

## From the "Selfish Gene" by Richard Dawkins

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Suppose a species of bird is parasitized by a particularly nasty kind of tick which carries a dangerous disease. It is very important that these ticks should be removed as soon as possible. Normally an individual bird can pull off its own ticks when preening itself. There is one place, however-the top of the head -which it cannot reach with its own bill. The solution to the problem quickly occurs to any human. An individual may not be able to reach his own head, but nothing is easier than for a friend to do it for him. Later, when the friend is parasitized himself, the good deed can be paid back. Mutual grooming is in fact very common in both birds and mammals.

This makes immediate intuitive sense. Anybody with conscious foresight can see that it is sensible to enter into mutual back-scratching arrangements. But we have learnt to beware of what seems intuitively sensible. The gene has no foresight. Can the theory of selfish genes account for mutual back-scratching, or 'reciprocal altruism', where there is a delay between good deed and repayment? Williams briefly discussed the problem in his 1966 book, to which I have already referred. He concluded, as had Darwin, that delayed reciprocal altruism can evolve in species that are capable of recognizing and remembering each other as individuals. Trivers, in 1971, took the matter further. When he wrote, he did not have available to him Maynard Smith's concept of the evolutionarily stable strategy. If he had, my guess is that he would have made use of it, for it provides a natural way to express his ideas. His reference to the 'Prisoner's Dilemma'-a favourite puzzle in game theory- shows that he was already thinking along the same lines.

Suppose B has a parasite on the top of his head. A pulls it off him. Later, the time comes when A has a parasite on his head. He naturally seeks out B in order that B may pay back his good deed. B simply turns up his nose and walks off. B is a cheat, an individual who accepts the benefit of other individuals' altruism, but who does not pay it back, or who pays it back insufficiently. Cheats do better than indiscriminate altruists because they gain the benefits without paying the costs. To be sure, the cost of grooming another individual's head seems small compared with the benefit of having a dangerous parasite removed, but it is not negligible. Some valuable energy and time has to be spent.

Let the population consist of individuals who adopt one of two strategies. As in Maynard Smith's analyses, we are not talking about conscious strategies, but about unconscious behaviour programs laid down by genes. Call the two strategies Sucker and Cheat. Suckers groom anybody who needs it, indiscriminately. Cheats accept altruism from suckers, but they never groom anybody else, not even somebody who has previously groomed them. As in the case of

the hawks and doves, we arbitrarily assign pay-off points. It does not matter what the exact values are, so long as the benefit of being groomed exceeds the cost of grooming. If the incidence of parasites is high, any individual sucker in a population of suckers can reckon on being groomed about as often as he grooms. The average pay-off for a sucker among suckers is therefore positive. They all do quite nicely in fact, and the word sucker seems inappropriate. But now suppose a cheat arises in the population. Being the only cheat, he can count on being groomed by everybody else, but he pays nothing in return. His average pay-off is better than the average for a sucker.

Cheat genes will therefore start to spread through the population. Sucker genes will soon be driven to extinction. This is because, no matter what the ratio in the population, cheats will always do better than suckers. For instance, consider the case when the population consists of 50 per cent suckers and 50 per cent cheats. The average pay-off for both suckers and cheats will be less than that for any individual in a population of 100 per cent suckers. But still, cheats will be doing better than suckers because they are getting all the benefits-such as they are-and paying nothing back. When the proportion of cheats reaches 90 per cent, the average pay-off for all individuals will be very low: many of both types may by now be dying of the infection carried by the ticks. But still the cheats will be doing better than the suckers. Even if the whole population declines toward extinction, there will never be any time when suckers do better than cheats. Therefore, as long as we consider only these two strategies, nothing can stop the extinction of the suckers and, very probably, the extinction of the whole population too.

But now, suppose there is a third strategy called Grudger. Grudgers groom strangers and individuals who have previously groomed them. However, if any individual cheats them, they remember the incident and bear a grudge: they refuse to groom that individual in the future. In a population of grudgers and suckers it is impossible to tell which is which. Both types behave altruistically towards everybody else, and both earn an equal and high average pay-off. In a population consisting largely of cheats, a single grudger would not be very successful. He would expend a great deal of energy grooming most of the individuals he met- for it would take time for him to build up grudges against all of them. On the other hand, nobody would groom him in return. If grudgers are rare in comparison with cheats, the grudger gene will go extinct. Once the grudgers manage to build up in numbers so that they reach a critical proportion, however, their chance of meeting each other becomes sufficiently great to off-set their wasted effort in grooming cheats. When this critical proportion is reached they will start to average a higher pay-off than cheats, and the cheats will be driven at an accelerating rate towards extinction. When the cheats are nearly extinct their rate of decline will become slower, and they may survive as a minority for quite a long time. This is because for any one rare cheat there is only a small chance of his encountering the same grudger twice: therefore the proportion of individuals in the population who bear a grudge against any given cheat will be small.

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