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In Defence of Selfish Genes

RICHARD DAWKINS

I have been taken aback by the inexplicable hostility of Mary Midgley's assault.[1] Some colleagues have advised me that such transparent spite is best ignored, but others warn that the venomous tone of her article may conceal the errors in its content. Indeed, we are in danger of assuming that nobody would dare to be so rude without taking the elementary precaution of being right in what she said. We may even bend over backwards to concede some of her points, simply in order to appear fair-minded when we deplore the way she made them. I deplore bad manners as strongly as anyone, but more importantly I shall show that Midgley has no good point to make. She seems not to understand biology or the way biologists use language. No doubt *my* ignorance would be just as obvious if I rushed headlong into *her* field of expertise, but I would then adopt a more diffident tone. As it is we are both in my corner, and it is hard for me not to regard the gloves as off. I will try to make my reply constructive, in the hope that it may interest those who have not read Midgley's article, as well as those who have. Unattributed quotations with page numbers will all be taken from her article. Since it was my book, *The Selfish Gene* (Oxford: Oxford University Press, 1976), which stimulated her attack, it will also be necessary for me to quote from it. I shall divide my reply into eight sections.

Definitional Misunderstanding

'[Dawkins'] central point is that the emotional nature of man is exclusively self-interested, and he argues this by claiming that all emotional nature is so. Since the emotional nature of animals clearly is not exclusively self-interested, nor based on any long-term calculation at all, he resorts to arguing from speculations about the emotional nature of genes . . .' (p. 439). Midgley raises the art of misunderstanding to dizzy heights. My central point had no connection with what she alleges. I am not even very directly interested in man, or at least not in his emotional nature. My book is about the evolution of life, not the ethics of one particular, rather aberrant, species.

I shall return to this misunderstanding of me, but for the moment let me concentrate on her more serious misunderstanding of the definitional

[1] M. Midgley, 'Gene-juggling', *Philosophy* **54** (October 1979).

conventions of the whole science of 'sociobiology', a science of which she aspires to be a serious scholar.[2] When biologists talk about 'selfishness' or 'altruism' we are emphatically not talking about emotional nature, whether of human beings, other animals, or genes. We do not even mean the words in a *metaphorical* sense. We *define* altruism and selfishness in purely behaviouristic ways: 'An entity . . . 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 . . . small . . . 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 . . . 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 presumed beneficiary' (*The Selfish Gene*, pp. 4–5).

It follows from such a behaviouristic definition of altruism and selfishness that 'calculation', whether long-term or not, is irrelevant, as is 'emotional nature'. I assume that an oak tree has no emotions and cannot calculate, yet I might describe an oak tree as altruistic if it grew fewer leaves than its physiological optimum, thereby sparing neighbouring saplings harmful overshadowing. A biologist would be interested in calculating the genetic and other conditions which would be necessary for such 'altruism' to be favoured by natural selection: for instance, it might be favoured if the saplings were close relatives of the tree. Philosophers may object that this kind of definition loses most of the spirit of what is ordinarily meant by altruism, but philosophers, of all people, know that words may be redefined in special ways for technical purposes. In effect I am saying: 'Provided I define selfishness in a particular way an oak tree, or a gene, may legitimately be described as selfish'. Now a philosopher could reasonably say: 'I don't like your definition, but given that you adopt it I can see what you mean when you call a gene selfish'. But no reasonable philosopher would say: 'I don't like your definition, therefore I shall interpret your statement as though you were using *my* definition of selfishness; by my definition your concept of the selfish gene is nonsense, therefore it *is* nonsense'. This is, in effect, what Midgley has done: 'Genes cannot be selfish or unselfish, any more than atoms can be jealous, elephants abstract or biscuits teleological' (p. 439). Why didn't she add to this witty little list, for the benefit of quantum physicists, that fundamental particles cannot have charm?

If I spoke of a 'selfish elephant' I would have to be very careful to state, over and over again, whether I meant the word in its subjective or its

[2] She recommends her own book (M. Midgley, *Beast and Man*, Hassocks: Harvester Press, 1979) 'For a fuller discussion of sociobiological ideas . . .'

behaviouristic sense. This is because a good case might be made that elephants subjectively experience emotions akin to our own selfishness. No sensible case can be made that genes do, and I therefore might have thought myself safe from misunderstanding. To make doubly sure, I still went to the trouble of emphasizing that my definition was behaviouristic. The many laymen who have read my book seem to have had little trouble in grasping this simple matter of definition.

Did Midgley, perhaps, just overlook my definition? One cannot, after all, be expected to read every single word of a book whose author one wishes to insult. But in the present case no such excuse can be made. 'My' definition is not private to me. It is essentially the same kind of definition as is used by all modern biologists who write about social behaviour in animals, and Midgley is supposed to know about these things. Actually I think it is arguable that we ethologists ('sociobiologists') have overdone our insistence on objective, behaviouristic definitions of words like 'hunger', 'fear' and 'selfishness'. Maybe one day we will all come round to the minority view of Donald Griffin (*The Question of Animal Awareness*, New York: Rockefeller University Press, 1976) that the present anti-subjective bias of ethological language constitutes 'an obsolete straitjacket'. But for the time being, whether we like it or not, it just is the case that biologists use these words in a special, restricted sense. A philosopher who wishes to understand biologists must, therefore, learn this basic feature of biological language, particularly a philosopher who aspires to write about biology. The imagination reels at what a mind labouring under Midgley's definitional misconception must make of almost any of the modern literature on animal behaviour.

Egoism

To Midgley it evidently follows from her misunderstanding of my words that I am advocating an egoistic view of human ethics, or at least that I 'would like to be an egoist' (p. 446). But even if, to grant the inconceivable, I really *was* saying that genes had a selfish 'emotional nature' (p. 439), it would not follow that I thought human beings had one too. And even if I *did* think human beings were fundamentally selfish, it would not follow that I welcomed the idea. In fact, of course, to the extent that I am interested in human ethics (a rather small extent), I disapprove of egoism. To the extent that I know about human psychology (again, a rather small extent), I doubt if our emotional nature is, as a matter of fact, fundamentally selfish. And I of course do not think genes have emotional natures at all.

Let me try to say again what I do think. The facts of ethology certainly deny individual egoism as a rule in nature. Every ethologist knows this, and examples abound in my book. How, then, is the Darwinian to explain

individual altruistic behaviour in animals? 'Group selection' is one possible answer: a species, or other group, may selfishly survive at the expense of rival groups if the individuals within it behave altruistically towards each other. But unfortunately, except under very special conditions, biologists now agree that group selection cannot work in nature. There is no authoritative support for the once fashionable habit of explaining animal adaptations, altruistic behaviour among them, as 'for the good of the species'. Midgley, incidentally, has this old biology A-level reflex well developed, as when she says 'What is maladaptive . . . damages the species's chances of surviving' (*Beast and Man*, p. 149), and '. . . there is a problem about evolution, which runs "Can a species survive if each member of it sometimes does things which do not (*in fact*) pay him?"' (op. cit., p. 117). The contemporary biologist would say that whether or not a species survives is, though doubtless an interesting question, nothing to do with Darwinian selection. Darwinian selection does not choose among species.

What, then, does it choose among? The favoured answer is 'individuals'. In a sense this is correct, but only if we put it very carefully; what matters is not differential *survival* of individuals, but differential inclusive genetic fitness of individuals. The fitness of an individual (again, this is a special technical usage, different from everyday usage) means its success in getting copies of its genes represented in future generations. Fitness is a difficult quantity to calculate and a difficult concept to understand (see, for instance, Midgley's own misunderstanding of it in *Beast and Man*, pp. 138–140). My suggestion is that we can lessen the risk of misunderstanding if we shift our attention from the organism as agent, to the gene itself. Inclusive fitness is, I have only half facetiously pointed out, 'that property of an individual organism which will appear to be maximized when what is really being maximized is gene survival'.[3] We may say, with the majority of modern specialists, that maternal care is favoured by natural selection because of its beneficial effects on the inclusive fitness of the mothers concerned. Or, we may say what is essentially the same thing in terms of the selfish gene: genes that make mothers care for their young are likely to survive in the bodies of the infants cared for; genes that make mothers neglect their infants are likely to end up in dead infant bodies; therefore the gene pool becomes full of genes that induce maternal care; this is why we see maternal care in nature.

In effect, what I have done is to reject 'the selfish group' as an explanation of individual altruism, to say 'the selfish individual' is a better, but more complex and easily misunderstood, alternative, and to offer 'the selfish gene' as a simple, correct alternative. The details are by no means

[3] R. Dawkins, 'Replicator Selection and the Extended Phenotype', *Zeitschrift für Tierpsychologie* **47**, 61–76.

simple, however, and my book is a working out, in various ways, of the complications and implications of this fundamental principle, that individual behaviour, altruistic or selfish, is best interpreted as a manifestation of selfishness at the gene level.

To illustrate the kind of argument I was making, I used an analogy: '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 . . . 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' (*The Selfish Gene*, p. 2). If anybody had suggested to me that it was possible to misread that passage as saying that people are essentially Chicago gangsters I would have laughed. Yet this superhuman feat of misunderstanding is exactly what Midgley manages to achieve, '. . . telling people that they are *essentially* Chicago gangsters is not just false and confused, but monstrously irresponsible' (p. 455). I ask Midgley to look again at my words, take a few deep breaths and read them calmly and quietly. See the role of my Chicago gangster analogy. The point was that knowledge about the kind of world in which a man has prospered tells you something about that man. It had nothing to do with the *particular* qualities of Chicago gangsters. I could just as well have used the analogy of a man who had risen to the top of the Church of England, or been elected to the Athenaeum. In any case it was not people but *genes* that were the subject of my analogy.

Reciprocal Altruism

Midgley's misunderstanding of the theory of reciprocal altruism is a special case of her more general muddle, already alluded to, about animals 'calculating'. The evolutionary theory of reciprocal altruism, largely due to R. L. Trivers, was the subject of J. L. Mackie's paper in this journal which was the immediate stimulus for Midgley's attack. Briefly, Trivers suggested that the principle of doing favours in the 'expectation' of their possibly being returned later, which *we* understand at the level of conscious calculation, can be made to work in an evolutionary model without assuming conscious calculation. The appropriate mathematics is the theory of games, as I illustrated in my simple explanatory model of three 'strategies' called 'cheat', 'sucker', and 'grudger' (*The Selfish Gene*, pp. 197–201). Now Midgley appears to think that reciprocal altruism can only work in animals that can 'calculate'. She quotes E. O. Wilson's surprising statement that 'Human behaviour abounds with reciprocal altruism consistent with genetic theory, *but animal behaviour seems to be almost devoid of it*' (Midg-

ley's italics, not in original, not acknowledged). Midgley goes on: '[Wilson] accounts for this (as I do) by the lack of calculation in animals, but seems not to see that, since these "animals" are the subjects we are dealing with for almost the whole of evolution, any "genetic theory" inconsistent with their capacities will have to be revised' (p. 444).

I would have been surprised if Wilson had really invoked 'the lack of calculation in animals', and indeed, as far as I can see, he does not. What he does suggest is that '... in animals relationships are not sufficiently enduring, or memories of personal behavior reliable enough, to permit the highly personal contracts associated with the more human forms of reciprocal altruism' (*Sociobiology*, p. 120). I think Wilson underestimates the power of animals to recognize and remember each other, but, be that as it may, he is talking about *memory*, which is quite different from Midgley's 'calculation'. More importantly, far from the theory of reciprocal altruism needing calculation, it doesn't even need memory, at least in the ordinary sense of the word. All that is required is some functional *equivalent* of a memory of past favours. It does not have to be a real memory residing in the nervous system. This is, indeed, the novelty of Trivers' contribution, since any fool can see that the principle of reciprocation will work in a species that is capable of remembering past favours and calculating debts. Midgley might have realized this if, instead of relying on her admittedly slightly misleading secondary source, she had gone back to the primary source (R. L. Trivers, 'The Evolution of Reciprocal Altruism', *Quarterly Review of Biology* **46** (1971), 35–57).

She might even have got the point from *The Selfish Gene* (pp. 201–202): 'Trivers discusses the remarkable symbiosis of the cleaner-fish. Some fifty species, including small fish and shrimps, are known to make their living by picking parasites off the surface of larger fish of other species. The large fish obviously benefit from being cleaned, and the cleaners get a good supply of food ... In many cases the large fish open their mouths and allow cleaners right inside to pick their teeth, and then to swim out through the gills which they also clean. One might expect that a large fish would craftily wait until he had been thoroughly cleaned, and then gobble up the cleaner. Yet instead he usually lets the cleaner swim off unmolested. This is a considerable feat of altruism because in many cases the cleaner is of the same size as the large fish's normal prey ... Each cleaner has his own territory, and large fish have been seen queueing up for attention like customers at a barber's shop' (not a real barber's shop with scissors and electric clippers, I suppose I now have to add). 'It is probably this site-tenacity which makes possible the evolution of delayed reciprocal-altruism in this case. The benefit to a large fish of being able to return repeatedly to the same "barber's shop", rather than continually searching for a new one, must outweigh the cost of refraining from eating the cleaner.'

The important point is that neither calculation nor memory of past

favours need be invoked. *Site-tenacity* on the part of both kinds of fish is sufficient. The site-tenacity, which, by the way, is a commonplace of fish ethology, acts as a kind of equivalent of a memory. In Darwinian terms we say that, *given* site-tenacity by both cleaners and cleaned fish, natural selection favours merciful behaviour by large fish towards their cleaners. Calculations of probable future benefit are done by the biologist, not by the fish (they *might* be done by the fish, but that is incidental). The fish simply do things which have consequences in given conditions, and natural selection judges them by those consequences.

The idea of animals behaving *as if* calculating odds without really doing so is fundamental to an understanding of the whole of sociobiology: 'Just as we may use a slide rule without appreciating that we are, in effect, using logarithms, so an animal may be pre-programmed in such a way that it behaves *as if* it had made a complicated calculation . . . This is not so difficult to imagine as it appears. When a man throws a ball high in the air and catches it again, he behaves as if he had solved a set of differential equations in predicting the trajectory of the ball. He may neither know nor care what a differential equation is, but this does not affect his skill with the ball' (*The Selfish Gene*, pp. 103–104; see also my reply to Marshall Sahlins: misunderstanding number 3 in R. Dawkins, 'Twelve Misunderstandings of Kin Selection', *Zeitschrift für Tierpsychologie* **51** (1979), 184–200).

There are other odd things in Midgley's section on reciprocal altruism. For instance she devotes a paragraph to a trenchant and forceful advocacy of the obviously undisputed proposition that 'The main source and focus of altruistic behaviour in animals is the care of the young, *which in most species will certainly never be repaid*' (p. 440, my italics). Who is supposed to be surprised? Not me, I am relieved to note, since reciprocation occupies a very small part of my book and kin-selected parental care rather a large one. Midgley's target in this case is J. L. Mackie ('The Law of the Jungle', *Philosophy* **53** (October 1978)), but her shot is aimed not at his main point (which she seems to have overlooked), but at his little aside about Nietzsche.

Before explaining why I think Mackie's paper may be an important contribution to biology, I cannot leave the subject of parental care without calling attention to the following, from Midgley: 'This persistent difficulty in reducing parents to the egoist pattern is just the kind of thing which makes Dawkins's typical readers—people with vaguely egoist leanings about individual human psychology—willing to follow him in losing touch with the observed facts of motivation altogether and taking off for the empyrean with the Gene' (pp. 443–444). It is one thing to insult the *author* of a book, but how *dare* Midgley pontificate about its 'typical readers'? I don't think I have had the pleasure of meeting any readers of Mrs Midgley's book, but no doubt they vary and would resent prejudiced generalizations about their 'leanings' and ill-informed slurs against their critical faculties.

Mackie's Contribution

Midgley's emotional reaction to a few words and phrases used by Mackie seems to have blinded her to the potentially important suggestion he was making. I shall explain this, since Mackie himself did not follow his train of thought to its conclusion. Group selection is the hypothetical process whereby natural selection chooses among whole groups of organisms, as opposed to choosing among individuals (see J. Maynard Smith, 'Group Selection', *Quarterly Review of Biology* **31**, 277–283). As I have explained, it is widely agreed to be an unworkable theory, but if it did work it would be important since it could explain altruistic behaviour: groups containing altruistic individuals are less likely to go extinct than groups of selfish individuals. Mathematical models by Maynard Smith himself and others have shown that the theoretical objections to group selection would largely vanish if we were allowed to assume the existence of high genetic variance among groups compared to within-group variance. This is a technical way of saying that there has to be a tendency for fellow group members to share more genes with each other than they share with random members of the population at large. This assumption will clearly be met if genetic relatives go about in family groups, but then we are dealing with the well-understood phenomenon of 'kin selection', not group selection at all. Mackie's contribution, though he does not put it like this, is to have offered us a new mechanism whereby the variance-differential necessary for group selection could be maintained. The argument is as follows.

My game-theoretic analysis of 'cheats, suckers and grudgers' led to two alternative stable solutions. A population dominated by cheats would not be invaded (evolutionarily speaking) by suckers or grudgers. If, however, a population chanced to acquire more than a critical frequency of grudgers, natural selection would suddenly start favouring grudgers, until they became a runaway majority. The concept of a bistable system is a slightly subtle one, and it is not surprising that Midgley misunderstood it in her summary: 'Dawkins concludes that Cheats and Grudgers would exterminate Suckers, and Grudgers might well do best of all' (p. 440). The whole point is not that grudgers might do better or worse than cheats, but rather that *whichever* of the two happened to attain more than a critical frequency in the population would, *by virtue of that fact*, do better than the other. For the present argument, the important consequence is that such a bistable system is a recipe for high between-group variance: some populations would stabilize at the grudger equilibrium; others would stabilize at the cheat equilibrium. Populations with intermediate relative frequencies would be inherently unstable, and natural selection at the individual level would push them to one extreme or the other. Selection within groups would thus see to it that variance between groups was high. Mackie's argument is that group selection would now have a real chance to work,

differentially extinguishing groups of cheats at the expense of groups of grudgers (reciprocal altruists). It is too early to say, yet, whether formal mathematical models will uphold this possibility, but if they do, Mackie's paper in *Philosophy* will have to be seen as a useful contribution to biology. I should add that a brief similar suggestion has been made independently by M. J. Wade ('A Critical Review of the Models of Group Selection', *Quarterly Review of Biology* **53** (1978)).

Models

Midgley describes my model of cheats, suckers and grudgers as an 'absurdly abstract and genetically quite impossible situation' (p. 440), and as a 'grossly simplified and distorted scheme' (p. 441). But *of course* it is abstract, simplified and distorted. This is what models are, and that is what gives them their usefulness. It is the very property which made my model useful to Mackie and which stimulated his useful contribution. Models do not aspire to mimic reality faithfully. If they did, they would not be models, they would be reality. In physics, for instance, it is sometimes convenient to imagine a body—it may even be described as a train—travelling at nearly the speed of light past an observer, who sees the passengers hideously foreshortened. Only a pedant would point out that trains can't go that fast, and that in any case the observer wouldn't have time to see the passengers. If a philosopher made such an objection against the writings of a particular physicist, we could justly conclude that he or she did not understand the first thing about physics, since all physicists make use of such simplified models. Yet this is almost exactly the nature of Midgley's objection to my 'grudger/sucker/cheat' model. If she had objected that it was a bad model I would have listened sympathetically, but that is not what she did. She appears not to have understood that it was a model at all.

In the present state of evolutionary biology, the preferred models embody various kinds of deliberate simplification, and one of the most fashionable of these deliberate simplifications is the 'one gene one strategy' model that worries Midgley so much. I am only one of many biologists for whom it is a convenient weapon in our theoretical armoury. Others who frequently wield it include J. Maynard Smith and E. O. Wilson, to name two biologists whom Midgley singles out for special praise in her article. It is ironic that she should compare my 'gene-selection' treatment of the paradox of sex, to its disadvantage, with a passage from John Maynard Smith's rightly praised *The Evolution of Sex* (Cambridge University Press, 1978). Like nearly all Maynard Smith's works, this book abounds in simplified models of exactly the kind Midgley castigates. If she had read beyond the Preface to page 113, Midgley would have found Maynard

Smith specifically endorsing gene-selection models of sexuality, invoking in his support the very passage from *The Selfish Gene* which Midgley describes as a 'clanger'.

If a philosopher attacked modern evolutionary biology as a whole for its reliance on over-simple models, again we would have to listen. But a philosopher who intemperately attacks one particular biologist for doing exactly what most of his professional colleagues do, and have done for decades, displays fundamental and profound ignorance of the methods of biology. It may be that we shall eventually find today's 'one gene one strategy' models too simple to be useful. The intuition of professionals varies here. My own hunch, for what it is worth, it that most of the major principles of present day 'strategy' models will survive future injections of genetic complexity, while the quantitative details of their predictions will not. We must patiently wait and see.

Genes

'There is nothing empirical about Dawkins. Critics have repeatedly pointed out that his notions of genetics are unworkable' (p. 439). No critic is named. The footnote refers only to a 1978 paper of mine.[3] Midgley says that in this paper I have 'eventually' made an 'attempt to answer some of these criticisms'. In fact I made no such attempt, because no such criticisms were known to me. If Midgley will cite the 'repeated' criticisms I will read them with attention and, if appropriate, reply to them.

My notions of genetics are actually much more conventional than Midgley thinks. She herself would have a great deal of trouble with the concept of the gene, as it is ordinarily used by geneticists: 'For selection to work as [Dawkins] suggests by direct competition between individual genes, the whole of behaviour would have to be divisible into units of action inherited separately and each governed by a single gene ... To convince us that this is so, Dawkins brings up once more the case of Rothenbuhler's Hygienic Bees, creatures which have been appearing in suspicious isolation as a stage army in all such arguments for some time ... Actually, not only does the bees' case stand alone, but it is certainly not proven. To show that even the simple behaviour it involves is really governed by only two genes would take something like seventy generations of outbreeding experiments to ensure that the effects described are not due to the close linkage of genes at a whole series of adjacent loci, and even this would not show that these genes affected nothing else' (p. 449). There are so many muddles interwoven here, it is hard to know where to start unravelling.

Probably the first point to make is that whenever a geneticist speaks of a gene 'for' such and such a characteristic, say brown eyes, he never means

that this gene affects nothing else, nor that it is the only gene contributing to the brown pigmentation. Most genes have many distantly ramified and apparently unconnected effects. A vast number of genes are necessary for the development of eyes and their pigment. When a geneticist talks about a single gene effect, he is always talking about a *difference* between individuals. A gene 'for brown eyes' is not a gene that, alone and unaided, manufactures brown pigment. It is a gene that, when compared with its alleles (alternatives at the same chromosomal locus), in a normal environment, is responsible for the difference in eye colour between individuals possessing the gene and individuals not possessing the gene. The statement 'G_1 is a gene for phenotypic characteristic P_1' is always a shorthand. It always implies the existence, or potential existence, of at least one alternative gene G_2, and at least one alternative characteristic P_2. It also implies a normal developmental environment, including the presence of the other genes which are common in the gene pool as a whole, and therefore likely to be in the same body. If all individuals had two copies of the gene 'for' brown eyes and if no other eye colour ever occurred, the 'gene for brown eyes' would strictly be a meaningless concept. It can only be defined by reference to at least one potential alternative. Of course any gene exists physically in the sense of being a length of DNA; but it is only properly called a gene 'for X' if there is at least one alternative gene at the same chromosomal locus, which leads to not X.

It follows that there is no clear limit to the complexity of the 'X' which we may substitute in the phrase 'a gene for X'. Reading, for example, is a learned skill of immense and subtle complexity. A gene for reading would, to naive common sense, be an absurd notion. Yet, if we follow genetic terminological convention to its logical conclusion, all that would be necessary in order to establish the existence of a gene for reading is the existence of a gene for not reading. If a gene G_2 could be found which infallibly caused in its possessors the particular brain lesion necessary to induce specific dyslexia, it would follow that G_1, the gene which all the rest of us have in double dose at that chromosomal locus, would by definition have to be called a gene for reading. Imagine a tribe in which almost everybody had G_2 and therefore could not learn to read. Now the rare possessors of G_1 would be the sole literates and, provided adequate educational opportunities were available to all, reading behaviour would be inherited according to the elementary laws of Mendelian genetics. Dyslexia would not, of course, be the only describable effect of such a gene. All genes are fundamentally 'genes for making proteins', but it is a routine convenience in genetics to accept other labels such as 'gene for brown eyes'. Which of the intricately ramified consequences of the fundamental protein effect we choose to use as a label is simply a matter of convenience. The hypothetical 'gene for dyslexia' would almost certainly have other psychological or perceptual effects, but in our world where reading is so important dyslexia might well

be its most salient effect, and the dyslexia label would therefore be convenient. The same gene, in a Pleistocene environment, might earn a different label, say 'gene for being unable to read animal footprints'. Similarly, a gene for total blindness would obviously prevent reading, but it would not be convenient to label it by this property since other effects of total blindness would be more noticeable. The normal alternative to a gene for total blindness could sensibly be called a gene for seeing, but not a gene for reading. This is, of course, a hypothetical example. I know of no evidence of a gene for dyslexia. My only point is that the complexity, *per se*, of a behaviour pattern such as reading is irrelevant to the plausibility of there being a single gene 'for' that behaviour pattern. To summarize the reason for this, it is that *differences* between behaviour patterns can have unitary and simple causes, even if the behaviour patterns themselves are highly complex.

It is no part of my world view that the whole of behaviour must be 'divisible into units of action inherited separately and each governed by a single gene'. Since Midgley is not the only person to have had trouble in grasping this point, let me use an analogy which others seem to have found helpful. The genetic code is not a blueprint for assembling a body from a set of bits; it is more like a recipe for baking one from a set of ingredients. If we follow a particular recipe, word for word, in a cookery book, what finally emerges from the oven is a cake. We cannot now break the cake into its component crumbs and say: this crumb corresponds to the first word in the recipe; this crumb corresponds to the second word in the recipe, etc. With minor exceptions such as the cherry on top, there is no one-to-one mapping from words of recipe to 'bits' of cake. The whole recipe maps on to the whole cake. But suppose we change one word in the recipe; what now emerges from the oven is a different cake, different through its whole substance. If we have 100 cakes baked according to the first version of the recipe and 100 cakes baked according to the second version of the recipe, it will be possible to say: although there is no one-word-one-crumb mapping from recipe to either cake, it is true that a one word difference between these two recipes is solely responsible for the only consistent differences between this set of 100 cakes and that set of 100 cakes.

To repeat, then, geneticists are not concerned with 'one gene one bit-of-animal' mapping. They are concerned with 'one gene-difference one animal-difference' mapping. And just as geneticists are concerned with inter-individual differences, so is natural selection. Natural selection can be said to choose individuals versus rival individuals, but it is only if the responsible differences between the individuals are due to genes that natural selection can have any evolutionary consequences. For instance, if selection favours fleetness of foot within a preyed-upon species, but individual differences in fleetness of foot are entirely non-genetic in origin, no evolutionary change will result from the selection: fast runners

will come to predominate among the survivors of each generation, but they will not pass their fleetness of foot on to the next generation, so no evolution will be seen. It follows that if we believe that X is a Darwinian adaptation, we are committing ourselves to the belief that, in the past anyway, there must have been at least one gene 'for' X. And Midgley's implication that the hygienic honey bee is the only known example of a gene effect on behaviour (it isn't, of course; it is just the most spectacular), and that even it may be suspect, is tantamount to a disavowal of the entire principle of the evolution of behavioural adaptation by natural selection!

We now come to the allegedly important distinction between a single gene and a linked series of adjacent genes, and the statement that it would take 'something like seventy generations of outbreeding experiments' to demonstrate a single gene effect as opposed to a close linkage effect. I hope nobody was impressed by the spurious impression of scientific precision conveyed by that 'seventy generations'. Why seventy, not seven hundred or seven thousand? No magic number of outbreeding experiments can settle the issue, because it is a non-issue, or, more precisely, because 'the gene', as I use the term, is an asymptotic, not an all or none, concept. If a series of adjacent genes is so closely linked that it takes n generations of breeding experiments to separate them, then for practical purposes we can treat them as one gene ('supergene' it is sometimes called), provided n is large in relation to the time span we are interested in. And the time span we are interested in here is the evolutionary time span. If we are examining a particular behaviour pattern as a possible Darwinian adaptation, we will be content to regard it as controlled by a single gene provided natural selection, too, 'regards' it as controlled by a single gene—that is, provided the risk of the supergene's being split into its component sub-genes is small compared to the risk of its being eliminated by the natural selection pressures we are investigating.

It is admittedly true that 'the gene' is an asymptotic rather than an all or none concept only if defined in a particular way. A molecular biologist might define it so that it became an all or none concept. But I am not a molecular biologist, and I made my definition very clear: 'A gene is defined as any portion of chromosomal material which potentially lasts for enough generations to serve as a unit of natural selection' (*The Selfish Gene*, p. 30). Midgley quotes this definition, expressing surprise that I got it from George Williams (whom she rightly admires), and adding, as though it were an objection, that I 'might be talking about any section of the DNA' (p. 451).[4]

[4] It is hard to resist a flourish as I quote almost exactly the same words from a recent, forward-looking review by Francis Crick, architect (with J. D. Watson) of the modern molecular concept of the gene: 'The theory of the "selfish gene" will have to be extended to any stretch of DNA' (F. H. C. Crick, 'Split Genes and RNA Splicing', *Science* **204** (1979), 270). Crick's point is elaborated in two

That is my point. I am not searching for an ideal, indivisible, atom-like unit. I am searching for a chunk of chromosomal material which, in practice, behaves as a unit for long enough to be naturally selected at the expense of another such fuzzy unit. I agree that there are difficulties in this way of looking at evolution, but I believe I have shown them to be less great than the difficulties inherent in any other way that has been suggested. The individual organism is a fuzzy unit too (think of vegetatively propagating plants), yet it is current orthodoxy that 'the individual is the unit of selection'. The group of individuals is even more fuzzy, and it is partly for this reason that it is no longer regarded as a significant unit of selection. The truth is that there is no hard atomic unit of natural selection, but I believe my 'fuzzy gene' or 'replicator' is the most convenient approximation.

Once again, philosophers should be particularly sympathetic towards special-purpose re-definitions of words, but actually the present case hardly deserves to be called *re*-definition at all. There never has been a generally agreed definition of the gene. Pre-molecular usage, in practice, amounted to the gene of the Williams definition, although in principle it was thought of as an indivisible 'bead' on a chromosomal string. In the 1950s, molecular biology showed that there were no atomistic beads, and Seymour Benzer[5] suggested that 'the gene' should be replaced by three terms: the muton was the minimum unit of mutational change; the recon was the minimum unit of recombination; and the cistron was defined in a way that was strictly applicable only to micro-organisms, but for practical purposes it amounted to the unit of protein synthesis. Which of the three gene definitions one used was to depend on one's purposes. But Benzer's purposes were all molecular. For the student of adaptation in whole organisms yet another unit, which I shall call the 'optimon', is required. The optimon is that unit to which we refer when we speak of a Darwinian adaptation as being 'for the good of' something. Williams, in effect,

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further molecular biological papers whose titles betray no coy reticence about applying the word 'selfish' to DNA molecules! (L. E. Orgel and F. H. C. Crick, 'Selfish DNA: the Ultimate Parasite', *Nature* **284** (1980); W. F. Doolittle and C. Sapienza, 'Selfish Genes, the Phenotype Paradigm and Genome Evolution', *Nature* **284** (1980). As for my definition of the gene, its derivation from Williams is not word for word, but I have conveyed the clear message of pp. 22–25 of his *Adaptation and Natural Selection* (New Jersey: Princeton University Press, 1966). My definition is a rendering, for laymen, of two technical sentences from these pages of Williams: 'I use the term *gene* to mean "that which segregates and recombines with appreciable frequency" '; and 'a gene could be defined as any hereditary information for which there is a favorable or unfavorable selection bias equal to several or many times its rate of endogenous change'.

[5] S. Benzer, 'The Elementary Units of Heredity', *The Chemical Basis of Heredity*, W. D. McElroy and B. Glass (eds) (Baltimore: Johns Hopkins, 1957).

defined the gene as equivalent to what I am calling the optimon. In *The Selfish Gene* I followed him, but I have since suggested substituting the more general term *replicator*, since 'gene' gives rise to confusion (and how!). This whole area of units of genetic function and units of adaptive benefit is fraught with important difficulties, but the alleged difficulties manufactured by Midgley are not among them. I do not claim that my essay on replicator selection[3] solves all the problems, but I think that it, and the paper of the philosopher David Hull[6] that follows it, are honest attempts to face up to the difficulties, and that some progress is being made.

Midgley (p. 454) quotes with approval Stephen Jay Gould's courteously expressed criticism: 'No matter how much power Dawkins wishes to assign to genes, there is one thing that he cannot give them—direct visibility to natural selection. Selection simply cannot see genes and pick among them directly. It must use bodies as an intermediary . . .'.[7] I find it impossible to imagine what it would even *mean* to say that genes were directly visible to natural selection. Of course they have to use bodies as an intermediary. That is why my book is mostly about the behaviour of individual bodies (see especially Chapter 4 for a discussion of the role of bodies as machines programmed to preserve genes, like computers programmed to win games of chess). Natural selection favours genes (replicators) versus their alleles by virtue of those genes' effects on bodies. But it is not the bodies that survive; they reproduce their genes and die. Only genes survive, in the form of information copies of themselves (why, by the way, does Midgley think the perfectly obvious fact that 'a gene cannot perpetuate *itself* but only likenesses of itself' (p. 446) is such a 'crashing' disaster for my case? It is one

[6] D. L. Hull, 'The Units of Evolution: a Metaphysical Essay', *Studies in the Concept of Evolution*, U. J. Jensen and R. Harré (eds) (Hassocks: The Harvester Press, in press). In view of her spirited remark that I should either learn to do metaphysics or retreat out of sight altogether, Midgley might be amused at the following from Hull's manuscript: 'Although he is likely to be shocked, if not offended, at being told so, Dawkins (1976, 1978) has made an important contribution to the metaphysics of evolution in his explication of "replicators". Like Monsieur Jourdain, who was astonished to discover that he had been speaking prose all his life, Dawkins may well be equally surprised to discover that he has committed an act of metaphysics.'

[7] S. J. Gould, 'Caring Groups and Selfish Genes', *Natural History* **86** (December 1977). Gould is a well-known palaeontologist who would probably be surprised at Midgley's description of him as 'a geneticist' (*Beast and Man*, 66). Midgley, in turn, might be surprised at some of the things Gould has written elsewhere, for instance: 'Natural selection dictates that organisms act in their own self-interest. They know nothing of such abstract concepts as "the good of the species". They "struggle" continuously to increase the representation of their genes at the expense of their fellows. And that, for all its baldness, is all there is to it; we have discovered no higher principle in nature' (S. J. Gould, *Ever Since Darwin* (London: Burnett Books, 1978), 261).

of the very linch-pins of my case!). Evolution consists in the differential copying success of genes relative to their alleles. The genes which exist in the world are, obviously, the genes whose replicas in previous generations were successful in getting themselves copied. Such success is achieved by means of influence on the development of bodies. Bodies, therefore, tend to have what it takes to propagate genes, and may properly be regarded as engines of gene propagation—'survival machines'.

Sociobiology

Midgley's malice at times becomes positively catty, as, for instance, when she gratuitously remarks that my 'pages are virgin of originality . . .' (p. 444), my material having all been drawn from 'evolutionists such as W. D. Hamilton, Edward O. Wilson, and John Maynard Smith who are not directly interested in individual psychology at all'. In another place she quotes a sentence from Wilson's *Sociobiology* (Harvard University Press, 1975; ironically the sentence is the very one on reciprocal altruism, which, as I showed above, Midgley so pathetically misunderstood). She then adds: 'Dawkins . . . ignores Wilson's reasoning here, as he does most other things that do not suit him' (p. 444). I did not 'ignore' Wilson's reasoning: at the time of writing (1975) I, together with most other people, had not had an opportunity of seeing Wilson's book. After completing my book in essentially its final form I obtained a copy of *Sociobiology*, and managed to slip into my final draft a brief mention of it (a criticism of Wilson's treatment of the theory of kin selection: I prophesied that he would muddle people, and p. 140 of Midgley's *Beast and Man* shows my forecast to have been amply fulfilled). This was the only change *Sociobiology* caused in my entire text. Only after *The Selfish Gene* had gone to press did I read Wilson's excellent work from cover to cover, and even then (early 1976) I must have been one of the first people in Britain to do so. Any claim that I was influenced by Wilson is simply false. The claim that I drew material from Hamilton and Maynard Smith is, of course, true. I am proud of it, and acknowledged my debt to them, and to George Williams and Robert Trivers. Like E. O. Wilson, I was trying primarily to synthesize and interpret our field (it wasn't called sociobiology then), and only incidentally trying to break new ground (although I think both Wilson and I would be disappointed if we were thought to have broken no new ground). Both Wilson and I would have been sadly remiss if we had not given great prominence to Hamilton's ideas on kinship and other topics. In my opinion[8] Wilson *was* rather

[8] In Hamilton's opinion too, as is clear from his reviews of both our books (and by the way, nobody in the world is better qualified to review either of them): W. D. Hamilton, review of *The Selfish Gene* (*Science* **196**, 1977, 757–759); W. D. Hamilton, review of *Sociobiology* (*Journal of Animal Ecology* **46**, 1977, 975–983).

remiss in virtually ignoring Maynard Smith's game-theoretic concept of the evolutionarily stable strategy. As for the statement that Wilson is 'not directly interested in individual psychology at all', hollow laughter seems the only appropriate response. Whatever does Midgley think the ballyhoo, the political demonstrations, the 'Sociobiology Study Group of Science for the People' are all about? If anyone remains in doubt, I recommend Wilson's *On Human Nature* (Harvard University Press, 1978).

Concluding Remarks

If the reader discerns in my reply signs of what appears to be undue rancour, I beg him or her to scan a few random sentences of Midgley's paper and judge the provocation. It is not an invited book review, remember, but a voluntarily contributed article. Her concluding footnote would be hard to match, in reputable journals, for its patronizing condescension toward a fellow academic (a fellow academic, moreover, who is a professional in the field under discussion, a field in which the critic herself is most charitably described as trying hard): 'Up till now, I have not attended to Dawkins, thinking it unnecessary to break a butterfly upon a wheel. But Mr Mackie's article is not the only indication I have lately met of serious attention being paid to his fantasies' (p. 458). Incidentally, when Midgley says she has not 'attended to' me before, this is not strictly accurate. In *Beast and Man* (e.g. p. 131) will be found criticisms of the concept of 'the selfish gene', but it is an orphaned concept, named but without a responsible author. Her readers were served up with the criticism, without being trusted with the information that 'the selfish gene' being criticized is, in fact, a real book, with an author, a date, and a publisher—a book that they might go away and judge for themselves against her criticism. Worse, in her Introduction (p. xxii), the concept of 'the selfish gene' is solemnly attributed to Edward Wilson, a fact which probably annoys him even more than it annoys me (he tells me he finds my ideas reductionist). What, in the circumstances, are we to make of her publisher's claim on the dustjacket that Midgley's comments on 'Wilson's concept of "the selfish gene" are the most serious and sustained criticism of Wilson yet published'?

Let me not end on a negative note. Midgley has a lot to say about metaphor, and I can end constructively by explaining why it was unnecessary for her to say it. She thought that I would defend my selfish genes by claiming that they were intended only as a metaphor, and assumed that I was speaking metaphorically when I wrote, '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' (*The Selfish Gene*, p. ix). But that was no metaphor. I believe it is the literal truth, provided certain key words are defined in the particular ways favoured by

biologists. Of course it is a hard truth to swallow at first gulp. As Dr Christopher Evans has remarked, 'This horrendous concept—the total prostitution of all animal life, including Man and all his airs and graces, to the blind purposiveness of these minute virus-like substances—is so desperately at odds with almost every other view that Man has of himself, that Dawkins' book has received a bleak reception in many quarters. Nevertheless his argument is virtually irrefutable' (*The Mighty Micro*, London: Gollancz, 1979, 171). For my part, what has gratified me is that the anticipated bleak reception has, in the event, been confined to so *few* quarters, and such unpersuasive ones.[9]

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[9] Some of the more constructive arguments in this paper are developed further in my forthcoming book, *The Extended Phenotype* (Oxford: W. H. Freeman & Co., 1982).

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[Footnotes]

[4] **Split Genes and RNA Splicing**
Francis Crick
Science, New Series, Vol. 204, No. 4390. (Apr. 20, 1979), pp. 264-271.
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[8] **Review: The Play by Nature**
Reviewed Work(s):
The Selfish Gene by Richard Dawkins
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[8] **Review: [Untitled]**
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