Generosity leads to evolutionary success, biologists show

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With new insights into the classical game theory match-up known as the "Prisoner's Dilemma," University of Pennsylvania biologists offer a mathematically based explanation for why cooperation and generosity have evolved in nature.

Their work builds upon the seminal findings of economist John Nash, who advanced the field of game theory in the 1950s, as well as those of computational biologist William Press and physicist-mathematician Freeman Dyson, who last year identified a new class of strategies for succeeding in the Prisoner's Dilemma.

Postdoctoral researcher Alexander J. Stewart and associate professor Joshua B. Plotkin, both of Penn's Department of Biology in the School of Arts and Sciences, examined the outcome of the Prisoner's Dilemma as played repeatedly by a large, evolving population of players. While other researchers have previously suggested that cooperative strategies can be successful in such a scenario, Stewart and Plotkin offer mathematical proof that the only strategies that succeed in the long term are generous ones. They report their findings in *PNAS* the week of Sept. 2.

"Ever since Darwin," Plotkin said, "biologists have been puzzled about why there is so much apparent cooperation, and even flat-out generosity and altruism, in nature. The literature on game theory has worked to explain why generosity arises. Our paper provides such an explanation for why we see so much generosity in front of us."

The Prisoner's Dilemma is a way of studying how individuals choose whether or not to cooperate. In the game, if both players cooperate, they both receive a payoff. If one cooperates and the other does not, the cooperating player receives the smallest possible payoff, and the defecting player the largest. If both players do not cooperate, they receive a payoff, but it is less than what they would gain if both had cooperated. In other words, it pays to cooperate, but it can pay even more to be selfish.

In the Iterated Prisoner's Dilemma, two players repeatedly face off against one another and can employ different strategies to beat their opponent. In 2012, Press and Dyson "shocked the world of game theory ," Plotkin said, by identifying a group of strategies for playing this version of the game. They called this class of approaches "zero determinant" strategies because the score of one player is related linearly to the other. What's more, they focused on a subset of zero determinant approaches they deemed to be extortion strategies. If a player employed an extortion strategy against an unwitting opponent, that player could force the opponent into receiving a lower score or payoff.

Stewart and Plotkin became intrigued with this finding, and last year wrote a commentary in PNAS about the Press and Dyson work. They began to explore a different approach to the Prisoner's Dilemma. Instead of a head-to-head competition, they envisioned a population of players matching up against one another, as might occur in a human or animal society in nature. The most successful players would get to "reproduce" more, passing on their strategies to the next generation of players.

It quickly became clear to the Penn biologists that extortion strategies wouldn't do well if played within a large, evolving population because an extortion strategy doesn't succeed if played against itself.

"The fact that there are extortion strategies immediately suggests that, at the other end of the scale, there might also be generous strategies," Stewart said. "You might think being generous would be a stupid thing to do, and it is if there are only two players in the game, but, if there are many players and they all play generously, they all benefit from each other's generosity."

In generous strategies, which are essentially the opposite of extortion strategies, players tend to cooperate with their opponents, but, if they don't, they suffer more than their opponents do over the long term. "Forgiveness" is also a feature of these strategies. A player who encounters a defector may punish the defector a bit but after a time may cooperate with the defector again.

Stewart noticed the first of these generous approaches among the zero determinant strategies that Press and Dyson had defined. After simulating how some generous strategies would fare in an evolving population, he and Plotkin crafted a mathematical proof showing that, not only can generous strategies succeed in the evolutionary version of the Prisoner's Dilemma, in fact these are the only approaches that resist defectors over the long term.

"Our paper shows that no selfish strategies will succeed in evolution," Plotkin said. "The only strategies that are evolutionarily robust are generous ones."

The discovery, while abstract, helps explain the presence of generosity in nature, an inclination that can sometimes seem counter to the Darwinian notion of survival of the fittest.

"When people act generously they feel it is almost instinctual, and indeed a large literature in evolutionary psychology shows that people derive happiness from being generous," Plotkin said. "It's not just in humans. Of course social insects behave this way, but even bacteria and viruses share gene products and behave in ways that can't be described as anything but generous."

"We find that in evolution, a population that encourages cooperation does well," Stewart said. "To maintain cooperation over the long term, it is best to be generous."

More information: From extortion to generosity, evolution in the Iterated Prisoner's Dilemma, www.pnas.org/cgi/doi/10.1073/pnas.1306246110

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