A Possible Mechanism of Repressing Cheating Mutants in Myxobacteria

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Abstract. The formation of fruiting bodies by myxobacteria colonies involves altruistic suicide by many individual bacteria and is thus vulnerable to exploitation by cheating mutants. We report results of simulations that show how in a structured environment with patchy distribution of cheating mutants the wild type might persist.

This work was inspired by experiments on myxobacteria *Myxococcus xanthus* reported in [1]. Under adverse environmental conditions individuals in an *M. xanthus* colony aggregate densely and form a raised "fruiting body" that consists of a stalk and spores. During this process, many cells commit suicide in order to form the stalk. This "altruistic suicide" enables spore formation by other cells. When conditions become favorable again, the spores will be released and may start a new colony.

Velicer et al. studied in [1] some mutant strains that were deficient in their ability to form fruiting bodies and had lower motility but higher growth rates than wild-type bacteria. When mixed with wild-type bacteria, these mutant strains were significantly over-represented in the spores in comparison with their original frequency. Thus these mutants are cheaters in the sense that they reap the benefits of the collective action of the colony while paying a disproportionally low cost of altruistic suicide during fruiting body formation. The authors of [1] ask which mechanism insures that the wild-type behavior of altruistic suicide is evolutionarily stable against invasion by cheating mutants.

We conjecture that a clustered distribution of mutants at the time of sporulation events could be a sufficient mechanism for repressing those mutants. One possible source of such clustering could be lower motility of mutants.

A detailed description of the program written to test this conjecture, the source code, as well as all output files, can be found at the following URL: www.math.ohiou.edu/~just/Myxo/. The program simulates growth, development, and evolution of ten *M. xanthus* colonies over 500 seasons (sporulation events). Each season consists on average of 1,000 generations (cell divisions). Each colony is assumed to live on a square grid, and growth of the colony is modeled by expansion into neighboring grid cells. At any time during the simulation, each grid cell is characterized by the number of wild-type and mutant bacteria that it holds. At the end of each season, fruiting bodies are formed in regions where sufficiently many wild type bacteria are present. After each season, the program selects randomly ten fruiting bodies formed in this season and

seeds the new colonies with a mix of bacteria in the same proportions as the proportions found in the fruiting body that was chosen for reproduction.

The proportion of wild-type bacteria in excess of carrying capacity that move to neighboring grid cells in the expansion step was set to 0.024. We run ten simulations each for parameter settings where mutants in excess of carrying capacity move to neighboring grid cells at rates of 0.006, 0.008, 0.012, and 0.024 and grow 1%, 1.5%, or 2% faster than wild-type bacteria. In the following table, the column headers show the movement rates for the mutants, row headers show by how much mutants grow faster than wild type bacteria, and the numbers in the body of the table show how many of the simulations in each run of ten simulations reached the cutoff of 500 seasons without terminating due to lack of fruiting body formation.

Table 1. Number of simulations that run for 500 seasons

	0.006	0.008	0.012	0.024
1%	9	7	5	0
1.5%	6	5	2	0
2%	5	4	2	0

These results show that for many of our parameter settings, wild-type bacteria can successfully propagate in the presence of cheating mutants. Successful propagation of wild-type bacteria over many seasons is more likely the less the discrepancy in growth rates of mutants and wild type is, and the less mobile the mutants are. This can be considered as a proof of principle for our conjecture.

All our simulations in which mutants have the same motility as wild-type bacteria terminated prematurely due to lack of fruiting body formation. The authors of [2] report that motility of mutant strains that are deficient in their ability to form fruiting bodies can be (partially) restored in the laboratory. If such mutants do occur in nature, then our findings suggest that another defense mechanism is necessary for the wild-type bacteria to prevail against them.

References

1. Velicer, G. J., Kroos, L., Lenski, R. E.: Developmental cheating in the social bacterium *Myxococcus xanthus.* Nature **404** (2000) 598–601.
2. Velicer, G. J., Lenski, R. E., Kroos, L.: Rescue of Social Motility Lost during Evolution of *Myxococcus xanthus* in an Asocial Environment. J. Bacteriol. **184**(10) (2002) 2719–2727.