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RICHARD DAWKINS

Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K.

Lucy Sullivan criticizes *The selfish gene* for its anthropomorphic language, quotes three recent papers to support her complaint that it has had a large and pernicious influence upon modern biology, and commends Darwin, by comparison, for eschewing such anthropomorphic excesses. In the course of this, she unfortunately demonstrates that she has never read *The selfish gene*, never read Darwin, never read two of the three papers supposed to have been influenced by *The selfish gene*, and misunderstood the third.

These are serious charges of poor scholarship and I must substantiate them before going any further. First, *The selfish gene* itself. Following her discussion of 'helping at the nest in bee-eaters', Sullivan says:

> '...here we find an interesting transformation of the supposed processes of gene selfishness into behavioural altruism. At the level of a society, as here, selfish gene theory ceases to function as a model for individualistic selfishness, but instead predicts social cooperativeness and helpfulness. True, the altruism is kinship-based, but it is altruism, nevertheless. After all, no one regards Shaftesbury as selfish rather than philanthropic because his legislative efforts were on behalf of English children, rather than, say, French children. Indeed, selfish-gene theory could well be entirely rewritten as a theory of consanguineally based altruism.'

Anybody who had read *The selfish gene* beyond the title page would know that Sullivan's point is not an 'interesting transformation' but precisely the main message of the entire book. It is not that she has overlooked a particular, buried passage, as anybody might. You'd have to overlook the whole book in order to talk of 'rewriting' it as 'a theory of consanguineally based altruism.' The whole purpose of the book is to explain how altruism at the level of the individual can emerge out of selfishness at the level of the genes. That is exactly why it is given the deliberately enigmatic title, *The selfish gene*. The suspicion that she has read the book by title only (she would not be the first vociferous critic to have subsequently admitted doing so) is borne out by her claim that *The selfish gene* is 'a challenge to the social morality of altruism.' In fact, in so far as the book admits to a moral message at all, it is a passionate plea in favour of the social morality of altruism. The last words of the original edition were 'We, alone on earth, can rebel against the tyranny of the selfish replicators.' Anthropomorphic, yes (I'm coming to that), but not a challenge to the social morality of altruism. Here is a passage from the beginning of the book that bears this out:

> '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.'

Second, it is hard to believe that Sullivan has read Darwin (she certainly hasn't understood him) despite her repeated invocation of him. She refers to my view that we should conceptualize survival of the fittest as operating at the genetic level 'rather than at the level of species as proposed by Darwin...'. This passage is not an accidental aberration. Her penultimate paragraphs make embarrassingly clear her astonishing belief that Darwin thought of natural selection as choosing among species, not within species:

> 'Darwin saw evolution as adaptation to changing ecological niches – to changes created by interspecies competition and species development – via individual random mutation preserved through its adaptiveness to the conditions of competition from other species. The significance of mutation for evolution is improved competitiveness, not within the species, but in relation to other species, or else a redirection of functioning so as to be less in competition with the dominant *modus vivendi* within the species.'

Again, we cannot laugh this off as a minor error of interpretation. It is a complete, root and branch, catastrophic misunderstanding of Darwin's central idea of natural selection. So is the following:

> 'The mutations that are instrumental in evolution, and the superior fitness which they achieve, are not, in Darwin's theory, primarily conceived as directed at achieving dominance and success in intraspecies competition. The intraspecies winner per se may be an interspecies loser, and the species, with all its selfish genes, will die out.'

The author of this passage reveals not only that she failed to understand *The origin of species*. She is also blissfully untouched by the vast subsequent literature, both philosophical and biological on 'levels of selection': that controversial literature which – in all its Byzantine and mathematical intricacy – forms the context in which *The selfish gene* belongs and must be understood (Wynne-Edwards 1962, 1986; Williams 1966, 1992; Maynard Smith 1976; Dawkins 1982; Brandon & Burian 1984; Cronin 1991; Wilson & Sober 1995).

Just as if you read *The selfish gene* by title only you might assume that it must be all about selfishness, so I suppose that if you read *The origin of species* by title only, you might come away with a vague idea that species were somehow important to Darwin – and therefore it is not a bad guess that he thought natural selection chose among species. But he did not: Darwin almost never flirted with group or species selectionism of any kind, and, as the historian Michael Ruse has convincingly shown, when he occasionally seemed to do so, it was anomalous and exceptional (Ruse 1980). This is in contrast to many of his lesser successors, for, to give Sullivan her due, she is in plentiful company: as W. D. Hamilton (1975) put it, '...almost the whole field of biology stampeded in the direction where Darwin had gone circumspectly or not at all.'

Sullivan severely criticizes papers by Haig, and by Hurst & Hamilton, but candidly admits that she has only read secondary accounts of them by Anderson. If she had read David Haig's own massively referenced and meticulously documented tour de force on maternal foetal conflict (Haig 1993), she would have hesitated before throwing in her two penn'orth of folk wisdom and apparent commonsense:

> 'Even in terms of selfish gene theory, it would not benefit the father's genes to curtail the mother's life through overtaxing her during pregnancy, because her presence is optimally required to raise the offspring to reproductive age (if the genes are to be transmitted further).'

A more conspicuous 'missing of the point' would be hard to devise. Parent–offspring conflict theory is subtle, difficult and, at first sight, paradoxical. That is why it is worth writing papers about it: there would be no point in writing them if you could do it all by commonsense. And that is why you have to read at least one of those papers before you launch into a criticism of the theory (see, *inter alia*, Trivers 1974, 1985; Haig 1993; or chapter 8 of *The selfish gene*).

The Hurst & Hamilton (1992) paper is also subtle, and you would need to have some sort of rudimentary idea of the basic difference between sexual and asexual reproduction to make so much as a start on it. In charity I do not know what to make of Sullivan's characterization of asexual reproduction: '...the two cells do not fuse but simply exchange genetic material, maintaining equality of cellular identity.' Which two cells? Which genetic material do they 'exchange'? The best guess I can make is that she is confusing asexual reproduction with isogamous sexual reproduction. Equally baffling is her opinion that the following statement, by Emlen and Wrege (in the third of her three criticized papers), is Lamarckian: '...the utility being maximized is fitness (survival and reproduction), measured in terms of the number of offspring equivalents produced during an individual's lifetime.' There is nothing remotely Lamarckian about that statement. It is as Darwinian as the most puritanically purist Darwinist (probably me) would wish for. Could it be that Sullivan, in some sort of knee-jerk reaction to the phrase 'produced during an individual's lifetime.' has confused 'offspring' with 'acquired characteristics'?

It is ironic that W. D. Hamilton, of all people, should be quoted in evidence of the pernicious influence of *The selfish gene*. More than ironic: embarrassing, because the influence is firmly the other way around. Hamilton is repeatedly acknowledged in *The selfish gene* as probably the most seminal inspiration of the book. I not only learned from Hamilton that the best level at which to think about natural selection is the gene. I also learned that this easily misunderstood truth can best be explained using anthropomorphic language (see his forthcoming volume of collected papers).

So, to anthropomorphism itself. I plead guilty to the charge as stated, but vigorously deny that there should be any such charge. On the contrary, anthropomorphism can be very helpful, both in teaching and in thinking, if cautiously used at the proper level. Whether I use it properly and helpfully will be for those that have read my book, at least partially, to say. But I will say that Darwin himself used it to great effect. For example, one of the best loved passages of *The origin* derives its power precisely from a poetic personification of nature,

> '...daily and hourly scrutinising, throughout the world, the slightest variations; rejecting those that are bad, preserving and adding up all that are good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being...'

Admittedly some people were misled. Wallace (1866) himself cautioned Darwin in a letter:

> My dear Darwin, – I have been so repeatedly struck by the utter inability of numbers of intelligent persons to see clearly, or at all, the self-acting and necessary effects of Natural Selection, that I am led to conclude that the term itself, and your mode of illustrating it, however clear and beautiful to many of us, are yet not the best adapted to impress it on the general naturalist public...Now, I think this arises almost entirely from your choice of the term Natural Selection, and so constantly comparing it in its effects to man's selection, and also to your so frequently personifying nature...To the few this is as clear as daylight, and beautifully suggestive, but to many it is evidently a stumbling block.

Wallace went on to recommend Spencer's term 'survival of the fittest' as more objective. Darwin (1866) agreed to adopt this more neutral language although he (rightly) doubted 'whether the use of any term would have made the subject intelligible to some minds.' Little could Wallace or Darwin guess that Spencer's term 'fittest' (to say nothing of its unfortunate political misuse) would later generate far more misunderstanding than Darwin's innocent personification of nature ever could.

Sullivan wisely quotes the late J. S. Kennedy, who has given us the most cogent and well-informed critique of anthropomorphic biology in recent years. We have to take note of what Kennedy says. His book develops the theme of his earlier classic paper, 'Is modern ethology objective?' (Kennedy 1954). Ethology is the tradition in which I was brought up, and the mental discipline of throwing out subjective language was an important part of our training. Ethology developed partly in reaction against subjectivist psychology (Tinbergen 1942). To the question, 'Why did the grasshopper leap?', the ethologist would distinguish at least two legitimate kinds of answer. First, answers of the form, 'Because a puff of air triggered sensory hairs which aroused the central nervous system which released the pent-up energy in stretched elastic in the legs.' Second, answers of the form, 'Because natural selection of the animal's ancestors favoured long leaps out of the way of ancestral predators.' Ethologists reject answers of the form, 'Because the poor creature was scared out of its wits and desperately wanted to get away from danger.' We do permit words like 'fear', 'anger', 'libido' and even 'hope', but only as formally defined 'intervening variables' or 'hypothetical constructs' (McCorquodale & Meehl 1948; Houston *et al.* 1977).

This kind of stringent objectivity, as policed by Kennedy (1954), Tinbergen (1951), Hinde (1970) and all the leading ethologists, is the more important because we do, at times, genuinely need to talk about whether our animals actually have subjective experiences. This is an important possibility to think about, and you cannot sensibly do so unless you are very clear about what you mean and what you do not mean. We take Donald Griffin and Marian Stamp Dawkins seriously when they tentatively discuss subjective experiences in animals, because we know that they have served out their apprenticeships as proper, paid up, objective (and distinguished) ethologists (Griffin 1992; Dawkins 1993). They know what is at stake, and they use their language advisedly and discerningly.

If I had written a book called *The selfish lion*, I would have been asking for trouble. Does it mean that lions really have selfish psyches: really think out consciously self-interested schemes? Or is it just a metaphor? If lions can be selfish, would you say the same of cockroaches? Where do you draw the line? It is for all these sorts of reasons that I would not dream of writing a book called *The selfish lion* unless I really did have a point to make about the subjective intentions of animals. But the selfish gene is another matter entirely. Genes are just DNA; they are dumb molecules. Nobody in their right mind could think that 'selfish', when applied to a molecule, could possibly have any subjective content at all. *The selfish gene*, one would have thought, should be as free from any suspicion of damaging antropomorphism as, say, the 'charm' which physicists attribute to fundamental particles. Apparently I was too sanguine. But only where a tiny minority of naive literalists (I do not say Gradgrindian pedants) is concerned (e.g. Midgley 1979; see reply by Dawkins 1981). The vast majority of readers (those that made it past the title) have taken the phrase selfish gene in the spirit which was intended – and which was carefully explained in the text.

Whenever we are dealing with an optimizing system, or a system that is maximizing some benefit or minimizing some cost, anthropomorphic language is going to be tempting. Control engineers speak of a feedback mechanism as 'hunting wildly' or 'seeking to track a target.' I once heard the late Jacques Monod, at a small conference on creativity in science, confess that he sometimes would tackle a chemical problem by asking: 'If I were a certain kind of atom, what would I do at this point?' Another Nobel prize winner, the physicist Richard Feynman, devoted one of his celebrated lectures to the benefits of treating inanimate nature as anthropomorphically pursuing a Principle of Least Action (Feynman 1964). An equally lucid explainer of physical science, Peter Atkins (1992), when dealing with the bending of light rays by refraction, encourages us to think of light as setting out to minimize the time it takes to travel. He is not the first to use the analogy of a man on the shore seeking to rescue a drowning swimmer:

> Suppose the victim is out to sea, and you are on the shore. What path brings you to him in the shortest time, bearing in mind that you can run faster than you can swim? One possibility is for you to select a geometrically straight path from your deckchair to where he is sinking: that involves a certain amount of running and swimming. Alternatively you could run to a point on the water's edge directly opposite him and swim out straight from there. That is greater in distance but it may be briefer in duration if you can run very much faster than you can swim. By trial and error, or trigonometry, you would find that the path involving the least time is one where you run at some angle across the beach, then change direction and swim at another angle in a straight line towards your target (if it is not too late by now). This is exactly the behaviour of light passing into a denser medium.
>
> But how does light know, apparently in advance, which is the briefest path? And, anyway, why should it care? The only way of discovering the briefest path appears to be to try them all, and then to eliminate all traces of having done so. There must be something about the nature of light which entails that it naturally tries all paths, and then eliminates all but the briefest.

Atkins goes on to explain how the wave nature of light makes it travel as if it deliberately set out to discover the briefest path. The very idea of a system maximizing or minimizing some quantity could affront a terminological purist as anthropomorphic. But it is helpful as a rule of thumb and physicists use it as a matter of course, fully understanding that particles, waves and inanimate objects don't really have aims and intentions.

Turning to biological systems adapted by natural selection, they are clearly maximizing something, but what? Here we have to think very distinctly about which level we are operating at. We can think like physicists or engineers about particular organs or systems. A bone, for example, might be seen as maximizing tensile strength while minimizing cost in calcium. But ultimately, when we speak of the survival of the fittest, what are we talking about? As Hamilton has memorably put it, 'the fittest what?' We have already seen that many biologists, though notably not Darwin himself, wrongly thought of it as the fittest group or the fittest species. This error was more or less unconscious in Konrad Lorenz (1966), and in others such as Julian Huxley, C. D. Darlington, W. C. Allee (quoted in Williams 1966), until V. C. Wynne-Edwards (1963) espoused group selection knowingly and brought it out into the open. This was one of the factors that provoked theorists such as G. C. Williams (1966) Hamilton (1964) and J. Maynard Smith (1964, 1976) into putting together a rigorous reformulation of the level at which natural selection acts. As Sullivan rightly perceives, this reformulation has become the current orthodoxy, an orthodoxy which is, except in certain special senses, hostile to all forms of group selection. *The selfish gene* and, more radically, *The extended phenotype*, pushed this low level neo-Darwinian view of life to its logical conclusion: some might say a little beyond.

None of the authors involved in the reformulation shrinks from anthropomorphic metaphors where these might aid exposition, nor from the sort of competitive, and conflict-laden language deplored by Sullivan. Thus Williams (1966), returning to Darwin's old problem of the evolution of sterility in social insects says: 'Yet I believe that the sterility of the workers is entirely attributable to the unrelenting efforts of Darwin's demon to maximize a mere abstraction, the mean.' Maynard Smith and Hamilton are noted for their vividly helpful, unashamedly anthropomorphic metaphors which, in Hamilton's case, grace his famous titles: 'Geometry for the selfish herd' (Hamilton 1971); 'Gamblers since life began: barnacles, aphids, elms' (Hamilton 1975). Successive generations of population genetics students are bewildered by the neutrally correct and unmemorable term 'linkage disequilibrium' (they confuse it with linkage), at the same time as they warm to and instantly understand, Maynard Smith's term (for a different phenomenon) 'genetic hitch-hiking.' For myself, I could point to the metaphor of the Arms Race as more constructively helpful than the neutral and inoffensive 'coevolution' (Dawkins & Krebs 1979).

But what are the positive benefits of using the language of selfish genes: of pretending to be a gene, and asking yourself what you would do if you were trying to maximize your long-term survival? Selfish gene terminology was introduced as a simple way of explaining to people why the tempting group selection fallacy is wrong. As we have seen, Lucy Sullivan herself is one of these who could benefit from such a simple explanation. The metaphor proved successful as an expository aid but then it turned out, more interestingly, that it could also save professional biologists from more subtle errors that stem from insufficiently clear application of 'individual level' thinking about selection.

Briefly, the history of this terminological minefield is as follows. Darwin, as we have seen, firmly fixated the individual organism as the locus of natural selection's action. When he adopted Spencer's 'survival of the fittest', fittest meant approximately what it says in everyday speech: the fastest, strongest, keenest of eye and sharpest of tooth. Obviously, however, organisms maximize not just their survival but their reproductive success. Survival is but a means to the end of reproduction. If the two conflict, reproduction may take precedence, as in Darwin's theory of sexual selection (Cronin 1991). Twentieth century population geneticists started to use 'fitness' as a technical term to combine both survival and reproductive success. Fitness came to mean 'that which is maximized by natural selection.' A trivial consequence of this is that the original phrase 'survival of the fittest' became a tautology, a point which was not lost on 'Creation Scientists' eager to bamboozle people already confused by a little philosophical learning – amateur philosophers 'educated far beyond their capacity to undertake analytical thought' (Medawar 1982).

More remarkably, the technical definition of individual fitness seems to have confused at least one noted ecologist. A. E. Emerson (quoted in Dawkins 1982) had been reading C. H. Waddington's exposition of the special Darwinian meaning of 'survival': '...survival does not, of course, mean the bodily endurance of a single individual... that individual "survives" best which leaves most offspring.' Emerson comments that: 'Critical data on this contention are difficult to find, and it is likely that much new investigation is needed before the point is either verified or refuted.' Emerson apparently thought that Waddington was alleging a testable correlation between longevity and fecundity. In fact, of course, Waddington was making a definitional point about the technical meaning of fitness (which he called 'survival' with quotation marks). Emerson's confusion deepens when he adds, 'It would be extremely difficult to explain the evolution of the uterus and mammary glands in mammals... as the result of natural selection of the fittest individual.' Emerson goes on to explain the uterus and mammary glands as adaptations to perpetuate the species. As I said above, Lucy Sullivan is in good company.

Emerson was an extreme case, however. Most biologists had no trouble in grasping the basic notion of fitness as capacity to reproduce: although it has been conflated, as Williams (1966) notes, with actual, observed reproductive success. When Hamilton (1964) came along to explain that kin relations other than direct descendants were also relevant, he recognised that biologists were well-disposed to the technical concept of fitness, and he therefore chose to introduce his innovation by devising a minimal bending of the familiar and comfortable notion of fitness. Hamilton's 'inclusive fitness' is a complicated mathematical function which has been much misunderstood and misused, as Alan Grafen (1982, 1991) has shown. It can be informally summarized as 'that quantity which an individual organism will appear to be maximizing when what is really being maximized is gene survival'

(Dawkins 1982). Inclusive fitness was Hamilton's brilliant last-ditch bid to rescue the concept of individual fitness when, in my view, it was already creaking beyond repair. Hamilton would have done better to stick by his alternative, anthropomorphic metaphor of the intelligent gene.

> 'A gene is being favored in natural selection if the aggregate of its replicas forms an increasing fraction of the total gene pool. We are going to be concerned with genes supposed to affect the social behavior of their bearers, so let us try to make the argument more vivid by attributing to the genes, temporarily, intelligence and a certain freedom of choice. Imagine that a gene is considering the problem of increasing the number of its replicas and imagine that it can choose between causing purely self-interested behavior by its bearer A (leading to more reproduction by A) and causing "disinterested" behavior that benefits in some way a relative, B.' (Hamilton 1972, p. 195)

The analogy to the physicist's anthropomorphic light waves should be clear.

Sullivan is shooting at the wrong target. The real problem, as she herself exemplifies, is not anthropomorphism but the level in the hierarchy of life at which we think, whether we think anthropomorphically or not. 'The gene uses individual organisms in order to maximize its own long-term survival in the form of copies' is usually (exceptions arise in cases such as meiotic drive) equivalent to 'Every organism maximizes its inclusive fitness: that is, the long term survival of copies of its genes.' Neither of these correct formulations is equivalent to any version of Sullivan's incorrect belief that the long term survival of the species is what is maximized. All three formulations may be phrased anthropomorphically, in terms of some entity striving to maximize something. Or, if we wish, we can express any of the three of them in a more pernickety, objective manner. I am less bothered about the dangers of anthropomorphism than I am concerned with finding the right level. I wrote *The selfish gene* in the way that I did, because I suspected that a judicious use of anthropomorphic language might actually straighten out people, like Lucy Sullivan, over this important question of the level at which natural selection acts. Her belief in the good of the species (albeit she explicitly shuns anthropomorphism) turns out to be the most truly anthropomorphic of all, for it implies evolutionary foresight: what J. B. S. Haldane dubbed 'Pangloss's theorem.' Sydney Brenner wittily recognized the point when he imagined a Cambrian species conserving a particular molecule because 'It might come in handy in the Cretaceous.'

In Hamilton's own sophisticated and safe hands, the difficult translation from gene level thinking to individual level thinking was accomplished without mishap. But others fell flat on their face. In the course of a somewhat desperate attack upon sociobiology, the highly regarded social anthropologist Marshall Sahlins (1977), for example, wrote the following, in an attempt to be sarcastic about the theory of kin selection:

> 'In passing it needs to be remarked that the epistemological problems presented by a lack of linguistic support for calculating *r*, coefficients of relationship, amount to a serious defect in the theory of kin selection. Fractions are of very rare occurrence in the world's languages, appearing in Indo-European and in the archaic civilisations of the Near and Far East, but they are generally lacking among the so-called primitive peoples. Hunters and gatherers generally do not have counting systems beyond *one*, *two*, and *three*. I refrain from comment on the even greater problem of how animals are supposed to figure out how that r [ego, first cousins] $= \frac{1}{8}$.'

As I unkindly put it when I first exposed this remarkable solecism:

> 'A pity, for Sahlins, that he succumbed to the temptation to 'refrain from comment' on how animals are supposed to 'figure out' *r*. The very absurdity of the idea he tried to ridicule should have set mental alarm bells ringing. A snail shell is an exquisite logarithmic spiral, but where does the snail keep its log tables; how indeed does it read them, since the lens in its eye lacks 'linguistic support' for calculating μ, the coefficient of refraction?' (Dawkins 1979).

Sahlins's trouble is that he was being anthropomorphic at the wrong level: ironically, the human level! If only he had chosen the level of the gene, he would have been spared this extraordinary blunder. The idea of genes maximizing something by conscious calculation has the virtue of being too absurd to be taken literally: it has got to mean something non-literal. Sahlin's fallacy is number 3 of 'Twelve misunderstandings of kin selection' (Dawkins 1979). I will not spell out the details, but others, among the twelve, that can be directly blamed on authors' attempts to think of natural selection as focused on the individual organism rather than the gene are number 5 (Washburn's fallacy), number 7 (the clonal lizard fallacy), number 11 (the ace of spades, or doting grandmother fallacy) and, I regret to say, number 12 (Dawkins's fallacy).

To summarize, there are two equally valid ways of expressing the correct alternative to Sullivan-style, 'good of the species' naiveté: the gene's eye view and the organism's eye view, but the gene's eye view has the advantage of being simpler and less vulnerable to error. Anthropomorphism at the gene level cannot sensibly be taken literally. Moreover, it is positively helpful in understanding, and thinking about, natural selection. The gene's eye view, however, raises interesting problems of its own, and I have made it my business, especially in *The extended phenotype*, to face these problems in detail and sort them out. I have argued that both the gene's eye view and the organism's eye view of selection, and also the species eye view which they replaced, are anthropomorphic personifications, but at different levels. My summing-up defence of *The selfish gene* against Lucy Sullivan's criticism is that she herself might benefit from reading it.

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