

SOCIOBIOLOGY

The Phoenix effect

Kevin R. Foster

A spore-forming bacterium can escape from social collapse and extinction with a single mutation that has a dramatic effect. Here is evidence that a cooperative system can recover from the very brink of destruction.

Where there is society, there are cheaters that threaten to ruin it. The evolution of such selfish behaviour can destroy cooperation, and may even drive a species to extinction¹. When Fiegna, Velicer and colleagues (page 310)² mixed a cheater strain with a cooperative strain of a bacterium, therefore, tragedy seemed assured. Many populations of the bacteria did indeed die out but, in one, a new social strain arose phoenix-like from the social collapse. This new strain resisted the cheater, produced more spores than the original strain and, most amazingly of all, evolved these abilities through just a single mutational change.

The bacterium concerned is *Myxococcus xanthus*. It earns its title of 'social' bacterium from the ability of starving cells to aggregate and form a fruiting body of hardy spores, in which many of the cells die³⁻⁵ (Fig. 1). This social behaviour has been put to good use by Velicer and colleagues in an intriguing story that has spanned almost a decade³⁻⁵. It began with an experiment that selected for mutant strains that grew rapidly under conditions in which they did not need to make spores⁵. Interestingly, several strains lost the ability to sporulate, and there was a further twist. Some could still form spores if mixed with the ancestral spore-former and, furthermore, produced more spores than the ancestor. Although socially inept when alone, these strains could exploit the shared resources in aggregations with the ancestor and use them to gain a selfish evolutionary advantage. Velicer and colleagues had inadvertently created cheater mutants⁴.

But would the cheaters completely replace the spore-former? To answer this, Fiegna and Velicer³ put mixtures containing one cheater strain and the social ancestor through several fruiting cycles in the lab by taking the spores from one cycle to seed the next. Two cheater strains persisted alongside the spore-former, but the more vigorous cheater rapidly increased in frequency and, as it did so, the results were devastating. By replacing the social ancestor, the cheater removed its own ability to produce spores. The result was population extinction: without spores, there was

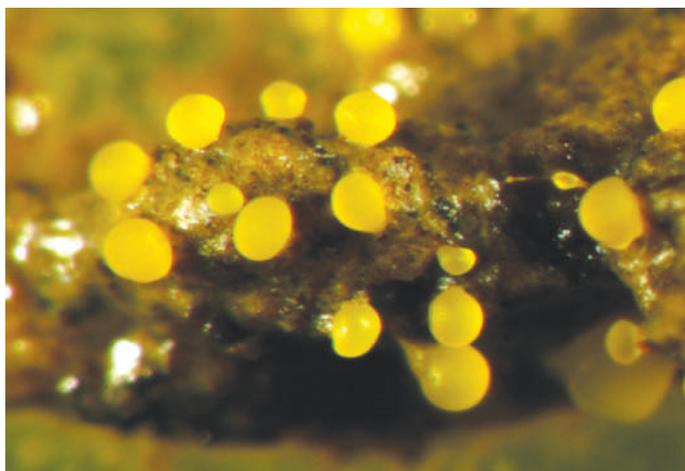


Figure 1 | Fruiting bodies of the social bacterium *Myxococcus xanthus* emerging from soil. Each fruiting body is about 100 μm in diameter, and contains a few thousand hardy spores that form through the aggregation of around 100,000 starving cells. (Photo by M. Vos.)

nothing to seed the next cycle of fruiting. These experiments provided a graphic illustration of what has come to be known as 'evolutionary suicide', where natural selection favours strategies that promote extinction. This process is alarming some conservation biologists, who worry that anthropogenic effects may be kick-starting spirals of selfish adaptations in some species that will drive their own destruction (Fig. 2b, overleaf)¹.

At least for the bacteria, however, all was not doom and gloom. Curiously, in one experiment, spores reappeared and the population recovered². It turned out that a new super-strain had evolved that could resist the cheater. This was named Phoenix after the mythical burning bird that can rise from its own ashes. In a tour de force of genetics, which involved the marathon task of sequencing the entire genome of the new strain, Fiegna *et al.*^{2,6} found that Phoenix arose with just a single mutation. This mutation simply increases the levels of one particular enzyme (an acetyl-transferase), but this is hypothesized to trigger a flood of subsequent changes in gene regulation and to drive a previously unrecognized route to sociality in *M. xanthus*.

To show that a social adaptation can escape from such a severe cheater, and can do so through a single mutation, makes this a landmark study^{2,6}. As with all studies, however,

there are caveats. Most importantly, this was all done in the lab, and strains were selected and mixed in ways that are unlikely to occur in nature. For example, natural aggregations of *M. xanthus* may only ever contain a single strain, which would mean that the lab cheaters that cannot develop alone would never spread. One must be cautious, therefore, when using these results to draw conclusions about the natural world. Nevertheless, the study represents a notable proof-of-principle that has intriguing implications for sociobiology.

First of all, it is quite amazing to find that a single mutation can drive such a dramatic social recovery, a result that underlines just how little we know about the genetic basis of social traits⁷. It is true that during a rapid population crash there may be little time for anything other than the most simple of genetic changes. However, a recovery mutation might also have resulted in only a slight initial improvement in spore production and a rather different evolutionary prognosis (Fig. 2c). If a new cooperator evolved to replace the cheater that was a poor sporulator, the way might be open for the original cooperator to re-evolve. This would mean the cheater could then re-invade, and perpetuate a potentially endless evolutionary game of rock-paper-scissors. Although this may seem to stretch credulity, such outcomes are known from both chemical

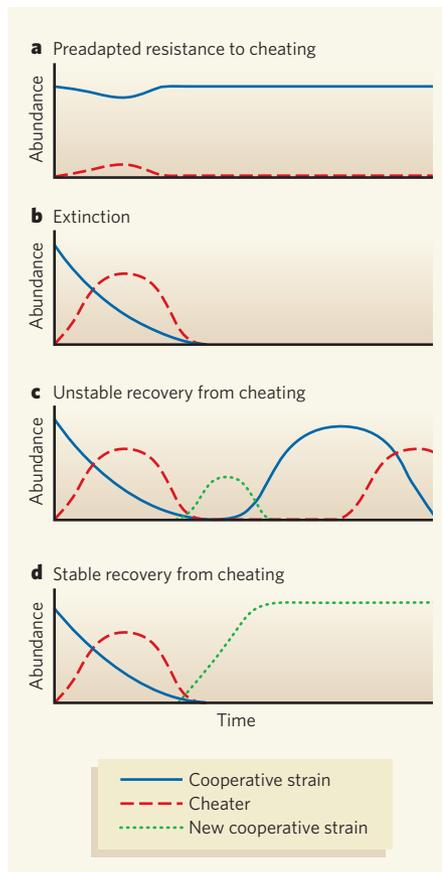


Figure 2 | Four possible outcomes when a cheater evolves in a social species. A cheater is an organism that exploits a cooperative adaptation for selfish gain. **a**, Preadapted resistance to cheating. It is typical to assume that social systems arise in such a way that cheaters can have only a limited impact (as shown), or do not succeed at all. Examples of preadaptations include high relatedness and pre-existing constraints that link cheating to a cost to the cheater¹¹. Policing and enforcement systems may evolve later to further constrain cheaters¹². **b**, Extinction. The cheater causes extinction of the social trait, or species (evolutionary suicide¹⁰). This selects for species preadapted to resist cheating¹⁰. **c**, Unstable recovery. A social strategy arises that resists the cheater but cannot out-compete the original strategy. The original strategy may reinvade and perpetuate a cycle of reinvasions in a rock–paper–scissors dynamic^{8,9}. **d**, Stable recovery. Sociality is restored by a strategy that out-competes both the cheater and the original strategy, as occurred with the Phoenix mutant². The result is a stable adaptation that protects the social system from the cheater. This process may be behind the policing and enforcement systems in other social species¹².

warfare in bacteria⁸ and male–male competition in lizards⁹.

This is not the case for Phoenix (Fig. 2d), which can out-compete the original strain and forms spores just fine. Such precipitous recoveries may turn out to be part of the evolutionary process. Extinctions play a key role in the history of life by removing species that are poorly adapted to persist, a process that favours both sexual reproduction and reduced

within-species conflict^{10,11}. However, the study by Fiegna *et al.*² shows that species may also escape from the very brink of disaster. There is some sense in this: a virulent cheater that threatens a population will necessarily result in strong natural selection for strategies that can re-evolve sociality in its wake. It was this effect that led to the rapid dominance of the Phoenix mutant, and one can speculate that it might also explain adaptations that police cheating in other societies¹². The final twist in the tale is that Phoenix actually produces more spores than the original strain. Escape from a virulent cheater is not just possible; it can even improve things. ■

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- Rankin, D. J. & López-Sepulcre, A. *Oikos* **111**, 616–619 (2005).
- Fiegna, F., Yu, Y.-T. N., Kadam, S. V. & Velicer, G. J. *Nature* **441**, 310–314 (2006).
- Fiegna, F. & Velicer, G. J. *Proc. R. Soc. Lond. B* **270**, 1527–1534 (2003).
- Velicer, G. J., Kroos, L. & Lenski, R. E. *Nature* **404**, 598–601 (2000).
- Velicer, G. J., Kroos, L. & Lenski, R. E. *Proc. Natl Acad. Sci. USA* **95**, 12376–12380 (1998).
- Velicer, G. J. *et al.* *Proc. Natl Acad. Sci. USA* **103**, 8107–8112 (2006).
- Robinson, G. E., Grozinger, C. M. & Whitfield, C. W. *Nature Rev. Genet.* **6**, 257–270 (2005).
- Kirkup, B. C. & Riley, M. A. *Nature* **428**, 412 (2004).
- Sinervo, B. & Lively, C. M. *Nature* **380**, 240 (1996).
- Nunney, L. in *Levels of Selection in Evolution* (ed. Keller, L.) 238–252 (Princeton Univ. Press, 1999).
- Foster, K. R., Shaulsky, G., Strassmann, J. E., Queller, D. C. & Thompson, C. R. *Nature* **431**, 693–696 (2004).
- Frank, S. A. *Evolution* **57**, 693–705 (2003).

EXTRASOLAR PLANETS

A neptunian triplet

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Three planets of Neptune mass have been discovered orbiting a Sun-like star known to have an asteroid belt. Exquisite measurements suggest that the search for habitable planets might be easier than assumed.

Our thirst for knowledge of planets orbiting stars similar to the Sun is tempered by the technological challenges of detecting them. We cannot see analogues of the Solar System directly; rather, the presence of extrasolar planets is inferred through effects that they induce on their parent star. The Doppler method, whereby astronomers search for subtle, periodic changes in the apparent speed of a star that result from its gravitational dance with an unseen planetary companion, has yielded all but a handful of the more than 180 known extrasolar planets¹. Heavier planets produce larger stellar wobbles, so it is not surprising that most of the worlds discovered so far have more in common with the distant gas and ice giants of the Solar System (Jupiter, Saturn, Uranus and Neptune) than with the smaller, closer terrestrial planets from Mercury to Mars.

But as techniques have been refined, so planets of lower mass have been revealed in increasing numbers¹. The current bestiary of extrasolar planets is therefore far from comprehensive. On page 305 of this issue, Lovis and colleagues² report unprecedentedly precise observations of the nearby, Sun-like star HD 69830. The fruit of their efforts is not one, but three orbiting planets (Fig. 1). The discovery is exciting for two reasons. First, the authors' technological advance implies that further low-mass planets will be spotted orbiting other stars. Second, the architecture of this particular planetary system bears some

intriguing similarities to that of our own Solar System.

The newly found planetary system is remarkable in that it possesses three planets located on nearly circular orbits within 1 astronomical unit of the star (1 AU is the Earth–Sun distance). The same is true of the Solar System. Where the HD 69830 system differs, however, is that the masses of the worlds range from 10 to 18 times that of Earth, and so are similar to that of Neptune. In the Solar System, the division between the low-mass terrestrial planets and massive gas giants was determined by the 'ice-line'. This is the distance beyond which the temperature in the protoplanetary nebula — the reservoir of gas and dust from which the planets formed — dipped below the freezing point of various hydrogen compounds. Beyond this point, much greater amounts of solid material, and so planets of much greater mass, were created.

The formation history of the HD 69830 system is thus a puzzle deserving of detailed study. Lovis and colleagues present² a preliminary calculation to show that the inner planets probably formed inside the ice line, and thus are likely to be predominantly rock, not gas. Their large masses require that HD 69830's protoplanetary nebula contained a larger quantity of solid material than did that of the Solar System. That inference is at odds with the observation that the star itself actually has a lower abundance of heavier elements, the stuff of planets.