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Cheating—and getting away with it: Gene allows amoebae to pass on more than their fair share of their genes

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A slice through a culture plates shows slugs (clumps) of the social amoebae *D. discoideum* (at left) on their way to becoming fruiting bodies (right). The photograph was shot in the lab of Joan Strassmann and David Queller by entomologist and photographer Alex Wild. For more of Wild's photos, visit http://www.alexanderwild.com/. Credit: Alexander Wild

We would all like to believe that there is a kind of karma in life that guarantees those who cheat eventually pay for their bad behavior, if not immediately, then somewhere down the line. But a study of a new gene in the amoeba *Dictyostelium discoideum* suggests that, at least for amoebae, it is possible to cheat and get away with it.

The experimental work was conducted by then graduate student Lorenzo Santorelli as part of a collaboration between evolutionary biologists David C. Queller and Joan E. Strassmann of Rice University and Gadi Shaulsky and Adam Kuspa of Baylor College of Medicine. Santorelli has since moved to Oxford University and his advisors to Washington University in St. Louis, where Queller is the Spencer T. Olin Professor of Biology and Strassmann is a professor of biology, both in Arts & Sciences.

The cheat in question is putting more than your clone's fair share of cells into a communal spore body, so that your genome dominates the next generation of amoebae. The idea has always been that cheating clones pay a price in the form of reduced evolutionary fitness in some other chapter of their lives.

In work described in the Jan. 9 issue of *BMC Evolutionary Biology*, the scientists tested the fitness of a knockout mutant (an amoeba with one disabled gene) called CheaterB. When mixed with equal parts of a wild-type clone, the cheater clone contributed almost 60 percent of the cells in the spore body, 10 percent more than its fair share.

The scientists ran CheaterB cells through exhaustive tests of their ability to grow, develop, form spores and germinate. CheaterB did just as well in these tests as its ancestor wild strain. Under laboratory conditions, at any rate, CheaterB didn't seem to be paying a fitness cost for cheating.

The study raises important questions about the tension between cooperation and cheating. Why would breaking something that is presumably functional (by knocking out a gene) confer an advantage in the first place? And if cheating benefits the cheater and has no hidden cost, what holds cheating in check?

Cheating is surprisingly easy

D. discoideum spend most of their lives as predatory single cells hunting bacteria through the leaf litter and upper soil layers of forests in eastern North America. But when they can't find bacteria and begin to starve, they gather to form fruiting bodies, a thin stalk of cells with a ball of spores at the top, like a miniature Space Needle. The amoebae that end up in the stalk die, giving up their lives to benefit the amoebae that become spores.

Importantly the cells that stream together to form the fruiting body can be clonal (genetically identical) or have two (or more) genetic makeups. If each clone in a two-clone fruiting body contributes half the cells to the spore body, both clones gain from cooperating because each must sacrifice fewer cells to the stalk.

But game theory suggests the clones should sometimes evolve strategies that allow them to gain the benefits of cooperation without paying the costs.

In 2008 Queller and Strassmann published a genome-wide screen of *D. discoideum* that found roughly 180 cooperation genes, genes that might produce cheaters if they mutated. The number of genes, and the number of different biological pathways they affected, suggested it might be easy to evolve cheating and difficult to control it fully.

At the time cheaters were believed to be held in check by mechanisms that made non-cooperation costly. The first *D. discoideum* cheater to be scrutinized, CheaterA, described in 2000, is not able to form fruiting bodies on its own. This is a crippling disability that would prevent it from surviving in the wild.

But the screen from 2008 selected only clones able to produce clonal fruiting bodies, thus passing a basic test of evolutionary fitness. These clones were what is called facultative cheaters, cheating only under favorable conditions, and not obligate cheaters, forced to cheat no matter what.

The overall robustness of knockout mutant CheaterB deepens the mystery. "No measurable laboratory trait revealed an Achilles heel," Strassmann says, "but that doesn't mean there isn't one in natural environments. Otherwise, why would a naturally occurring mutation that duplicated the knockout not take over amobae populations?"

Provided by Washington University in St. Louis

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