# Putting Game Theory to the Test

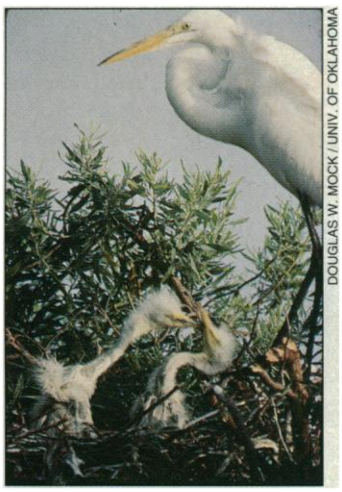
Animal behavior—from aggression in mole rats to cooperation among guppies—is providing field tests of this tool for understanding games of all kinds, from poker to politics

When three game theorists won the Nobel Prize in economics last October, the award spotlighted a theoretical tool that has quietly spread across several areas of science, gaining power as it goes. Game theory, which untangles complex situations in which the best strategy of one player depends on the actions of another, was originally devised to study poker, chess, and the like. Later, economists adapted it to explain markets and competition, and since the 1970s it has attracted researchers from other areas, including animal behavior. In the last few years, some evolutionary biologists have taken game theory the next step: testing its predictions in the field.

These empiricists are turning the tables on the traditional approach: applying game theory to explain existing data on, say, fighting or cooperative hunting. Instead, these researchers have been making field observations and doing lab experiments specifically to test game-theory models—and finding good agreement with the calculations in everything from spiders fighting over web sites to naked mole rats obeying a dominant female. The new give-and-take between theory and data, says Lee Dugatkin of the University of Missouri, Columbia, is allowing researchers to sharpen their models and get an increasingly detailed understanding of a wide range of animal behavior.

This effort is also reverberating outside biology, says Peter Hammerstein, a theorist at the Max Planck Institute for Physiology of Behavior in Seewiesen, Germany, who collaborates with both animal behaviorists and economists. After all, game theory's predictions have generally been quite difficult to verify for humans. The problem, explains Oxford University zoologist Martin Nowak, lies in knowing what the payoffs are for a particular "game." Is making a large profit, say, more desirable than driving a competitor out of business? With animals, however, the reward for a successful strategy is easy to identify: an advantage, such as more food, a higher rank in a social hierarchy, or less competition for mates, that ends up increasing the animal's reproductive success.

As a result, says Hammerstein, "it's now very fashionable for economists to work in evolutionary game theory," and game theorists from other fields have also taken note. Social scientists, for example, hope that understanding how a behavior such as cooperation is maintained in animals will give them insights into the origins of similar behavior in human systems.



DOUGLAS W. MOCK / UNIV. OF OKLAHOMA

**Making sense of strife ...** Egret nestmates can turn murderous.

Biologists had left game theory to the economists until 1973, when John Maynard Smith of the University of Sussex, U.K., used the technique to explain when and why some animals, such as stags or fish, fight with each other. Maynard Smith proposed treating a given behavior as a strategy in a game and assuming that strategies evolve just as physical characteristics do. Thus, any well-adapted population will follow the "best" strategy in this sense: Any mutants practicing a different strategy will reap a lower reproductive payoff and will die out. Maynard Smith named that optimum strategy an evolutionarily stable strategy, or ESS.

RAYMOND A. MENDEZ / ANIMALS ANIMALS

**... and oppression.** Naked mole rat queen threatens a balky worker.

Over the past 20 years theorists have modeled nearly every imaginable animal behavior as an ESS: aggression, cooperation, foraging, hunting, rivalry, and many more. "It was very exciting that the models seemed to predict all this," Hammerstein says. "But to see that it was more than just a superficial correspondence, they had to be tested." To demonstrate that an animal really does follow an ESS, researchers would have to collect enough data to calculate the exact reproductive payoff for the observed strategy and the alternatives.

### A spider's stratagems

Among the first to do so was Susan Riechert, a spider expert at the University of Tennessee. Early in Riechert's work with the desert spider *Agelenopsis aperta*, she faced a puzzle. She had noticed that the spiders' reproductive success depended greatly on where their webs were located: Some spots offered much more prey, allowing the spiders to eat better and lay more eggs. Riechert wasn't surprised to find that the spiders squared off over webs in these prime sites, but she saw no pattern to these conflicts. Sometimes an invader would leave almost as soon as it arrived, sometimes it would engage in a series of bizarre displays and counterdisplays with the current occupant, and sometimes the two would fight.

While she was mulling over this puzzle, Riechert read Maynard Smith's paper. Perhaps, she thought, the behavior could be understood in terms of an ESS. Because she had no experience in game theory, she collaborated with Hammerstein, who had worked with Maynard Smith and who had earlier published an abstract game-theory model that held promise for explaining the spider's strategies. "We took some existing data about spiders and created a model that could reproduce the data," Hammerstein says. "But did it [do so] for the right reasons?"

Answering that question took a full 6 years. Riechert measured how much food a spider gained by occupying a prime web site in different kinds of environments and worked out the implications for egg production. She also found that when spiders fight over these prime sites, the probable outcome depends mostly on the spiders' weights. If one spider outweighs the other by 10% or more, it has a 90% chance of winning the fight. She discovered that a spider loses a leg in about 30% of fights, and the loss of a leg costs it 10% in food intake per day and makes it 25% less likely to win its next fight.

When Riechert was done, she and Hammerstein could estimate the lifetime reproductive payoff for various confrontation strategies, depending on the site in dispute and the size of the opponent. For spiders in an arid area with few prey, they found, good web sites were so important that neither spider in a contest should withdraw right away; both should at least mount a display. And unless a spider was outweighed by 10% or more, it should be willing to fight. (Two spiders on a web can judge each other's weight very accurately, she says.)

By contrast, for areas close to water with many good web sites, they calculated that a smaller spider's best strategy is always to withdraw immediately and take no chances. Between spiders of equal weight, the occupant should display and the intruder, which has nothing invested in the web, should withdraw. A heavier intruder should display, hoping the web-owning spider will leave. Neither should escalate into a fight—the risks aren't worth it.

When Riechert took these predictions back to the field, she found that the spiders in the arid areas "behave very close to prediction." The spiders who lived in areas near water "had a lot more fighting than predicted," she says, but that seems to be explained by the fact that they interbreed with more combative spiders from the arid areas.

### New players

The depth and detail of Riechert and Hammerstein's model, which they finished in the mid-1980s, helped convince other researchers that game theory's appeal was more than just intuitive. It could provide numbers that could be tested against observation. At the University of Oklahoma, for instance, Douglas Mock was attracted by the chance to replace "squishy verbal arguments" with "the rigor of a quantitative approach." So he approached game theorist Geoffrey Parker at the University of Liverpool to help solve the puzzle of avian siblicide—the tendency of many young birds to kill others in the nest.

Because the victim shares half the killer's genes, siblicide would seem to hurt the killer's reproductive fitness, but Mock knew from field observations that it's a common practice among young egrets and other birds. With Parker's help he created a relatively simple model to explain it based on sibling rivalry for food, which is often scarce in egret nests. They posited an ESS for young birds that strikes a balance between ensuring their own survival and allowing their siblings to live and reproduce. Whether the birds resort to siblicide, Mock and Parker predicted, should depend on how quickly the birds grow, how much food is available, and how many siblings share the nest. By studying hundreds of egret nests, Mock and Parker were able to confirm their model: Larger nestlings begin to kill smaller ones at the point where their own survival may be threatened by a shortage of food.

At Cornell University, Kern Reeve is taking the same quantitative approach to the social behavior of wasps and naked mole rats, a burrowing species from East Africa. Among the mole rats, for example, only one queen and one to three breeding males take part in reproduction, while the remaining members of the colony, typically about 80 in number, do all the work: digging and clearing tunnels, finding food, and guarding against predators. This work puts the laborers at risk of being eaten by a snake. But the nonbreeding members are willing to take risks on behalf of the queen and breeding males because they are all closely related, which gives the laborers a

PHOTOS BY STEPHEN AND MELINDA PRUETT-JONES

**Nice guys finish last.** For male bowerbirds *(top)*, marauding—destroying rivals' bowers *(bottom)*—is the best strategy.

stake in the queen's reproductive success.

There are limits, however. Even a nonbreeding individual has an incentive to stay alive, and not just because it can continue to serve the queen. If the queen or top males die, the worker may move up the hierarchy and become a breeding member itself. This creates a conflict of interests: The queen wants all colony members to work as hard as possible, while her subjects are smart to slack off.

Using a game theory model, Reeve predicted that a worker's best strategy should depend on two factors: relatedness to the queen and likelihood of becoming a breeding member. Individuals less related to the queen have less to gain from her reproductive success and so should be lazier. And the colony's larger members, which are the most likely to rise to breeding status, should also avoid work to improve their chances of surviving to breed later. Thus, Reeve reasoned, the queen should be in particular conflict with both the larger workers and her more distant relatives.

Experiments on naked mole rat colonies showed just the pattern of conflicts predicted by game theory. The queen shoves members through the tunnels, sometimes as far as a meter, in order to get them back to work—and she has to concentrate her efforts on the larger and less related animals. When the queen was temporarily removed, moreover, those animals slacked off much more than the others did.

### Prisoner's Dilemma

To social scientists, such successes are encouraging, but still more intriguing are cases in which game theory can explain why animals cooperate. A traditional game theory model called the Prisoner's Dilemma, for instance, shows that cooperation is often not the favored strategy. As originally conceived, the Prisoner's Dilemma refers to a situation in which two prisoners are charged with a crime. If neither confesses—they "cooperate"—each will serve a minor prison term, say 1 year. If one cooperates while the other "defects," blaming the first prisoner for the crime, the defector goes free while the cooperator serves 10 years. If both defect, both serve 4 years. The alternative with the least total jail time is joint cooperation. Neither knows how the other will behave, however. So each reasons that no matter what his fellow does, he'll serve less time if he defects (zero versus 1 year if his partner stays silent, 4 versus 10 years if his partner sings). So both defect, and both do 4 years of hard time.

Humans face a Prisoner's Dilemma in a variety of situations, from business contracts to international arms-control agreements, and social scientists have been intrigued and bothered by the implication that the logical strategy is to cheat. Among animals, too, cheating can be a stable strategy, as shown by work done on bowerbirds by Stephen and Melinda Pruett-Jones at the University of Chicago. Male bowerbirds build elaborate bowers—structures of twigs, leaves, and other objects—to attract females, but they also spend part of their time "marauding," or seeking out the bowers of other males and damaging or destroying them. If all the male bowerbirds cooperated and left one another's bowers intact, all would benefit. But if any of the birds are marauders, they increase their chances for success with females at the expense of their nonmarauding rivals, making cooperation a losing strategy.

Game theorists did predict a version of the game in which cooperation can become a stable strategy, however. If the players interact again and again in an "iterated Prisoner's Dilemma," so that each player knows which other players are cooperating and which are not, tit for tat should be a viable strategy: Cooperate at first and then do what the other player did on the previous turn. But could a tit-for-tat strategy work in the real world? In 1987 Manfred Milinski at the University of Bern in Switzerland suggested that one place to look was among certain small fish that face an iterated Prisoner's Dilemma naturally.

When a large fish nears a school of these fish, one or more of the school will approach it to see how dangerous it is. This "predator inspection" is risky for the scouts, but the information can benefit them as well as the rest of the school—if the interloper is not a predator or if it's not hungry, the smaller fish don't need to scatter. A group of scouts approaching a predator, Milinski noted, is playing out a Prisoner's Dilemma: Each has a strong incentive to defect and let the others take all the chances, but if all defect, they learn nothing about the predator. Full cooperation, on the other hand, minimizes the risks because the predator becomes confused if it can't focus on a single target. Because potential predators approach the school again and again, Milinski thought that a tit-for-tat strategy might have evolved among the fish.

Milinski and Dugatkin have independently tested the idea—Milinski in sticklebacks and Dugatkin in guppies—and both find that the fish do indeed use a tit-for-tat strategy in predator inspection. Guppies that are paired up in a tank with a predator confined at one end will approach the predator in a sequence of moves, Dugatkin says. "If one of them is trailing, the lead fish will turn around and head back. It will wait for the other to head out, and then it will go by its side." In other words, if one fish defects (holds back), the other will, too, and it then waits for the first one to cooperate (swim forward) before cooperating itself. The guppies even remember from day to day what other guppies did, Dugatkin found. If one of a pair defects in one trial, the other will defect in turn on a second trial the next day.

The verification of the tit-for-tat strategy has led to new and more detailed models of the guppies' behavior, Dugatkin says. "After doing that experiment, watching the fish, and thinking about the model, I realized that guppies should prefer to associate with cooperators because it would be in their interest to be near cooperators if a predator appeared." He later found that, given a choice, guppies did indeed spend more time with fish that had cooperated than with defectors. "These models make some new and very interesting predictions about the evolution of cooperation," Dugatkin says, "and we hope they will spur even more empirical work."

Researchers from other fields will be watching this work unfold, says Hammerstein. Take economists, who have a hard time explaining how markets end up in Nash equilibrium, in which no competitor can gain an advantage by unilaterally changing strategy. Studies of markets suggest that Nash equilibria—the equivalent of ESSs in animals—do arise, but the theory predicting them assumes that the players act in a perfectly rational fashion, which is impossible.

As a result, says Hammerstein, a number of economists are "looking to evolutionary game theory for processes other than rational decision making that could lead to a Nash equilibrium." Perhaps, he says, these stable strategies arise in much the same way as cooperation arises among guppies: People base their behavior not on rational calculation but on experience.

Robert Axelrod, a political scientist at the University of Michigan, raises the possibility that evolutionary game theory might even offer insights into the election-year strategies deployed by candidates for the U.S. Congress. Perhaps politicians imitate the strategies of others, or perhaps some other process from evolutionary game theory is at work. One can only hope that negative campaigning does not prove to be an evolutionarily stable strategy.

–Robert Pool

PHYSICS

# Making Light Work of Brownian Motion

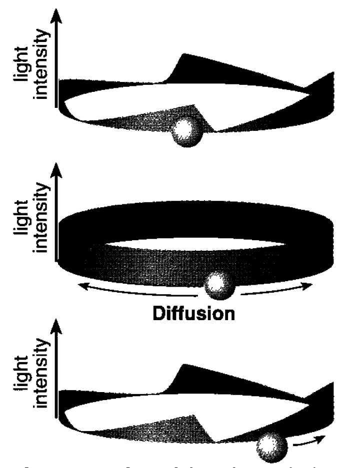
The bacteria *Listeria monocytogenes* are notorious for causing dangerous illnesses such as meningitis. Among a small group of biophysicists and physicists, however, they are famous for a different talent: their ability to swim by harnessing the random jitter called Brownian motion, generated by millions of water molecules constantly striking the bacteria. The trick is in their tails—bushy appendages that ordinarily hold the bacteria steady. When Brownian motion jostles a bacterium forward, explains biophysicist George Oster of the University of California, Berkeley, the microbe briefly sheds its tail. Then it quickly fills in the gap, fixing itself in place until it gets another push forward.

*Listeria*'s scheme for turning random thermal motion into net movement has fascinated researchers because it extracts work out of something long regarded as useless "noise." Over the last 2 years, inspired by *Listeria* and a few other examples from biology, scientists have conceived simple laboratory schemes that could harness Brownian motion and even turned a few of them into working systems. The 27 February issue of *Physical Review Letters* reports the latest and, say some researchers, the most elegant: an "optical thermal ratchet," invented by Albert Libchaber and his colleagues at Princeton University and the NEC Research Laboratory in Princeton, New Jersey, that uses light itself to convert Brownian motion into directed movement of a plastic bead.

Systems like Libchaber's ratchet could provide a novel way to separate various-sized particles and molecules. And, coming full circle to biology, they provide a model of a process that some researchers think might be integral to the work of so-called motor proteins such as myosin, which drives muscle contraction as it moves along filaments of the protein actin. "Can these mechanisms possibly explain how biological motors work? That's the $64,000 question," says Steven Block of Princeton University, a physicist who studies motor proteins.

Although these recent laboratory systems were inspired by biology, they also take a cue from a centuries-old mechanism consisting of a toothed ratchet wheel and a pawl, which engages the teeth of the ratchet and allows it to spin in one direction only. In the Princeton system, the wheel is replaced by a microscopic plastic sphere in water, illuminated by an infrared laser beam that rotates rapidly, tracing a circle 7 micrometers in diameter. The beam induces a fluctuating electric charge in the sphere, which traps it where the light's electromagnetic field is strongest—the perimeter of the circle. Ordinarily, the bead is free to diffuse around the circle as it is pushed this way and that by Brownian motion.

That freedom ends when Libchaber's team sends the laser light through a "chopper," a filter that modulates the intensity of the beam so as to create a series of sawtooth-shaped "hills" around the circle. Each hill has a gentle slope of increasing intensity on one side and a steep drop-off in intensity on the other. Because the sphere's fluctuating charge makes it want to reach the brightest spot, says Libchaber, the bead rolls up the nearest hill and then stops at the peak—just as if a pawl had been engaged.




**Laser ratchet.** A bead caught in an optical trap's intensity peak *(top)* drifts randomly when the intensity is evened out *(middle)*. Recreating the peaks either returns the bead to the same peak or advances it one step *(bottom)*.

SOURCE: FAUCHEUX *ET AL*./PRL ILLUSTRATION: C. FABER SMITH

By periodically removing the chopper, Libchaber and his colleagues can force the bead to travel in one direction around the circle. When the chopper is turned off, the sphere diffuses away from the peak where it had been trapped. If it diffuses down the gentle side of the same peak, the sphere will slowly return to its original posi-