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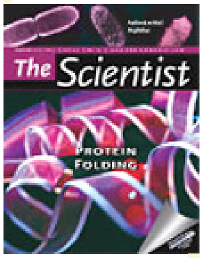

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Rooting out the cheats

Crime doesn't pay for nitrogen-fixing bacteria | By Stuart Blackman

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...perative relationship between legumes (peas, beans, and their ...) and the nitrogen-fixing bacteria (rhizobia) that live in nodules ... roots is a textbook example of mutualism. However, it has been ... why this cooperation is maintained, given the evolutionary ...on to cheat the system. New research led by Ford Denison of ...ersity of California, Davis, provides evidence that legumes ... good behavior among their rhizobia by imposing sanctions against cheats.

In the legume rhizobium system, the bacteria fix atmospheric nitrogen for use by the host plant in return for accommodation in root nodules. But because nitrogen fixation is energetically expensive, any rhizobium strain that withholds this service should increase its own growth and fitness at the expense of cooperative strains and its host. "If free riders can obtain benefits while letting others pay the costs, that can undermine cooperation between species, just as it undermines cooperation among humans," says Denison.

In the September 4 Nature, Kiers et al. show that the soybean *Glycine max* discourages cheating by its rhizobial partner *Bradyrhizobium japonicum* by imposing sanctions against noncooperative bacteria. In what Regis Ferriere, professor of mathematical ecology at the University of Paris VI, describes as "an extremely elegant set of experiments," Denison's team followed the fate of rhizobia that they forced to cheat by exposing nodules to air in which the nitrogen had been replaced with the inert gas argon (*Nature*, 425;78-81, September 4, 2003).

The reproductive success of bacteria in noncooperative, argon-treated nodules was about 50% that of controls exposed to normal air, even when experimental and control nodules were on the same plant. This effect is, the authors say, unlikely to be due to the lack of nitrogen—they estimate that there was enough in the system to cover the needs of the rhizobia. Rather, lower O_2 concentrations within experimental nodules and a reduction in their permeability to O_2 suggested that the soybean withholds oxygen from noncooperative nodules.

Such sanctions are analogous to the policing that can stabilize cooperation within species, according to the authors. But "cooperation by rhizobia apparently depends on evolutionary changes in bacterial populations, not changes in the behavior of individuals," writes Denison. "Host sanctions ensure that better cooperators… will be more common

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in the next generation."

In Denison's experiments, nodules contained only a single bacterial strain by design, but noncooperative strains of *B. japonicum* are widespread in nature. Ferriere points out that the system would be complicated by the occurrence of multiple strains within a single nodule: "In mixed populations of rhizobia—good mutualists and not-so-good ones—sanctions applied to one nodule affect… the bad bacteria and the good ones as well."

However, the occurrence of some mixed nodules would, says one of Denison's coauthors, Stuart West from the University of Edinburgh, "make sanctions less effective, but far from ineffective," and might even explain the persistence of noncooperative strains. "The really clever thing," he says, "would be to be a good nitrogen-fixing rhizobia when you are alone in a nodule, and then a noncooperating cheat when in a nodule with another rhizobia who was fixing nitrogen."

Links for this article
E.T. Kiers et al., "Host sanctions and the legume-rhizobium mutualism," *Nature*, 425;78-81, September 4, 2003.
http://www.nature.com/nature

University of California, Davis
http://www.ucdavis.edu/

S.A. Frank, "Mutual policing and repression of competition in the evolution of animal groups," *Nature,* 377:520-522, October 12, 1995.
http://www.nature.com/nature

University of Paris VI
http://www.upmc.fr

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