

## Contentious genes: a commentary on *The Selfish Gene* by Richard Dawkins

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In the preface to *The Selfish Gene*, Richard Dawkins tells us that ‘three imaginary readers looked over my shoulder while I was writing’: the layman, the student, and the expert. I recently asked Dawkins how he had fared with each of his target readers.

Lay readers, he believes, ‘have been moderately enthusiastic, but have quite often misunderstood’ the book. Students have received it very favourably. But the response of the expert, ‘which is the one I’m most interested in’, came as something of a surprise. Dawkins thought his colleagues would agree that ‘the gene’ is ‘the level at which selection operates’ and did not expect to find himself debating ‘individual selectionists’, nor did he anticipate that the metaphor of a *volitional* gene would stick in so many throats.

The writing style of *The Selfish Gene* is popular to the point of cuteness—Dawkins now finds himself ‘positively embarrassed when students parrot the quaint anthropomorphic way of speaking’—but this probably has not greatly influenced expert response. Scientific reviewers who like the contents call the style ‘superbly readable’. Those who do not substitute ‘gushing’. The popular style is by no means inconsequential, however. Favourable reviews in such periodicals as the *New Yorker*, the *Economist*, and the *New York Times Review of Books*, as well as the hundreds of letters that the author has received, attest to Dawkins’s success with the public.

Students truly enjoy the book. Text-book publishers, please take note. Without irrelevant photographs, coloured type-faces or any other pandering to the alleged minimal attention spans of a television-reared generation, indeed without a single illustration or subdivision beyond his eleven chapters, Dawkins has written a book which students (according to my informal survey of instructors in biology, psychology and anthropology) are almost unanimous in praising.

It is of course precisely because of Dawkins’s success with his lay and student readers that expert opinion becomes important. What exactly has he popularized and has he got it right?

It must first be remarked that Dawkins is more interested in explaining theory than in presenting evidence. Sometimes this seems particularly

unfortunate, as in Chapter 7, where he counters Wynne-Edwards's group selection theory with selfish gene accounts of each allegedly group-adaptive phenomenon. The naïve reader would hardly suspect that Lack's theory, for example, has inspired a great deal of *empirical* work and has been supported and refined. Critics who brand sociobiology an armchair enterprise of fanciful story-weaving may be regrettably reinforced in their erroneous prejudices by Dawkins's treatment. And accepting the bias toward theoretical treatment, there are still flaws evident in retrospect: *contra* Dawkins, Alexander's (1974) parental manipulation theory is alive and well (see Craig, 1979; Harpending, 1979), and Zahavi's (1975) handicap principle has been successfully modelled (Bell, 1978). But if Dawkins was occasionally too assertive (and he now regrets his 'impoliteness' to authors with whom he disagreed), he nevertheless summarized a rapidly developing field of theory with considerable synthetic skill and with a flair that did not displease his principle sources, W.D. Hamilton, R.L. Trivers, J. Maynard Smith and G. C. Williams.

Dawkins was (and remains) in some doubt about the extent to which *The Selfish Gene* might constitute an original contribution to theory. According to his preface, 'my greatest hope is that even (the expert) will find something new here'. To his surprise, the book thrust him into the role of radical advocate of a position endorsed by few sociobiologists: the view that discussions of 'group', 'kin' and 'individual' selection all obfuscate the fact that 'gene selection' is what is really at issue (Dawkins, 1978). Critics have responded that this sort of reductionism obscures principles of higher structural organization, a point made with unusual clarity by Michael Wade:

Dawkins' misconception of the role of population structure in the evolution of social behaviors stems from his confusion of the *effects* of selection with the *process* of selection. He reasons as follows (Chapter 3): Because evolution consists of changes in gene frequency and because genes persist unchanged longer than chromosomes, genomes, or gene pools, the gene must therefore be the unit of selection.

'Since genes reside on the chromosomes of individuals, all forces which affect gene frequencies can be reduced to increments or decrements in the fitness of individuals as a matter of mathematical convenience. This reductionist approach (employed by Hamilton in his mathematical formulation of kinship theory), however, does not mean that all selective changes can be attributed strictly to selection at the genic level. The differential proliferation of the various units of population structure can be the actual mechanism of gene frequency change. And, it is the variance between the units of population structure which determines the relative rates of gene frequency change caused by selection at any level' (Wade, 1978, pp. 220–221).

I believe that Wade's criticism has some validity, but the disagreement may be more semantic than substantive. Dawkins and several of his critics accept as meaningful the question 'What is the unit of selection?' and give different answers, without apparently differing on matters of fact. Perhaps the question is not valid as posed. We all might find it easier to think clearly about these matters if we bear in mind that natural 'selection' is itself a metaphor, chosen by Darwin to parallel the artificial selection performed by breeders. 'Selective agents', 'selective *vs.* non-selective deaths' and many related concepts are not direct descriptions of natural phenomena. They are metaphorical models at a high level of abstraction, invoked to help understand certain statistical properties of classes of natural phenomena. Like all metaphors, 'selection' as a model of differential proliferation of types can obscure as well as clarify.

(That is why Stephen Jay Gould, 1977, is unconvincing when he claims that the 'fatal flaw' in Dawkins's argument is that genes lack 'direct visibility to natural selection', evoking images of a malevolent selective agent bashing undesirable phenotypes as they reveal themselves.) If 'selection' means differential survival and reproduction, there is no question that it occurs between alleles. But the processes by which it occurs include (at the least) differential survival and reproduction (selection) of individuals.

The question, then, should not be whether Dawkins's particular form of reductionism is correct, but whether it is useful. Wade argues that it obscures higher-level structure. Dawkins argues that it clarifies certain thorny evolutionary problems. Presumably, we should maintain the mental flexibility to move back and forth. But Dawkins, perhaps pushed to an extreme position by critical response, has written 'The time has come to carry (Hamilton's) "selfish gene" revolution to its conclusion, and give up the habit of speaking of adaptation at the individual level' (Dawkins, 1978, p. 75). I do not think he noticed what a *reductio ad absurdum* this sounds' even if it were desirable, such a mental leap is almost unimaginable. All the game theoretic analyses in *The Selfish Gene* focus on individual strategists (hawk, dove, etc.), and Dawkins's own research has always focussed upon individual decision-making by chickens, crickets, and wasps. The individual is unquestionably *an* appropriate focus for the study of adaptation and perhaps even *the* appropriate focus. I will give that last word on this to Richard Alexander:

It is almost always possible to build a better system of water balance, a better locomotory mechanism, a better extruder of toxic products, or a better temperature control device. What stops the evolutionary process at any particular point is the difficulty in building a better organism. Any study of function which fails to take into account the reproductive strategy of the whole organism—no matter how clear the actions and effect of chemicals, organelles, or organs may seem to be—necessarily must lack focus (Alexander, 1975, pp. 83–84).

Even more surprising to Dawkins than the 'unit of selection' dispute has been the response to his anthropomorphising of the gene. He knew well enough that theorists who described animals as strategists striving to maximize their inclusive fitness were in danger of being taken literally, but as he told me, he had hoped to obviate misunderstanding by 'the shift of volition from a level where it is plausible to one where it is manifestly absurd'. The metaphor of a wilful gene is certainly a handy rhetorical device and it may even be a useful stimulus to theory, but is it also mischievous? I think it can be. Certainly Dawkins leaps from a technical definition of gene 'selfishness' to the claim 'we are born selfish' without scrutinizing the intervening logic. And certainly, the selfish genes are sometimes portrayed as *seeking* novel ways to exploit the environment for their own replication, when it would be more consistent to say that extant genes seek no innovation but instead fear being supplanted by inventive alleles. How much this sort of thing really matters I cannot say. It would be a critical feat beyond my abilities to dissect each use of the 'volitional gene' metaphor and say when it misleads. But one example must surely be Dawkins's inspirational vision of man becoming 'emancipated' from his genes, a notion that is literally nonsensical, but which follows from attributing a will to the genes, a will which we may then defy. I hasten to add that I can think of no

theory in the behavioural sciences that is not to some degree similarly encumbered with the two-edged sword of beguiling metaphor.

*The Selfish Gene* was written before the wave of controversy that followed the publication of Wilson's *Sociobiology*. (Indeed, most of the writing was done before Dawkins had even heard of Wilson's book.) Had he anticipated the politicization of the field, Dawkins says he would have dealt explicitly with the allegation of genetic determinism. One may doubt whether he could thereby have altered the peculiar mixture of glowing and vituperative notices that his book received. Many biologists would still take exception to his way of geneticizing ethology.

Let me quickly dismiss one such criticism. Gould (1977) would have it that the probability of selectively neutral mutations argues against the paramount importance of selection at the genetic level. But surely neutral alleles are simply members of a single class from Dawkins's perspective. What, after all, does it mean to say that two genes are 'the same'? There is no magical categorical criterion. We could categorize genes at a particular locus according to the isotope of oxygen at site  $x$ , but we ignore that difference and call them 'the same' because the difference is irrelevant to our interests. (Better to protest an overemphasis of allelic substitution models on the grounds that significant evolutionary change seems always to involve gross modification of the karyotype, but that is a problem for the whole field of theoretical population genetics and not just for Dawkins.)

Let us for the moment follow Dawkins's (1978) lead and define sociobiology as that branch of animal behaviour study influenced by W. D. Hamilton's (1964) genetical theory of social behaviour. Even so, most good sociobiological research is really no more 'genetic' than is the study of functional morphology. Although in both fields one might investigate the Mendelian genetics of a trait and perhaps even developmental genetics, more often researchers do neither, but proceed directly to the study of adaptive function. Engineering principles can be brought to bear upon the question of the adaptive function of a wing or a femur, and sometimes of a discrete act too, but how to deal with complex behaviour? Hamilton's 'inclusive fitness' provided the field of animal behaviour with a conceptual tool for the measurement and analysis of adaptive function. (Following the lead of David Lack and others, some animal behaviourists were already measuring simple fitness consequences.) Now we had a way to begin to ask, for example, to what extent the behaviour of a Florida scrub jay who helped at his parents' nest instead of breeding was adaptive; nothing more 'genetic' than that. Is it any wonder that sociobiologists are dismayed by the vulgar characterization of their discipline as that which attributes behaviour to genes?

Dawkins, like E. O. Wilson before him, must bear some of the responsibility for that vulgar characterization, for both authors are frequently guilty of perpetuating a confusion about what it means to say that a gene is a 'determinant' of behaviour. The population genetical sense is essentially one of variance partitioning: a proportion of phenotypic variance is 'attributable' to correlated genotypic variance, quite irrespective of the causes of that correlation. 'Genetic determination' can also refer to gene action in development, a causal meaning that cannot be translated into the population genetical meaning. I believe that virtually all of us in animal behaviour occasionally lose sight of this distinction,

and that that is a major reason why nature-nurture disputes are so persistent and perplexing. In one place, Dawkins writes, 'If genes really turn out to be totally irrelevant to the determination of modern human behaviour. . . ' (p. 3). This can only be the population genetical sense: that genes play no causal role in human development is absurd, but we can at least imagine that allelic differences might be altogether unrelated to behavioural differences. Yet earlier in the same paragraph we have 'Our genes may instruct us to be selfish. . . ' and here allelic differences are clearly *not* the point: a species-wide attribute is now imagined and the genes' role can only be of the causal developmental sort. This confusion pervades not just *The Selfish Gene* but the entire field. The causal developmental gene and the population genetical gene are two incongruent concepts that have converged at the same bit of DNA. That Dawkins's genes perform this double duty seems to me a profound theoretical problem.

Richard Dawkins has begun work on a second book in which he hopes to clarify several of the issues discussed above. The result may be anticipated pleurably, for his first book, its several faults notwithstanding, is remarkably readable, educative and thought-provoking. It contains much wit and insight. (The dissection of 'speciesism' in chapter one, for example, is alone worth the price of the book.) I shall continue to recommend *The Selfish Gene* to students at all levels because it stimulates them to think, and that is no faint praise.

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