

could be released, the OMEGA results described by Bibring *et al.* exclude any possibility that the southern perennial cap could appreciably affect the atmospheric pressure.

The search for the existence of water on Mars, past and present, will continue. Future reports will often confirm less-direct evidence, as is the case with the information about the widespread existence of water ice at the martian south pole provided by OMEGA. But this does not lessen the importance of these discoveries.

Did Mars ever support life? Will Mars support human life in the future? The answers depend on understanding the past and present distribution of both water and CO₂. Life, as we know it, requires liquid water. Yet the long-term stability of liquid surface water requires a thicker atmosphere than Mars has at present. OMEGA's observations show that its past atmosphere, predominantly CO₂, is not locked up in the polar caps. We can hope that OMEGA and her sister instruments on Mars Express, Mars Global Surveyor and Mars Odyssey, along with reports from the

rovers Spirit and Opportunity, will deliver the necessary information to tell us where that ancient atmosphere went.

Human exploration and ultimate colonization of Mars depend on accessibility of one resource — water. Martian water is necessary not only for human consumption, but is also the key to making breathable air and fuel for a return trip to Earth. For life on Mars, water is the elixir. ■

Timothy N. Titus is at the US Geological Survey, 2255 North Gemini Drive, Flagstaff, Arizona 86001, USA.

e-mail: ttitus@usgs.gov

1. Christensen, P. R. *et al.* *J. Geophys. Res.* **105**, 9623–9642 (2000).
2. Bibring, J.-P. *et al.* *Nature* **428**, 627–630 (2004).
3. Jakosky, B. M. & Barker, E. S. *Icarus* **57**, 322–334 (1984).
4. Nye, J. F. *et al.* *Icarus* **144**, 449–455 (2000).
5. Boynton, W. V. *et al.* *Science* **297**, 81–85 (2002).
6. Titus, T. N., Kieffer, H. H. & Christensen, P. R. *Science* **299**, 1048–1051 (2003).
7. Byrne, S. & Ingersoll, A. *Science* **299**, 1051–1053 (2003).
8. Prettyman, T. H. *et al.* *J. Geophys. Res.* (in the press).
9. Smith, D. E. *et al.* *Science* **284**, 1495–1503 (1999).

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Behavioural evolution

Cooperate with thy neighbour?

Peter D. Taylor and Troy Day

What gives cooperation an evolutionary edge? Two features of a population — spatial structure and finite size — are factors in the success of any strategy, although more subtle than we thought.

In thinking about the evolution of cooperative behaviour¹, there is one main stumbling block: that cooperative individuals can be exploited by 'defectors', who benefit from cooperation while avoiding the costs that it entails. Solutions to this problem typically find ways for cooperative individuals to interact with one another more often than they would purely by chance. There are two basic ways in which this can happen. One involves the population having a spatial structure with local reproduction and dispersal, so that neighbours of a cooperative individual are themselves more likely to be cooperative^{2,3}. The other relies on some form of information transfer whereby players can assess the behaviour of a prospective partner and decide accordingly how, or even whether, to play. The assessment might be made on the basis of traits that are reliable indicators of likely behaviour^{4,5} or through a phase of negotiation^{6,7}.

Two papers in this issue^{8,9} add further insight. Hauert and Doebeli⁸ (page 643) propose that, under certain conditions, spatial structure might actually hinder cooperative behaviour. It has long been understood that population structure can be a mixed blessing for cooperation, because the gains that it provides through positive assortment are

countered by competition between like individuals^{2,10,11}. Hauert and Doebeli have uncovered yet another limitation of population structure, one that also gives a fascinating geometric distinction between games such as Hawk–Dove — in this case, in the guise of the snowdrift game — and the Prisoner's Dilemma, or blizzard game (Box 1, overleaf).

For a spatially structured population of players, with their choice of strategy displayed as a particular colour on a grid, Hauert and Doebeli see a shift in the geometry of clusters of cooperators at the point where the cost and benefit of the encounter are equal. In the Prisoner's Dilemma, when the cost is greater than the benefit, globular clusters form (Fig. 1a), which give cooperators enough protection to persist at a small frequency. But in playing the snowdrift game, when benefit outweighs cost, the clusters become more finger-like, or dendritic (Fig. 1b). Here the cooperators are vulnerable to exploitation and they die out. The transition is perplexing, but it is clear that spatial structure in a population might not always work in favour of cooperation.

In the second article, Nowak *et al.*⁹ (page 646) suggest that finite population size is also crucial in the evolution of cooperation. These authors focus on the Prisoner's Dilemma



100 YEARS AGO

A New Mineral from Ceylon. In the beginning of February I bought from Mr. Holland 5 cwt. of the mineral described by Prof. Dunstan in last week's NATURE (p. 510)... I had hoped to have positive and definite results to communicate before describing its constituents, but the publication by Prof. Dunstan of an analysis, and his statement that he is still engaged in its investigation, makes it necessary to write this letter...

Fractionation shows that the oxalate precipitate (the portion soluble in ammonium oxalate) gives equivalents between 25.0 (the most insoluble portion of the double sulphate) and 44.7 (the most soluble portion); by far the major part of the element has the last mentioned equivalent...

Assuming that the element is a tetrad, which is probable from its behaviour, it undoubtedly possesses an equivalent approaching the highest number (44.7), and for this there is a gap in the periodic table between cerium and thorium; one at least of the elements present (supposing that there is more than one present) will probably have an atomic weight of about 177, preceding tantalum (182.5) in the horizontal row of the periodic table...

Within the limits of this letter I am obliged to omit many more characteristics of this curious ore... I regret to have been obliged to tell an imperfect story.

William Ramsay

From *Nature* 7 April 1904.

50 YEARS AGO

The brain mechanisms which serve the sun navigation of the animals mentioned are presumably of a similar nature in all species and are probably based on the same principles as human sun orientation.

They can also be expected to share certain properties with other time-keeping mechanisms (internal clocks) which are of wide occurrence. They keep time fairly well on their own and they are set and kept in pace by light stimuli. Their metabolic nature has in certain cases been established. A third property of such systems is that they regulate motor activities. *Drosophila*, for example, normally emerge from their pupæ before dawn. If a bottle with larvæ and pupæ of *D. melanogaster* is artificially illuminated during three consecutive nights and kept in darkness during daytime, the flies which emerge during the following week will 'remember' the time of the artificial dawn and emerge in the evenings, even when now kept in perpetual darkness.

H. Kalmus

From *Nature* 10 April 1954.

to highlight dramatically the difference between evolutionary stability in a finite and an infinite population, and at the same time suggest a new factor that bears on the evolution of cooperation.

In the Prisoner's Dilemma, defectors always outcompete cooperative individuals when encounters are random. Axelrod and Hamilton demonstrated¹², however, that cooperative strategies can be enhanced if multiple encounters with the same partner are allowed and if current behaviour is based on past experience. Of all such conditional strategies, 'tit-for-tat' seems to be one of the best: a player cooperates initially but continues to cooperate only if its partner cooperated in the previous encounter. It turns out that if the number of encounters with the same partner is large enough, tit-for-tat can outperform a uniform all-defect strategy once its frequency is high enough. This means that there is an unstable mixed equilibrium at some particular frequency: above it, tit-for-tat dominates; below it, all-defect takes over. At least, this is true of an infinite population (in which changes in frequency are deterministic in evolutionary time). For example, with a benefit of 3, a cost of 4, and 10 encounters per partner, this unstable equilibrium is at a frequency of 1/8 tit-for-tat.

But what if the population is finite, say of size 80? Treated as an infinite population, we'd expect to need ten individuals playing tit-for-tat before this strategy could become more fit than all-defect; and by the standard definition, all-defect is evolutionarily stable (no rare mutant tit-for-tat-er can invade). In contrast, as a finite population, the stochastic nature of random sampling leads us to expect that, after many generations, all individuals will be descended from exactly one of the original members. With neutral strategies, each individual would have the same

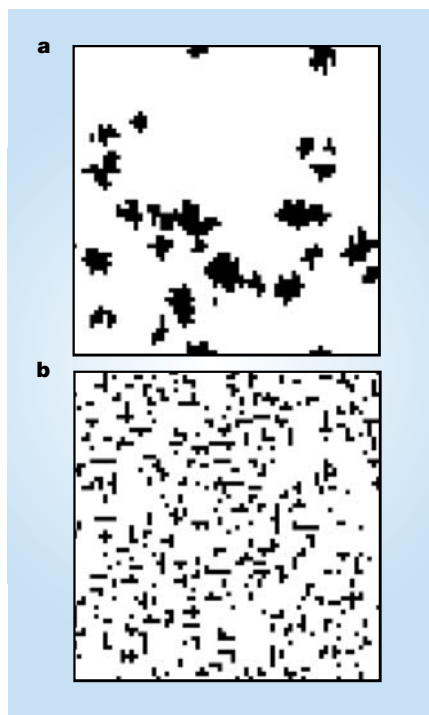


Figure 1 Cooperators versus defectors. With the spatial structure of a population represented by a grid, Hauert and Doebeli⁸ find different equilibrium configurations for two slightly different games that test the evolution of cooperation. Cooperators are shown in black, defectors in white. a, In the Prisoner's Dilemma game, clusters of cooperators develop and can offer protection to those in the interior of each cluster, increasing the fitness of cooperators. b, In the snowdrift game, however, the cooperative clusters develop into dendritic fingers that poke out into defector territory, exposing their members to exploitation. Cooperators can actually be worse off than if they had formed partnerships at random.

probability of being the founder, which suggests an alternative way of comparing the fitness of tit-for-tat versus all-defect — calculate the probability that an individual of each kind will be the founder¹³.

It turns out that, for the example of one lone tit-for-tat-er in a population of 79 all-defect players, the probability that the tit-for-tat individual is the founder is almost twice that of an all-defect individual (M. Nowak, personal communication). Should we still regard all-defect, then, as an evolutionarily stable strategy? In fact, Nowak *et al.*⁹ use this example to propose an extension of the standard definition of evolutionary stability for finite populations. The mutant strategy must be less fit in two ways: no rare mutant can invade (the traditional sense), and a rare mutant individual must have a lower than normal chance of being the founder of the ultimate population. Certainly, in a finite population such an extension is needed, but it's not at first so clear how to do this, nor exactly what role fixation probability should play. In a population subject to the forces of mutation and drift, what are the states that we might expect to observe? ■

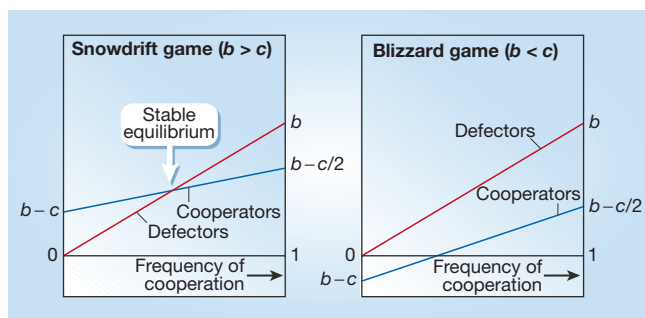
Peter D. Taylor and Troy Day are in the Department of Mathematics and Statistics, Queen's University, Kingston, Ontario K7L 3N6, Canada. e-mail: taylorp@post.queensu.ca

- Dugatkin, L. A. *Cooperation Among Animals* (Oxford Univ. Press, 1997).
- Hamilton, W. D. in *Man and Beast: Comparative Social Behavior* (eds Eisenberg, J. F. & Dillon, W. S.) 59–91 (Smithsonian Inst. Press, Washington, 1971).
- Wilson, D. S. *Proc. Natl Acad. Sci. USA* **72**, 143–146 (1975).
- Nowak, M. A. & Sigmund, K. *Nature* **393**, 573–577 (1998).
- Riolo, R. L. *et al. Nature* **414**, 441–443 (2001).
- McNamara, J. M. *et al. Nature* **401**, 368–371 (1999).
- Taylor, P. D. & Day, T. *Proc. R. Soc. Lond. B* **271**, 669–674 (2004).
- Hauert, C. & Doebeli, M. *Nature* **428**, 643–646 (2004).
- Nowak, M. A. *et al. Nature* **428**, 646–650 (2004).
- Wilson, D. S. *et al. Evol. Ecol.* **6**, 331–341 (1992).
- Taylor, P. D. *Proc. R. Soc. Lond. B* **249**, 299–302 (1992).
- Axelrod, R. & Hamilton, W. D. *Science* **211**, 1390–1396 (1981).
- Proulx, S. R. & Day, T. *Selection* **2**, 1–16 (2001).

Box 1 Snowdrifts and blizzards

Imagine two car drivers caught in a snowdrift. The total cost of shovelling out of the drift is c and the benefit to each of getting home is b . The drivers might follow either of two strategies — cooperate with the other, or defect. If both drivers cooperate, they split the cost of shovelling and both get home. If one cooperates and one defects, they will both get home, but the cooperator will bear the whole cost. Two defectors bear no cost but get no benefit.

It is reasonable to assume that $b > c/2$ — that getting home is worth more than the cost of half the shovelling (or the game is pointless). That leaves two interesting cases: $b > c$ and $b < c$. The first case is



known as the snowdrift game and (in the spirit of comparison) we call the second the blizzard game. In the latter, the shovelling is so hard that a driver who does it all suffers a net loss. The snowdrift game is a version of Hawk–Dove, and the blizzard

game is a version of the Prisoner's Dilemma, both of which are much studied in behavioural evolution.

In a biological population in which the payoff contributes to fitness, we are interested in comparing the average fitness

of a cooperator and a defector. Fitness is illustrated here as a function of frequency of cooperative encounters. There is a stable equilibrium where the lines intersect. For random encounters between drivers/players, the snowdrift game supports a stable mixture of cooperators and defectors (roughly half-and-half). The blizzard game does not: the only point of stable equilibrium is an all-defector population. But if there were some mechanism that increased the frequency of cooperative encounters, the lower portion of the cooperation line would rise, creating a point of stable equilibrium for the blizzard game as well. **P.D.T. & T.D.**