MAR10-2009-000346

Abstract for an Invited Paper
for the MAR10 Meeting of
the American Physical Society

Games microbes play: The game theory behind cooperative sucrose metabolism in yeast

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The origin of cooperation is a central challenge to our understanding of evolution. Microbial interactions can be manipulated in ways that animal interactions cannot, thus leading to growing interest in microbial models of cooperation and competition. In order for the budding yeast *S. cerevisiae* to grow on sucrose, the disaccharide must first be hydrolyzed by the enzyme invertase. This hydrolysis reaction is performed outside of the cytoplasm in the periplasmic space between the plasma membrane and the cell wall. Here we demonstrate that the vast majority ($\sim$99%) of the monosaccharides created by sucrose hydrolysis diffuse away before they can be imported into the cell, thus making invertase production and secretion a cooperative behavior [1]. A mutant cheater strain that does not produce invertase is able to take advantage of and invade a population of wildtype cooperator cells. However, over a wide range of conditions, the wildtype cooperator can also invade a population of cheater cells. Therefore, we observe coexistence between the two strains in well-mixed culture at steady state resulting from the fact that rare strategies outperform common strategies—the defining features of what game theorists call the snowdrift game. A simple model of the cooperative interaction incorporating nonlinear benefits explains the origin of this coexistence. Glucose repression of invertase expression in wildtype cells produces a strategy which is optimal for the snowdrift game—wildtype cells cooperate only when competing against cheater cells. In disagreement with recent theory [2], we find that spatial structure always aids the evolution of cooperation in our experimental snowdrift game.

[1] Gore, J., Youk, H. & van Oudenaarden, A., *Nature* **459**, 253 – 256 (2009)
[2] Hauert, C. & Doebeli, M., *Nature* **428**, 643 – 646 (2004)