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Book reviews

The Selfish Gene. By RICHARD DAWKINS. New Revised Edition. Oxford University Press. 1989. 352 pages. Cloth £17.50, Paper £5.95. ISBN 0 19 217773, 0 19 286092 5.

The first edition of this book, published in 1976, was hailed with fulsome praise even in non-scientific papers ('the sort of popular science writing that makes the reader feel like a genius' wrote the New York Times), and it became an 'international best seller', with 150000 sales in English and translation into 13 languages. This first edition retains quite a lot of its original interest, but is clearly out-of-date, and author and publishers thought the book was due for revision. In revising it, however, Dawkins has taken the easy way out by leaving the original text of 200 pages unchanged and adding no less than 66 pages of endnotes, together with two new chapters and an extended bibliography. These endnotes, which add 33% to the length of the original text, are a serious imposition on the reader's time and temper, and I think Oxford University Press should have insisted on a properly updated and integrated text, which would have been of much greater value.

Dawkins' argument, briefly, is that natural selection does not act on the species, group or the individual organism, but on the genes – or rather on the 'replicators' which are the fragments of DNA on which natural selection acts through their effects on phenotype. He generally equates 'replicators' with genes, and contrasts the 'ruthlessly selfish genes' with the vehicles alias machines alias 'lumbering robots' alias organisms. Only the 'genes' are passed on from generation to generation (I think he has forgotten the cytoplasm), while the soma or rest of the organism is just a vehicle, discarded once gene transfer has been achieved. Successful genes are those that produce organisms which survive to pass them on to the next generation, and the most successful genes are those which have survived for millions of years and now reside in Richard Dawkins and other members of *H. sapiens*.

Dawkins writes:

> The predominant quality to be expected of the successful gene is ruthless selfishness. This will usually give rise to selfishness in individual behaviour... Universal love and the welfare of the species as a whole are concepts that simply do not make evolutionary sense... 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, however much we may deplore something it does not stop it being true. Be warned that if you wish, as I do, to build a society in which individuals cooperate generously and successfully towards a common good, you can expect little help from biological nature. Let us *teach* generosity and altruism, because we are born selfish.'

The reader may well brood gloomily on this gloomy picture and wonder how it is that there is a fair amount (if far too little) of altruism detectable in many human societies. I also feel tempted to accuse Richard Dawkins of undue optimism in supposing that we few who realise the threat posed by our selfish genes can persuade societies to reach levels of altruism far beyond any achieved by Old and New Testament Prophets, Christ, Divines, Preachers, Philosophers, Politicians and anyone else except when war is delared, whereupon nearly everyone becomes maddened by patriotism (which is a kind of restricted altruism).

We now have to consider Dawkins' replicators and vehicles. Clearly an organism (survival vehicle or lumbering robot) is an obvious concept which can usually be defined unambiguously for operational and experimental purposes. But the replicator is operationally a nebulous concept which is not amenable to experimental study. It might be a complete chromosome, linked genes held together by an inversion, an operon or even a homeobox. It may change radically in size and constitution as natural selection wafts it onwards, under the pressure of recombination, mutation, etc. and, whatever it is, it is entirely misleading to call it a 'gene'. This word has a perfectly definite operational meaning in genetics, and to equate gene and replicator will only confuse the many readers of Dawkins' book who are beguiled by its attractive title. If asked 'What, then, is a replicator?', I would answer that at present it is only a 'Meme' in Dawkins' brain (read his chapter 11 to discover what a meme is), and that it is up to him to identify a few, follow their progress as they change under the influence of natural selection, and so prove that they can have an operational and experimental reality.

The book describes a number of complex behaviour patterns and inter-specific interactions, which will make fascinating reading for those who do not know the literature. Examples include the cuckoos and their various victims, large carnivorous fish with the small, brightly striped fish which clean them (and mimics of the latter), naked mole rats, a variety of social insects, wasps which dig solitary burrows and lay one egg in each, and caddis larvae which build houses some of which, in well-chosen stone, should be of interest to the Prince of Wales. These can be fitted into the grand Dawkins scheme without too much difficulty, but there is very little genetic analysis of any of these cases and insufficient other data are available for one to make any critical assessment.

In the absence of experimental tests, the theorists have been busy with their computers. One example is a hypothetical population of birds infected with ticks carrying a lethal virus. The birds can groom each other but not their own heads (see chapter 10: entitled 'You scratch my back and I will sit on yours'). Mutual head cleaning is of obvious benefit to all, and the birds who clean any proffered head ('Suckers') form a stable population until a mutant 'Cheat' appears who won't clean any other head. He wins because of the energy he saves, but then gets killed off because he cannot get his head cleaned. So the theorist invents a third class of 'Grudgers' who clean the heads of any birds who have never refused to clean theirs (they have long memories!). Computer simulation of populations with these three classes yields interesting results, but we never learn whether Grudgers have actually been seen in Nature. One would like to know whether birds could develop a Grudger-type memory: if not, the example is a little academic.

A more intriguing case is the control of sex ratio in honey bees and social ants. Because males are haploid and females (workers and queens) diploid, in single-queen hives or nests two workers have $\frac{3}{4}$ of their genes in common while a worker has only $\frac{1}{4}$ of her genes in common with a brother and $\frac{1}{2}$ her genes in common with the queen. This leads to the deduction that, to best propagate her own genes, a queen needs a 1:1 and workers a 3:1 sex ratio of females to males. I am not clear whether the queen or workers control the sex ratio, but presumably it is the workers who persuade the queen to fertilize the right proportion of her eggs from her reservoir of sperm. There is some disputed evidence that a 3:1 ratio is actually found in social ants, but the neat theory does not fit the case of honey bees. Dawkins produces a clever theory which just might possibly explain away the wrong sex ratio in bees, and that seems to satisfy him; but I would like to propose another hypothesis. This is that worker bees, which obviously have to be able to count to get the sex ratio right, have their counting ability distorted by the need to count in a different way when performing their famous (and essential) dances. In any case, it has to be pointed out that, if a 3:1 sex ratio were definitely established in bees and ants then this sex ratio could be explained by the selfish gene theory but would certainly not prove it.

A word should be said about 'Memes'. These are tunes, ideas, catch-phrases, etc. etc. which, once planted in a brain, tend to stick and to spread to other brains – i.e. they multiply by a process analogous to natural selection. Dawkins enthusiastically promotes this 'concept', and seems to think it will be of value in analysing brain functions and thought processes. My own view is that it is an ill-considered and superficial concept which will not help (but may hinder) brain scientists, Psychologists and Philosophers; and my guess is that this concept, being a meme itself, is already firmly implanted in Dawkins' own mind and will not be easily dislodged.

Of the two new chapters in the second edition, Chapter 12 ('Nice Guys Finish First') is quite the best chapter in the book and is well worth study. It discusses the Axelrod-Hamilton computer simulation study of the 'Prisoner's Dilemma' game, with Axelrod's further developments. Tests of different strategies against each other show that, at least in the games examined, 'nice' strategies in which the player's aggression is limited to retaliation and the player has a short memory generally win in the long run over 'nasty' strategies which throw in aggression more frequently. An essential factor here is, of course, the ability of the 'nice' player to react just as aggressively as his opponent, so that the odds are not loaded against him, e.g. he does not have to cope with a large bully or a multinational corporation. It should be of particular interest to theologians that one of the most successful strategies was recommended by Jesus. John Maynard Smith named it 'Tit for two Tats', without, I suspect, realising its New Testament significance: it actually consists of turning the other cheek to the opponent before retaliating against further aggression, and no doubt its success in Axelrod's struggle for survival between strategies surprised everyone. Before you choose this as your personal strategy, however, you need to check whether Jesus would have allowed you to retaliate after turning both cheeks.

Chapter 13 'The long reach of the gene' is described as a distillation of a few of the themes from Dawkins' 1982 book 'The Extended Phenotype', which he would like us to read in full (this I have not found time for). I don't find his concept here, that genes can reach out beyond their own vehicles when these are parasites by modifying the phenotypes of their hosts, at all novel, since if they could not they would not be parasites. Dawkins sums it all up thus:

> The gene reaches out through the individual body wall and manipulates objects in the world outside, some of them inanimate, some of them other living beings, some of them a long way away. With only a little imagination we can see the gene as sitting at the centre of a radiating web of phenotypic power.... The long reach of the gene knows no

obvious boundaries. The whole world is criss-crossed with causal arrows joining genes to phenotypic effects, far and near.... But the individual body, so familiar to us on our planet, did not have to exist. The only kind of entity that has to exist in order for life to arise, anywhere in the universe, is the immortal replicator.

After reading this somewhat mystical passage, you may feel, as I do, that you *don't* want to read the enormous extension of this chapter which you can expect to find in the 300 pages of 'The Extended Phenotype'.

To sum up my view of 'The Selfish Gene' (revised), while the book contains many interesting behaviour case histories, some of which are good enough to help push the Dawkins' thesis along but not to prove it or provide critical data, the author is so fond of emotive terms and phrases such as the 'ruthless selfishness' of successful genes, genes 'ganging up in the primeval soup', 'survival vehicles', 'lumbering robots' and so on, and is so quick to fit any example into his particular selfish-gene straightjacket, that I keep on thinking I am reading an advertisement by Saatchi & Saatchi, who are also very persuasive.

My selfish genes evidently differ from those of Dawkins, or I would find myself forced to recommend his book. It certainly contains much attractive material for reaching out to numerous phenotypes via television: nevertheless, I have to remind the reader that (to use the author's own term) it was written by a "lumbering robot".

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Evolution and Animal Breeding: Reviews on Molecular and Quantitative Approaches in Honour of Alan Robertson. Edited by WILLIAM G. HILL and TRUDY F. C. MACKAY. Wallingford, Oxon, UK: C.A.B. International. 1989. 313 pages. Cloth £45.00. ISBN 0 85198 639 0.

For many years the Institute of Animal Genetics at Edinburgh has been a mecca for visitors with an interest in quantitative genetics. Of particular influence was the institution of the coffee hour in Alan Robertson's room where problems arising from the interaction of animal breeding, quantitative genetics and evolution were discussed, and which is remembered in this volume as 'paradise lost' by Joe Felsenstein and as 'having an aura similar to that of the Columbia University Fly Room' by Dick Frankham. Of course, Alan Robertson was also highly influential in more orthodox ways, through his characteristically lucid papers, through those of his students now scattered through the world, and through his advice to animal breeders. The volume under review is a series of essays by his students and collaborators intended as a festschrift in his honour; sadly, Alan died just before its publication after a prolonged period of deteriorating health.

The book is divided into four sections, reflecting the breadth of Alan Robertson's scientific interests in population genetics, quantitative genetics, and the application of quantitative genetic and molecular techniques to animal breeding. Each section begins with a chapter reviewing Alan's own contributions in the field, followed by a series of minireviews covering recent developments in subjects in which he was interested. The format works very well, making a valuable and fascinating survey, though I suspect that many readers with narrower interests will wish to concentrate either on the evolutionary topics in the first half or on the animal breeding topics in the second half of the book.

The first section opens with a chapter by Felsenstein reviewing Alan Robertson's work on population genetics. He argues that it derives its strength from its origin from practical concerns in animal breeding, eschewing unnecessary regard for mathematical rigour; there is a lesson here. Many of the following reviews concern aspects of molecular evolution: neutral theory and possible alternatives (Kimura, Langley), evolution at 'silent' sites (Sharp), DNA sequence polymorphisms (Lewontin), restriction map analysis (Leigh-Brown), transposable elements (Charlesworth), multigene familes (Ohta). Other reviews are on disequilibrium coefficients (Weir and Cockerham), phenotypic models of evolution (Maynard Smith) and population structure (Barker).

In the second section Frankham reviews Alan's contributions to quantitative genetics, the field on which he has probably had most impact. This is a valuable and balanced account of both his theoretical and experimental work, and of the relation between the two, and of his influence on colleagues and students. The reviews discuss the measurement of fitness (Crow, Sved), mutation and its significance for quantitative genetic variation (Hill, Mackay), selection experiments (Falconer, López-Fanjul), selection for growth (McCarthy & Roberts) and the identification of individual genes for metric traits (Mayo, Piper & Shrimpton).

In introducing the third section on quantitative approaches to animal breeding, King stresses that theory and application were closely linked in Alan Robertson's work, as they are in many areas of applied scientific work. The reviews cover the statistical estimation of genetic parameters (Meyer, Thompson, McGuirk, Dempfle) and the design of animal breeding programmes (James, Webb), including the impact of artificial insemination and embryo transfer (Nicholas). This leads on naturally to the fourth section on the application of genetic manipulation to livestock improvement. In the introductory chapter, Roger Land (who sadly died soon after completing it) discusses Alan Robertson's maxim that catching the right genes to transfer would be more difficult than the technical problems of transfer and would require detailed understanding of the