pruitt's paper might help to promote this perspective, he said. In the case of the social spiders, "even though group and individual selection may be going in the same direction, group level is stronger," Nonacs said. "This might be an interesting paper because it will be high-profile and will get people to think about this and not just accept the common paradigm."

Figuring out how social-spider colonies maintain their ratios might help to convince some skeptics. Do group members kill or exile spiders whose personalities throw the colony out of balance? Or do they encourage breeding of spiders with the underrepresented traits? Docile mothers tend to produce docile offspring, but it's unclear whether this is genetically encoded, or if it's a flexible trait that mothers can shape during development.

Though the social spiders present strong evidence for group-level selection in the wild, researchers aren't sure if it's a common occurrence in nature. "Whether or not it gets out of the insect and spider world into birds and mammals, we'll see," Nonacs said. Others feel that it is more widespread than previously believed. "I don't think this is rare at all," said Jennifer Fewell, a behavioral ecologist at Arizona State University in Tempe. Researchers are looking more and more at personality differences among members of a group, and they often find a mix of aggressive and less aggressive members, she said. Social spiders may be rare, but their behavior could prove to be a model for many other species across the animal kingdom.

Correction: This article was revised on October 3, 2014, to reflect that Andy Gardner is a biologist at the University of St Andrews, not the University of Oxford. In addition, he stated that the researchers over-interpreted the results as evidence of "group-level adaptation," not "group-level selection," as originally quoted.

Editor's note: *Feb. 6, 2020*
Since the time of this article's publication, the research about social spiders described here has

come under scrutiny for data irregularities, along with other other papers by Jonathan Pruitt that have already been retracted.

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