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 subtly than we thought

In thinking about the evolution of cooperative behaviour[1], 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 Doebeli[8] (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).

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 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 demonstrated[12], 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 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 founder[13].

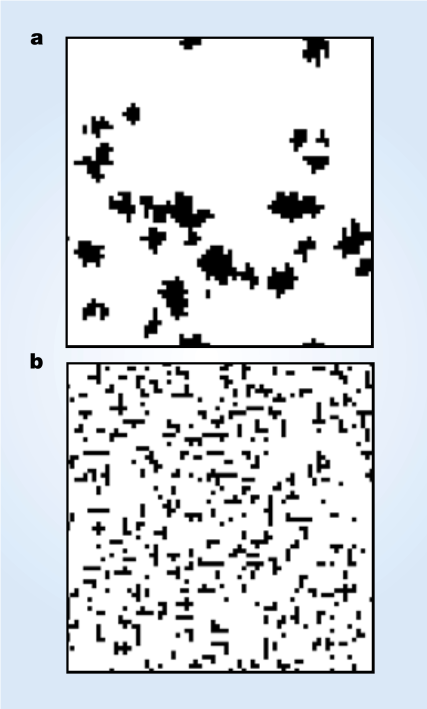

Figure 1 **Cooperators versus defectors. With the spatial structure of a population represented by a grid, Hauert and Doebeli[8] find different equilibrium configurations for two slightly different games that test the evolution of cooperation. Cooperators are shown in black, defectors in white.** a, **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 might actually be worse off than if they had formed partnerships at random.**

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. In this case, faced with mutation and drift, in what sense will an evolutionarily stable strategy be what we expect to observe? Is finite-population evolutionary stability perhaps a contradiction in terms? ■

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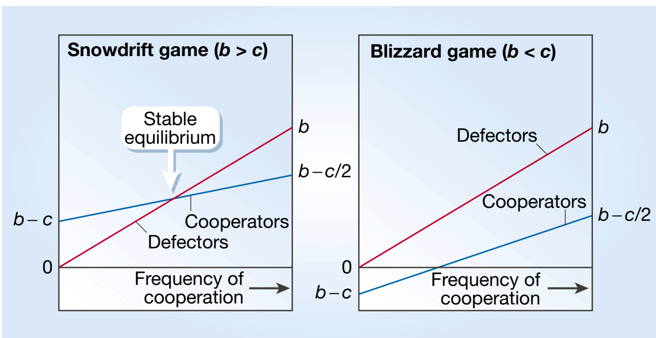
Box 1 Snowdrifts and blizzards

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. One cooperator and one defector 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.