

# The Selfish Gene



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# The Selfish Gene

RICHARD DAWKINS

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## Preface to 1976 edition

THIS book should be read almost as though it were science fiction. It is designed to appeal to the imagination. But it is not science fiction: it is science. Cliché or not, 'stranger than fiction' expresses exactly how I feel about the truth. We are survival machines—robot vehicles blindly programmed to preserve the selfish molecules known as genes. This is a truth which still fills me with astonishment. Though I have known it for years, I never seem to get fully used to it. One of my hopes is that I may have some success in astonishing others.

Three imaginary readers looked over my shoulder while I was writing, and I now dedicate the book to them. First the general reader, the layman. For him I have avoided technical jargon almost totally, and where I have had to use specialized words I have defined them. I now wonder why we don't censor most of our jargon from learned journals too. I have assumed that the layman has no special knowledge, but I have not assumed that he is stupid. Anyone can popularize science if he oversimplifies. I have worked hard to try to popularize some subtle and complicated ideas in non-mathematical language, without losing their essence. I do not know how far I have succeeded in this, nor how far I have succeeded in another of my ambitions: to try to make the book as entertaining and gripping as its subject matter deserves. I have long felt that biology ought to seem as exciting as a mystery story, for a mystery story is exactly what biology is. I do not dare to hope that I have conveyed more than a tiny fraction of the excitement which the subject has to offer.

My second imaginary reader was the expert. He has been a harsh critic, sharply drawing in his breath at some of my analogies and figures of speech. His favourite phrases are 'with the exception of'; 'but on the other hand'; and 'ugh'. I listened to him attentively, and even completely rewrote one chapter entirely for his benefit, but in the end I have had to tell the story my way. The expert will still not be totally happy with the way I put things. Yet my greatest hope is that even he will find something new here; a new way of looking at familiar ideas perhaps; even stimulation of new ideas of his own. If this is too high an aspiration, may I at least hope that the book will entertain him on a train?

The third reader I had in mind was the student, making the transition from layman to expert. If he still has not made up his mind what field he wants to be an expert in, I hope to encourage him to give my own field of zoology a second glance. There is a better reason for studying zoology than its possible 'usefulness', and the general likeableness of animals. This reason is that we animals are the most complicated and perfectly-designed pieces of machinery in the known universe. Put it like that, and it is hard to see why anybody studies anything else! For the student who has already committed himself to zoology, I hope my book may have some educational value. He is having to work through the original papers and technical books on which my treatment is based. If he finds the original sources hard to digest, perhaps my non-mathematical interpretation may help, as an introduction and adjunct.

There are obvious dangers in trying to appeal to three different kinds of reader. I can only say that I have been very conscious of these dangers, but that they seemed to be outweighed by the advantages of the attempt.

I am an ethologist, and this is a book about animal behaviour. My debt to the ethological tradition in which I was trained will be obvious. In particular, Niko Tinbergen does not realize the extent of his influence on me during the twelve years I worked under him at Oxford. The phrase 'survival machine', though not actually his own, might well be. But ethology has recently been invigorated by an invasion of fresh ideas from sources not conventionally regarded as ethological. This book is largely based on these new ideas. Their originators are acknowledged in the appropriate places in the text; the dominant figures are G. C. Williams, J. Maynard Smith, W. D. Hamilton, and R. L. Trivers.

Various people suggested titles for the book, which I have gratefully used as chapter titles: 'Immortal Coils', John Krebs; 'The Gene Machine', Desmond Morris; 'Genesmanship', Tim Clutton-Brock and Jean Dawkins, independently with apologies to Stephen Potter.

Imaginary readers may serve as targets for pious hopes and aspirations, but they are of less practical use than real readers and critics. I am addicted to revising, and Marian Dawkins has been subjected to countless drafts and redrafts of every page. Her considerable knowledge of the biological literature and her understanding of theoretical issues, together with her ceaseless encouragement and moral support, have been essential to me. John Krebs

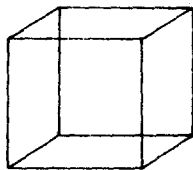
too read the whole book in draft. He knows more about the subject than I do, and he has been generous and unstinting with his advice and suggestions. Glenys Thomson and Walter Bodmer criticized my handling of genetic topics kindly but firmly. I fear that my revision may still not fully satisfy them, but I hope they will find it somewhat improved. I am most grateful for their time and patience. John Dawkins exercised an unerring eye for misleading phraseology, and made excellent constructive suggestions for re-wording. I could not have wished for a more suitable 'intelligent layman' than Maxwell Stamp. His perceptive spotting of an important general flaw in the style of the first draft did much for the final version. Others who constructively criticized particular chapters, or otherwise gave expert advice, were John Maynard Smith, Desmond Morris, Tom Maschler, Nick Blurton Jones, Sarah Kettlewell, Nick Humphrey, Tim Clutton-Brock, Louise Johnson, Christopher Graham, Geoff Parker, and Robert Trivers. Pat Searle and Stephanie Verhoeven not only typed with skill, but encouraged me by seeming to do so with enjoyment. Finally, I wish to thank Michael Rodgers of Oxford University Press who, in addition to helpfully criticizing the manuscript, worked far beyond the call of duty in attending to all aspects of the production of this book.

RICHARD DAWKINS

## Preface to 1989 edition

IN the dozen years since *The Selfish Gene* was published its central message has become textbook orthodoxy. This is paradoxical, but not in the obvious way. It is not one of those books that was reviled as revolutionary when published, then steadily won converts until it ended up so orthodox that we now wonder what the fuss was about. Quite the contrary. From the outset the reviews were gratifyingly favourable and it was not seen, initially, as a controversial book. Its reputation for contentiousness took years to grow until, by now, it is widely regarded as a work of radical extremism. But over the very same years as the book's *reputation* for extremism has escalated, its actual *content* has seemed less and less extreme, more and more the common currency.

The selfish gene theory is Darwin's theory, expressed in a way that Darwin did not choose but whose aptness, I should like to think, he would instantly have recognized and delighted in. It is in fact a logical outgrowth of orthodox neo-Darwinism, but expressed as a novel image. Rather than focus on the individual organism, it takes a gene's-eye view of nature. It is a different way of seeing, not a different theory. In the opening pages of *The Extended Phenotype* I explained this using the metaphor of the Necker cube.



This is a two-dimensional pattern of ink on paper, but it is perceived as a transparent, three-dimensional cube. Stare at it for a few seconds and it will change to face in a different direction. Carry on staring and it will flip back to the original cube. Both cubes are equally compatible with the two-dimensional data on the retina, so the brain happily alternates between them. Neither is more correct than the other. My point was that there are two ways of looking at

natural selection, the gene's angle and that of the individual. If properly understood they are equivalent; two views of the same truth. You can flip from one to the other and it will still be the same neo-Darwinism.

I now think that this metaphor was too cautious. Rather than propose a new theory or unearth a new fact, often the most important contribution a scientist can make is to discover a new way of seeing old theories or facts. The Necker cube model is misleading because it suggests that the two ways of seeing are equally good. To be sure, the metaphor gets it partly right: 'angles', unlike theories, cannot be judged by experiment; we cannot resort to our familiar criteria of verification and falsification. But a change of vision can, at its best, achieve something loftier than a theory. It can usher in a whole climate of thinking, in which many exciting and testable theories are born, and unimagined facts laid bare. The Necker cube metaphor misses this completely. It captures the idea of a flip in vision, but fails to do justice to its value. What we are talking about is not a flip to an equivalent view but, in extreme cases, a transfiguration.

I hasten to disclaim any such status for my own modest contributions. Nevertheless, it is for this kind of reason that I prefer not to make a clear separation between science and its 'popularization'. Expounding ideas that have hitherto appeared only in the technical literature is a difficult art. It requires insightful new twists of language and revealing metaphors. If you push novelty of language and metaphor far enough, you can end up with a new way of seeing. And a new way of seeing, as I have just argued, can in its own right make an original contribution to science. Einstein himself was no mean popularizer, and I've often suspected that his vivid metaphors did more than just help the rest of us. Didn't they also fuel his creative genius?

The gene's-eye view of Darwinism is implicit in the writings of R. A. Fisher and the other great pioneers of neo-Darwinism in the early thirties, but was made explicit by W. D. Hamilton and G. C. Williams in the sixties. For me their insight had a visionary quality. But I found their expressions of it too laconic, not full-throated enough. I was convinced that an amplified and developed version could make everything about life fall into place, in the heart as well as in the brain. I would write a book extolling the gene's-eye view of evolution. It should concentrate its examples on social behaviour, to help correct the unconscious group-selectionism that then pervaded



popular Darwinism. I began the book in 1972 when power-cuts resulting from industrial strife interrupted my laboratory research. The blackouts unfortunately (from one point of view) ended after a mere two chapters, and I shelved the project until I had a sabbatical leave in 1975. Meanwhile the theory had been extended, notably by John Maynard Smith and Robert Trivers. I now see that it was one of those mysterious periods in which new ideas are hovering in the air. I wrote *The Selfish Gene* in something resembling a fever of excitement.

When Oxford University Press approached me for a second edition they insisted that a conventional, comprehensive, page by page revision was inappropriate. There are some books that, from their conception, are obviously destined for a string of editions, and *The Selfish Gene* was not one of them. The first edition borrowed a youthful quality from the times in which it was written. There was a whiff of revolution abroad, a streak of Wordsworth's blissful dawn. A pity to change a child of those times, fatten it with new facts or wrinkle it with complications and cautions. So, the original text should stand, warts, sexist pronouns and all. Notes at the end would cover corrections, responses and developments. And there should be entirely new chapters, on subjects whose novelty in their own time would carry forward the mood of revolutionary dawn. The result was Chapters 12 and 13. For these I took my inspiration from the two books in the field that have most excited me during the intervening years: Robert Axelrod's *The Evolution of Cooperation*, because it seems to offer some sort of hope for our future; and my own *The Extended Phenotype* because for me it dominated those years and because—for what that is worth—it is probably the finest thing I shall ever write.

The title 'Nice guys finish first' is borrowed from the BBC *Horizon* television programme that I presented in 1985. This was a fifty-minute documentary on game-theoretic approaches to the evolution of cooperation, produced by Jeremy Taylor. The making of this film, and another, *The Blind Watchmaker*, by the same producer, gave me a new respect for his profession. At their best, *Horizon* producers (some of their programmes can be seen in America, often repackaged under the name *Nova*) turn themselves into advanced scholarly experts on the subject in hand. Chapter 12 owes more than just its title to my experience of working closely with Jeremy Taylor and the *Horizon* team, and I am grateful.

I recently learned a disagreeable fact: there are influential scientists in the habit of putting their names to publications in whose composition they have played no part. Apparently some senior scientists claim joint authorship of a paper when all that they have contributed is bench space, grant money and an editorial read-through of the manuscript. For all I know, entire scientific reputations may have been built on the work of students and colleagues! I don't know what can be done to combat this dishonesty. Perhaps journal editors should require signed testimony of what each author contributed. But that is by the way. My reason for raising the matter here is to make a contrast. Helena Cronin has done so much to improve every line—every word—that she should, but for her adamant refusal, be named as joint author of all the new portions of this book. I am deeply grateful to her, and sorry that my acknowledgment must be limited to this. I also thank Mark Ridley, Marian Dawkins and Alan Grafen for advice and for constructive criticism of particular sections. Thomas Webster, Hilary McGlynn and others at Oxford University Press cheerfully tolerated my whims and procrastinations.

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## Why are people?

Intelligent life on a planet comes of age when it first works out the reason for its own existence. If superior creatures from space ever visit earth, the first question they will ask, in order to assess the level of our civilization, is: 'Have they discovered evolution yet?' Living organisms had existed on earth, without ever knowing why, for over three thousand million years before the truth finally dawned on one of them. His name was Charles Darwin. To be fair, others had had inklings of the truth, but it was Darwin who first put together a coherent and tenable account of why we exist. Darwin made it possible for us to give a sensible answer to the curious child whose question heads this chapter. We no longer have to resort to superstition when faced with the deep problems: Is there a meaning to life? What are we for? What is man? After posing the last of these questions, the eminent zoologist G. G. Simpson put it thus: 'The point I want to make now is that all attempts to answer that question before 1859 are worthless and that we will be better off if we ignore them completely.'\*

Today the theory of evolution is about as much open to doubt as the theory that the earth goes round the sun, but the full implications of Darwin's revolution have yet to be widely realized. Zoology is still a minority subject in universities, and even those who choose to study it often make their decision without appreciating its profound philosophical significance. Philosophy and the subjects known as 'humanities' are still taught almost as if Darwin had never lived. No doubt this will change in time. In any case, this book is not intended as a general advocacy of Darwinism. Instead, it will explore the consequences of the evolution theory for a particular issue. My purpose is to examine the biology of selfishness and altruism.

Apart from its academic interest, the human importance of this subject is obvious. It touches every aspect of our social lives, our loving and hating, fighting and cooperating, giving and stealing, our

greed and our generosity. These are claims that could have been made for Lorenz's *On Aggression*, Ardrey's *The Social Contract*, and Eibl-Eibesfeldt's *Love and Hate*. The trouble with these books is that their authors got it totally and utterly wrong. They got it wrong because they misunderstood how evolution works. They made the erroneous assumption that the important thing in evolution is the good of the *species* (or the group) rather than the good of the individual (or the gene). It is ironic that Ashley Montagu should criticize Lorenz as a 'direct descendant of the "nature red in tooth and claw" thinkers of the nineteenth century . . .'. As I understand Lorenz's view of evolution, he would be very much at one with Montagu in rejecting the implications of Tennyson's famous phrase. Unlike both of them, I think 'nature red in tooth and claw' sums up our modern understanding of natural selection admirably.

Before beginning on my argument itself, I want to explain briefly what sort of an argument it is, and what sort of an argument it is not. If we were told that a man had lived a long and prosperous life in the world of Chicago gangsters, we would be entitled to make some guesses as to the sort of man he was. We might expect that he would have qualities such as toughness, a quick trigger finger, and the ability to attract loyal friends. These would not be infallible deductions, but you can make some inferences about a man's character if you know something about the conditions in which he has survived and prospered. The argument of this book is that we, and all other animals, are machines created by our genes. Like successful Chicago gangsters, our genes have survived, in some cases for millions of years, in a highly competitive world. This entitles us to expect certain qualities in our genes. I shall argue that a predominant quality to be expected in a successful gene is ruthless selfishness. This gene selfishness will usually give rise to selfishness in individual behaviour. However, as we shall see, there are special circumstances in which a gene can achieve its own selfish goals best by fostering a limited form of altruism at the level of individual animals. 'Special' and 'limited' are important words in the last sentence. Much as we might wish to believe otherwise, universal love and the welfare of the species as a whole are concepts that simply do not make evolutionary sense.

This brings me to the first point I want to make about what this book is *not*. I am not advocating a morality based on evolution.\* I am saying how things have evolved. I am not saying how we humans

morally ought to behave. I stress this, because I know I am in danger of being misunderstood by those people, all too numerous, who cannot distinguish a statement of belief in what is the case from an advocacy of what ought to be the case. My own feeling is that a human society based simply on the gene's law of universal ruthless selfishness would be a very nasty society in which to live. But unfortunately, however much we may deplore something, it does not stop it being true. This book is mainly intended to be interesting, but if you would extract a moral from it, read it as a warning. Be warned that if you wish, as I do, to build a society in which individuals cooperate generously and unselfishly towards a common good, you can expect little help from biological nature. Let us try to *teach* generosity and altruism, because we are born selfish. Let us understand what our own selfish genes are up to, because we may then at least have the chance to upset their designs, something that no other species has ever aspired to.

As a corollary to these remarks about teaching, it is a fallacy—incidentally a very common one—to suppose that genetically inherited traits are by definition fixed and unmodifiable. Our genes may instruct us to be selfish, but we are not necessarily compelled to obey them all our lives. It may just be more difficult to learn altruism than it would be if we were genetically programmed to be altruistic. Among animals, man is uniquely dominated by culture, by influences learned and handed down. Some would say that culture is so important that genes, whether selfish or not, are virtually irrelevant to the understanding of human nature. Others would disagree. It all depends where you stand in the debate over 'nature versus nurture' as determinants of human attributes. This brings me to the second thing this book is not: it is not an advocacy of one position or another in the nature/nurture controversy. Naturally I have an opinion on this, but I am not going to express it, except insofar as it is implicit in the view of culture that I shall present in the final chapter. If genes really turn out to be totally irrelevant to the determination of modern human behaviour, if we really are unique among animals in this respect, it is, at the very least, still interesting to inquire about the rule to which we have so recently become the exception. And if our species is not so exceptional as we might like to think, it is even more important that we should study the rule.

The third thing this book is not is a descriptive account of the detailed behaviour of man or of any other particular animal species. I

shall use factual details only as illustrative examples. I shall not be saying: 'If you look at the behaviour of baboons you will find it to be selfish; therefore the chances are that human behaviour is selfish also'. The logic of my 'Chicago gangster' argument is quite different. It is this. Humans and baboons have evolved by natural selection. If you look at the way natural selection works, it seems to follow that anything that has evolved by natural selection should be selfish. Therefore we must expect that when we go and look at the behaviour of baboons, humans, and all other living creatures, we shall find it to be selfish. If we find that our expectation is wrong, if we observe that human behaviour is truly altruistic, then we shall be faced with something puzzling, something that needs explaining.

Before going any further, we need a definition. An entity, such as a baboon, is said to be altruistic if it behaves in such a way as to increase another such entity's welfare at the expense of its own. Selfish behaviour has exactly the opposite effect. 'Welfare' is defined as 'chances of survival', even if the effect on actual life and death prospects is so small as to *seem* negligible. One of the surprising consequences of the modern version of the Darwinian theory is that apparently trivial tiny influences on survival probability can have a major impact on evolution. This is because of the enormous time available for such influences to make themselves felt.

It is important to realize that the above definitions of altruism and selfishness are *behavioural*, not subjective. I am not concerned here with the psychology of motives. I am not going to argue about whether people who behave altruistically are 'really' doing it for secret or subconscious selfish motives. Maybe they are and maybe they aren't, and maybe we can never know, but in any case that is not what this book is about. My definition is concerned only with whether the *effect* of an act is to lower or raise the survival prospects of the presumed altruist and the survival prospects of the presumed beneficiary.

It is a very complicated business to demonstrate the effects of behaviour on long-term survival prospects. In practice, when we apply the definition to real behaviour, we must qualify it with the word 'apparently'. An apparently altruistic act is one that looks, superficially, as if it must tend to make the altruist more likely (however slightly) to die, and the recipient more likely to survive. It often turns out on closer inspection that acts of apparent altruism are really selfishness in disguise. Once again, I do not mean that the

underlying motives are secretly selfish, but that the real effects of the act on survival prospects are the reverse of what we originally thought.

I am going to give some examples of apparently selfish and apparently altruistic behaviour. It is difficult to suppress subjective habits of thought when we are dealing with our own species, so I shall choose examples from other animals instead. First some miscellaneous examples of selfish behaviour by individual animals.

Blackheaded gulls nest in large colonies, the nests being only a few feet apart. When the chicks first hatch out they are small and defenceless and easy to swallow. It is quite common for a gull to wait until a neighbour's back is turned, perhaps while it is away fishing, and then pounce on one of the neighbour's chicks and swallow it whole. It thereby obtains a good nutritious meal, without having to go to the trouble of catching a fish, and without having to leave its own nest unprotected.

More well known is the macabre cannibalism of female praying mantises. Mantises are large carnivorous insects. They normally eat smaller insects such as flies, but they will attack almost anything that moves. When they mate, the male cautiously creeps up on the female, mounts her, and copulates. If the female gets the chance, she will eat him, beginning by biting his head off, either as the male is approaching, or immediately after he mounts, or after they separate. It might seem most sensible for her to wait until copulation is over before she starts to eat him. But the loss of the head does not seem to throw the rest of the male's body off its sexual stride. Indeed, since the insect head is the seat of some inhibitory nerve centres, it is possible that the female improves the male's sexual performance by eating his head.\* If so, this is an added benefit. The primary one is that she obtains a good meal.

The word 'selfish' may seem an understatement for such extreme cases as cannibalism, although these fit well with our definition. Perhaps we can sympathize more directly with the reported cowardly behaviour of emperor penguins in the Antarctic. They have been seen standing on the brink of the water, hesitating before diving in, because of the danger of being eaten by seals. If only one of them would dive in, the rest would know whether there was a seal there or not. Naturally nobody wants to be the guinea pig, so they wait, and sometimes even try to push each other in.

More ordinarily, selfish behaviour may simply consist of refusing



to share some valued resource such as food, territory, or sexual partners. Now for some examples of apparently altruistic behaviour.

The stinging behaviour of worker bees is a very effective defence against honey robbers. But the bees who do the stinging are kamikaze fighters. In the act of stinging, vital internal organs are usually torn out of the body, and the bee dies soon afterwards. Her suicide mission may have saved the colony's vital food stocks, but she herself is not around to reap the benefits. By our definition this is an altruistic behavioural act. Remember that we are not talking about conscious motives. They may or may not be present, both here and in the selfishness examples, but they are irrelevant to our definition.

Laying down one's life for one's friends is obviously altruistic, but so also is taking a slight risk for them. Many small birds, when they see a flying predator such as a hawk, give a characteristic 'alarm call', upon which the whole flock takes appropriate evasive action. There is indirect evidence that the bird who gives the alarm call puts itself in special danger, because it attracts the predator's attention particularly to itself. This is only a slight additional risk, but it nevertheless seems, at least at first sight, to qualify as an altruistic act by our definition.

The commonest and most conspicuous acts of animal altruism are done by parents, especially mothers, towards their children. They may incubate them, either in nests or in their own bodies, feed them at enormous cost to themselves, and take great risks in protecting them from predators. To take just one particular example, many ground-nesting birds perform a so-called 'distraction display' when a predator such as a fox approaches. The parent bird limps away from the nest, holding out one wing as though it were broken. The predator, sensing easy prey, is lured away from the nest containing the chicks. Finally the parent bird gives up its pretence and leaps into the air just in time to escape the fox's jaws. It has probably saved the life of its nestlings, but at some risk to itself.

I am not trying to make a point by telling stories. Chosen examples are never serious evidence for any worthwhile generalization. These stories are simply intended as illustrations of what I mean by altruistic and selfish behaviour at the level of individuals. This book will show how both individual selfishness and individual altruism are explained by the fundamental law that I am calling *gene selfishness*. But first I must deal with a particular erroneous explanation for altruism, because it is widely known, and even widely taught in schools.