'Policing' stops cheaters from dominating groups of cooperative bacteria

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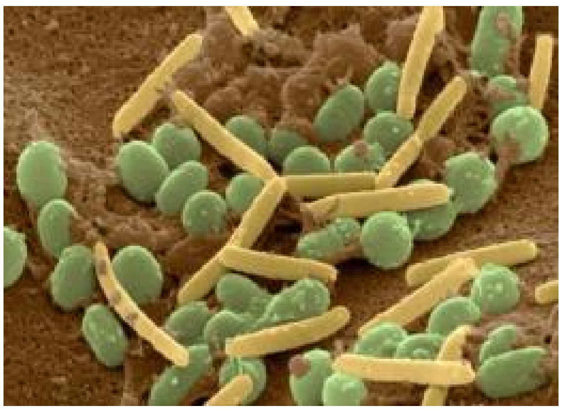

When environmental conditions are hospitable, *Myxococcus xanthus* takes a rod-shaped form (yellow), swarming, dividing, and competing with other cells for nutrients. When stressed, the bacterium becomes more social, collaborating with other cells to produce spherical spores (green) that can withstand stress. Credit: Image courtesy of Juergen Berger and Supriya Kadam

For cooperation to persist in the often violently competitive realm of bacteria, cheaters must be kept in line.

Two Indiana University Bloomington biologists have learned that in one bacterium, at least, bacterial cooperators can evolve to "police" the cheaters and arrest their bids for dominance.

"Even simple organisms such as bacteria can evolve to suppress social cheaters," said Gregory Velicer, who with Ph.D. student Pauline Manhes has reported the policing behavior in the Proceedings of the National Academy of Sciences.

Their laboratory experiments suggest that cooperative bacteria in nature may evolve to behave in ways that thwart the increase of selfish cheaters. In complex multicellular organisms such as ourselves, cancer cells can be viewed as cheaters that proliferate at the expense of the larger organism. If cancer cells are not successfully "policed" by our healthy cells (and/or medical intervention), the results can be catastrophic. Similarly, the long-term fate of cooperator lineages can be threatened by neighboring cheater lineages in the same social group unless the cooperators are able to migrate away from cheaters or evolve to suppress them.

"Mechanisms that prevent, mitigate or eliminate social conflict among interacting individuals are required for cooperation or multicellularity to succeed," Velicer said. "Policing is one such mechanism. This study shows that bacteria have the potential to evolve behaviors that eliminate fitness advantages derived from cheating within social groups."

Myxococcus xanthus is a predatory bacterium that swarms through soil, killing and eating other microbes by secreting toxic and digestive compounds. When food runs out, cells aggregate and exchange chemical signals to form cooperative, multi-cellular fruiting bodies. Some of the cells create the fruiting body's structure. Other cells are destined to become hardy spores that can survive starvation and other difficult conditions.

In mixed fruiting bodies containing both "cheater" and "cooperator" strains, the cheater strain utilized by Manhes and Velicer does not contribute a social signal required for making spores, whereas the cooperative strain does. Defection from making a social contribution allows cheater cells to "steal" the social signal from cooperators and convert a larger proportion of their cells into spores than do cooperators.

Thus, the cheater strain loses to the cooperator strain when they develop in separate groups, but the cheater wins in mixed groups where they directly interact with cooperators.

The scientists mixed cooperative and cheating strains of M. xanthus and allowed cooperator lineages -- but not the cheater -- to evolve under starvation conditions in which cooperative construction of fruiting bodies is important for survival. They then watched to see how replicate lineages descended from the cooperator strain would evolve while repeatedly encountering the same non-evolving cheater over many consecutive cycles of fruiting body development.

Both strains were exposed to an antibiotic during a growth phase after each cycle of development. Cheater cells are sensitive to the antibiotic and were killed off, whereas cooperator cells were resistant to the antibiotic and their populations could continue growing and evolving. The same non-evolving cheater strain was reintroduced to the evolving cooperator lineages at the beginning of each cycle of fruiting body development and removed at the end of each cycle.
The evolution experiment was allowed to run for 20 cycles of development.

"We tested whether cooperators adapted to the presence of a cheater mainly by changing their social interactions with that cheater or by improving their spore production in a way that is independent of their social environment," Manhes said. "We found that the lineages descended from the cooperative ancestor evolved novel interactions with the cheater that improved their fitness."

The policing behavior was described as "selfish" because suppression of the cheaters directly benefited the evolved populations themselves rather than being self-sacrificial for the benefit of others. That being said, the selfish police actually do strongly benefit cooperator cells in at least one social context. In mixed groups that include three players -- the evolved cells, the cheater and the ancestral cooperator -- the ancestor produced far more spores than it did when it was mixed with only the cheater.

The evolving populations might have gained the ability to suppress cheaters by a variety of mechanisms, Velicer said.

For example, the descendants of the ancestral cooperator might have evolved a general anti-competitor trait that generically harms a variety of potential competitors to a similar degree, but this did not occur. Rather, the cooperator lineages evolved behaviors that are particularly harmful to the non-evolving cheater. "We would like to investigate the molecular basis of cheater suppression," Velicer said, "in particular whether it is due to the positive production of a compound that is uniquely detrimental to the cheater or some other mechanism."

The scientists competed the strains that evolved to deal with the cheater against their cooperative ancestor, both with the cheater present in the same group and without the cheater. They found that most evolved populations strongly outcompeted their ancestor only when the cheater was present. This result showed that much of the adaptation that took place during the evolution experiment was a specific evolutionary response to the presence of cheater cells.

In an intriguing reversal of fate, some of the replicate populations that evolved from the cooperative ancestor actually became cheaters themselves, but of a new kind. These new cheaters differed from the non-evolving cheater (the one that was mixed with the evolving populations during every round of development) and in some cases could socially exploit both the cooperative ancestor and the non-evolving cheater itself.

This study may cast a shadow on recent proposals that cheaters might be used to thwart infections of bacteria that cooperate with each other to cause disease in humans. The basic idea of such proposals is to introduce cheaters that will disrupt the social cohesion of infecting bacterial populations. However, just as bacteria readily evolve resistance to antibiotics, cooperative bacteria that infect humans or animals may evolve to beat the cheats.

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