Perspectives and Hypotheses

Vol. 9, No.2 (2026)
ISSN: 2532-5876
Open access journal licensed under CC-BY
DOI: 10.13133/2532-5876/19646

A re-look at *The Selfish Gene* after 50 years

Vidyanand Nanjundiah[a*]

[a] *Centre for Human Genetics and International Centre for Theoretical Sciences, Bangalore, India*

***Corresponding author:** Vidyanand Nanjundiah, Email: vidyan@alumni.iisc.ac.in

Abstract

This is an informal account of reflections evoked by being asked about the impression that Richard Dawkins's book *The Selfish Gene* made on me initially when I first read it. The 50th anniversary of the publication of what became an international and much discussed bestseller has reignited comments on it. Overall, they have been extremely laudatory. I have tried to go back to my initial acquaintance with the book to touch on questions that it raised then, and raises now, regarding several interrelated issues. They concern how biological evolution takes place, how meaningful it is to take a gene-centric view of evolution, and how to make sense of the evolution of cooperative social behaviour, in particular seemingly altruistic behaviour. As much as the science, Dawkins's language attracted attention; the metaphors he used were a hit with lay readers. But for good reasons, a number of biologists criticised both. It is evident that his framing of the evolution of cooperation was not nuanced enough.

Keywords: Dawkins, gene-centric, selfish gene, altruism, evolution

Citation: Nanjundiah, V 2026, "A re-look at *The Selfish Gene* after 50 years", *Organisms. Journal of Biological Sciences*, vol. 9, no. 2, pp. 13–21. DOI: 10.13133/2532-5876/19646

1. Background

The news that *The Selfish Gene* (Dawkins, 1976), Richard Dawkins's racy account of how cooperation evolves, is 50 years old, came as the first of three surprises. Memory said I had read it at the urging of my colleague Madhav Gadgil in 1974. A second surprise was that the familiar paperback with Desmond Morris's vaguely menacing cover illustration was missing from my library. Instead, there was a 1978 reprint, and a different, albeit equally unsettling, cover. This one shows a bird holding out a beak full of worms to clamouring chicks; provider and recipients have eyes all over their bodies. In words that sit well with the general tenor of the book, Google's AI overview explains it thus: "The parent bird feeding its chicks is not necessarily acting out of conscious love, but rather, its genes are commanding it to feed the chicks because the chicks carry copies of those same 'selfish' genes." I come to the third surprise later (in "How does *The Selfish Gene* look today?").

The present essay deals with the first, 1976, edition of the book. Being asked how I reacted to it then, made me think about how it was, and could have been, critiqued at the time. Its publication attracted a mix of acclaim and criticism, and that applied to the science as well as the manner in which the science was conveyed. Both opinions were expressed strongly, and it is of interest to enquire why. This is not meant to be a discussion of the evolution of social behaviour, whether from the standpoint of 1976 or 2026. For the reason given, I confine myself to the pre-1976 literature except when the later work throws light on

what was done earlier. Citations to the literature are indicative, not comprehensive, and are merely meant to serve as signposts.

2. The Science

The anthropomorphic overtones of the language in *The Selfish Gene* appealed to many; they made it seem that the science was easy to follow. The notion of genes as master computer programs for building organisms had begun to take hold; 'Selfish gene' raised the question whether genes too had minds of their own, as it were. We begin with a look at the biology behind that belief.

The science in *The Selfish Gene* relates to two issues: whether the gene-centric view of natural selection is appropriate; and whether cooperative behaviour, in particular so-called altruism, requires either kinship or reciprocity in order to evolve. The larger issue, which is unexamined in the book because the answer is taken for granted, is whether natural selection is a near-universal explanation for evolutionary change. According to the Evolutionary or Modern Synthesis, evolution takes place mostly through the route first proposed by Darwin and Wallace, that is, natural selection, buttressed by Mendelian genetics, the laws of chance (whose importance rises in small populations) and migration. With natural selection accorded primacy, that appears to be Dawkins's view, as indeed it is of most biologists.

But the explanatory sufficiency of natural selection—and the Modern Synthesis—has been questioned in interesting ways ever since the days of Darwin and Wallace. So has its necessity. In both cases the questioning has been on varied grounds. See for example (Berg, 1926; Müller, 2017), one old, one recent. However, in order to stay focussed on the essentials, I take it for granted here that the Modern Synthesis is a sufficient explanation for evolution, and confine myself to commenting on the gene's-eye angle, because it reveals the sense in which Dawkins attributes selfishness to genes—whether he was right or wrong to use such a word, is something else (see 'The Language'). Also, so as to keep things simple, and unless the context demands otherwise, throughout this essay I gloss over distinctions between the word pairs gene-DNA, gene-allele, and organism-individual.

We can interpret the adjective 'selfish' in four ways. They rest on two starting points: on the whole, evolution takes place through natural selection via the differential reproduction of individuals, and hereditary traits that impinge on reproduction are correlated with the individual's genetic constitution. In order, the interpretations involve (a) a shift of perspective, which manifestly makes 'selfish' a modifier of 'gene'; (b) the belief that natural selection is best understood as acting at the level of the gene; (c) directing attention to the participation of genes in processes that further their own reproduction but do not affect the reproduction of the organism in which they reside; and (d) explaining seemingly altruistic behaviour as a consequence of shared genes among relatives. Taken together, the steps (a) to (d) that follow indicate a plausible route for arriving at Dawkins's use of 'selfish' in *The Selfish Gene*. The upshot is that if a gene-centred view of evolution is thought through, an explanation of 'selfish' follows (though that does not automatically justify using the word).

(a). An altered perspective suggests an interpretation of 'selfish gene'. If a behaviour has evolved by natural selection, its performance must be in the individual's self-interest; ergo, it can be termed selfish. This is epitomised in two quotes by famous sportsmen. One is by Paavo Nurmi, the athlete: "No, I ran for myself, not Finland" (Whitman, 1973). The other, by the cricketer Kapil Dev, goes "If somebody says, I played for the nation, no, first I played for myself" (The Hindu, 2026). It is worth remarking that E. O. Wilson made use of the first quote in a chapter titled "Group selection and altruism" (Wilson, 1975; he called Nurmi the ultimate individual selectionist).

By that reasoning, can a trait such as the ability of the eye to sense light, which has also evolved because it is in the individual's self-interest, be thought of likewise, as reflecting a selfish tendency? On the part of whom? It feels strange to think of a physical or mental trait as one would a behavioural act. If forced, one might concede that the trait could be said to reflect a form of selfishness on the part of the genes involved in its expression; in the present instance, the genes that encode photoreceptor proteins (besides others). Why not apply similar reasoning to all genes in an individual? Seen thus, every gene that is a result of natural selection is, in a trivial sense, a selfish gene. As we will see in section (b), that fits well with the view that a life cycle marks the passage of genes from one generation to the next.

Trivial or not, to say that every gene is selfish demands a shift in perspective. Conventionally, natural

selection is thought to be manifested by the differential reproduction of *organisms*; and the word organism stands for an adult, or a characteristic stage through which an embryo passes on its way to adulthood. The construction of normal tables of development, as exemplified by the terms blastula, gastrula, neurula, etc., testifies to that. Properly speaking, though, the organism extends continuously across time; the mental image we have is only a 'frozen snapshot'—or set of snapshots—from the entire life cycle (Bonner, 1965). By saying life cycle, we tacitly acknowledge that what we think of as an organism is a small part of a continuous process in the course of which one generation follows another. In a sexually reproducing species, the passage from one life cycle to the next involves fertilisation, embryonic development, the attainment of reproductive maturity, and the onset of the next generation (unless death intervenes before reproduction, in which case the cycle ends there).

Conventionally, a life cycle begins with fertilisation and finishes with the production of gametes (accompanied by a random shuffling of alleles on the two chromosomes and allelic combinations on the same chromosome), and the reproductively mature adult holds centre stage. It makes no difference if, instead, a life cycle is reckoned from the pre-reproductive adults of one generation to adulthood in the next generation, and focus of attention is directed at gametes. To complete the circuit, one can start from gametes or adults. To paraphrase Dawkins, a life cycle can be seen either in terms of organisms transiting across generations by using genes as their vehicles, or genes transiting across generations by using organisms as their vehicles. The difference is that the organism does not retain its identity across generations, whereas, in a sense, the gene does. Subject to that qualification, the two standpoints are equivalent. That said, depending on the situation, one may be more insightful than the other.

For instance, as the aptly-named *grandchildless (gs)* gene of *Drosophila subobscura* shows, counting children is not always the correct way to measure reproductive success. It may be necessary to count grandchildren, which seems strange at first. The reason is that for a life cycle to be completed, it is not enough for the embryo to develop to adulthood, mate, and produce ostensibly normal offspring. In addition to all that, the offspring must also be fertile; gametes must succeed in finding partners (Spurway, 1948).

There are other subtleties. Children born to *gs/gs* females are infertile because, as embryos, they were unable to form primordial gametes. *grandchildless* and other such 'maternal effect' mutations raise the intriguing possibility that a mutation might affect the reproductive success of a descendant two or more generations down the line, but not before that.

The converse viewpoint, which focusses on the organism, not its genes, is common. Even then, genes remain central. For example, large body size helps animals in defence against predators. Environmental factors as well as genetic makeup impact adult size. Directly or indirectly, genes that influence size can interact with other genes that affect diverse traits, which means the notion of 'genes for traits' is untenable. Yet, the relevant gene frequencies can be moulded by natural selection (more on that below). So a gene whose action promotes growth on the average, spreads in the population: on either viewpoint, one can justify the use of 'selfish' on the grounds that the life cycle, which is the right way to think of an organism, can be seen as a gene-generation cycle.

(b). The altered perspective also leads to a gene-centric view of natural selection. To hold that the two ways of looking at life cycles are equivalent, could also be taken as implying that the differential reproduction of individuals amounts to the differential reproduction of alleles. The assumption is that after averaging over all environments encountered by the species, each allele makes its own, quantifiable, contribution to the survival and reproduction of the organism. It implies that the interaction between genes and the environment is additive and separable into distinct gene-by-gene components. To stretch a point, it means thinking of organisms "as" the genes in them, or to think of the genome as an implicit representation the organism (in the way a 3-base stretch of DNA that codes for an amino acid is an implicit representation of the amino acid). If correct, it means that the genetic makeup of an organism fully decides its life cycle. The properties of chromosomes, organelles, cells and tissues that are not genetically specified, cannot act as independent inputs into deciding evolutionary success. That conclusion is a corollary of a gene-centred neo-Darwinian or Modern Synthesis. It has perennially been questioned. I. I. Schmalhausen (1946) and C. H. Waddington (1953) are often cited in this regard, but the questioning goes back to the early years of the 20th century (Nanjundiah, Geeta

& Suslov, 2026; Thompson, 1942 [1917]). The .concept of genes as implicit representations of organisms does not hold good in other situations too. It fails when genes and environments interact inextricably, as they do when traits involve inter-individual interactions (as many behavioural traits do), and when a phenotypic change that is initially driven by the environment, subsequently becomes assimilated, as it were, into the genome (Nanjundiah, 2020; Woltereck, 1909).

All the same, focussing on genes one at a time might be rationalised as a pragmatic way of dealing with messy reality. As such, it was used successfully in the early 20th century to construct mathematically tractable models for the tempo and mode of evolution (the title of a landmark book; Simpson, 1944), and how population effects can modify the process. Those models, to which R. A. Fisher was a prominent contributor, form the bedrock of the Modern Synthesis (Fisher, 1918). Dawkins's attitude to evolution is uncompromisingly Fisherian; indeed, he calls Fisher the greatest biologist of the 20th century. The models of classical population genetics were not praised by everyone, not even all selectionists. In a derisive description, Ernst Mayr (1959) said that measuring evolutionary change by counting genes was to pretend that they were like separate beans in a bag (he elicited a spirited response from J B S Haldane, 1964). Fisher handled gene-gene interactions and gene-environment correlations by taking the average effect of each allele in all possible genotypes and environments. The assumptions were that primary genetic change determines phenotypic change through miniscule additive steps, and that evolutionary change via natural selection involves large populations, free mating, and long times. If those assumptions, and the further assumption that environmental effects can be factored out, hold good, the gene-centric view of natural selection is worth taking as a useful first approximation.

(c). The view of genes as autonomous entities strengthens the gene-centric view. In certain conditions, genes appear to exhibit autonomous behaviour, independently of the organisms that house them. The well-known nomenclature of jumping genes, as applied to mobile genetic elements, carries the suggestion of autonomy (McClintock, 1950). It was taken as support for the widely held though mistaken belief that DNA can copy itself, all on its own. The error lies in thinking that the requirements for the replication of DNA can be reduced to a physically permissible environment and molecular building blocks (which can lead to the error of conflating the problems of the origin of life and the origin of the first DNA molecule). From there, it is easy to persuade oneself that genes or DNA qualify for the label 'selfish' in the same sense that individual organisms do.

But there is evidence for gene-level autonomy in a certain sense. Gershenson (1928) found an X-chromosome in *Drosophila obscura* that, during male meiosis, is transmitted preferentially vis-à-vis its Y counterpart. Such a violation of the fair meiotic lottery mandated by Mendel's law can be interpreted as self-favouring behaviour. The males in question mostly, and sometimes only, sire daughters. In wild populations, the trait co-exists with normal meiosis, indicating a balanced outcome on account of selection against the trait at the organismal level (Fisher, 1930). The earliest unambiguous recognition of what may be labelled selfish behaviour by genetic material is in a publication by Östergren (1945), which also happens to be an excellent example of theoretical biology without mathematics. He pointed to the redundant B chromosomes, found in several plant species, that spread both within a plant and between plants (that is, within the species), and concluded that natural selection on the host plant was unlikely to be involved initially. However, as their spread was also deleterious to the host, they reached a stable frequency. Östergren's summary of B chromosome behaviour is worth quoting: "…it is not necessary that they are useful for the plants. They need only be «useful» to themselves".

The same thing can be said of restriction-modification DNA elements found in bacteria and eukaryotes. Many functional roles have been proposed for them, but the point to grasp is that they need not have any 'function' besides the ability to hitch-hike on a host so as to ensure their own propagation. Various adaptations can favour that, one of them being that living without them can be lethal for the host. Aptly, they have been termed addiction modules (Naito, Kusano & Kobayashi, 1995). In the spirit of *The Selfish Gene*, one might say such genes run a protection racket. Once the process of parasitising gets going, the operation of natural selection on the host can, post facto, endow a hitherto purely selfish element with one or more functions: parasitism can transition smoothly into symbiosis.

(d). The gene-centric, 'selfish gene' view offers one explanation for altruistic behaviour. In numerous

cases of group living, individual members of the group display traits that are, at first glance, paradoxical: the traits reduce the individual's chances of reproduction relative to that of another individual. The obligate sterility of social insect workers is a much-cited example. It would seem that such traits could never evolve by natural selection. Wisely, Darwin, who discusses the puzzle extensively, restricts himself only to saying that if there is a comparable situation among individuals of different species, "it would annihilate my theory" (Darwin, 1859, chap. VI, "What natural selection can do", p. 301). At the same time, he proposes several solutions to the corresponding problem within species. Among them is something long known to breeders: when two individuals are related, selection can operate on one them via the reproduction of the other. The outcome can be reproductive asymmetry; it may even happen that the unsuccessful member—the seeming altruist—does not reproduce at all. For instance, in order to improve milk yield, a dairy farmer crosses a cow that produces milk in abundance with a bull whose mother or sister is a good producer too. Darwin makes the same point pithily: "…a well-flavoured vegetable is cooked, and the individual is destroyed; but the horticulturist sows seeds of the same stock, and confidently expects to get nearly the same variety" (Darwin, 1859, chap. VII, "Instinct", pp. 237–238). As both examples show, the relationship between actor and beneficiary has to be via recent common descent. If a gene whose effect is to favour self-sacrificing behaviour is present in everyone, there is no sense in which the trait, or it, can spread. On the contrary, it is easy to see that then, 'selfish' behaviour is likely to be favoured by natural selection.

The best understood explanation of how indirect selection works, is through a gene-centred view. It is encapsulated in the concept of inclusive fitness, which temporarily blurs the distinction between individuals (Hamilton, 1964). According to it, one must count all replicas of a shared gene that is correlated with a trait, not just those that are passed on by direct reproduction. Known as kin selection (Maynard Smith, 1964), this is the explanation most often cited for 'altruistic' behaviour in groups. The upshot is that altruist's reproductive success is lowered but that of the gene correlated with altruistic behaviour is enhanced: what looks like individual altruism is a mask for genetic selfishness. Fisher (1930) had put forward the same hypothesis for explaining the evolution of distastefulness in insect larvae, when distastefulness is signalled by odour or colour or body pattern. The first distasteful larva to be eaten would not benefit, obviously. But its siblings would gain protection from the sacrifice, because the predator would learn from the signal and avoid repeating the mistake. Fisher also pointed out that the idea could be put quantitatively by paying attention to the proportion of shared genes, a concept Haldane (1955) conveyed in a throwaway line quoted by Maynard Smith: "I would lay down my life for two brothers or eight cousins". The detailed theory was fleshed out by (Hamilton, 1964).

Dawkins also cites symbiosis and reciprocal altruism as possible explanations for individual altruism; neither of them requires kinship. Symbiosis can evolve from parasitism, as we have seen before. In reciprocal altruism, an altruistic act is repaid, conceivably on a later occasion (Trivers, 1971). The fact that it is repaid, means that here too the impression of altruism is mistaken, and reflects ignorance of subsequent interactions.

Summary of points (a) to (d). Dawkins states that much of the time, so-called altruistic behaviour is perfectly in accord with natural selection, but appears altruistic because we are not scrupulous in maintaining the focus on genes. That can happen either because of ignoring indirect inheritance and shared genes, or by overlooking behavioural reciprocity between unrelated individuals (reciprocal or indirect altruism too is supposed to have a genetic basis, but not necessarily based on genes shared via kinship). The last statement comes along with a rider: altruistic behaviour cannot evolve simply by virtue of its being 'for the good of the group'.

3. Omissions

Under the theme "Toleration and cooperation in the absence of kinship" Hamilton (1972) had pointed out that apparently altruistic behaviour can evolve in the absence of either kinship or reciprocity, and cited examples from the cellular slime moulds and other organisms. As possible explanations he brought up likely advantages related to outbreeding, dispersal, and symbiosis (and also cited cases that were difficult to explain). Dawkins acknowledges that symbiotic associations exist and mentions reciprocal altruism, but ignores other possibilities. After drawing attention to the fact that there are serious objections to treating groups as units of selection, he does not ask whether the difficulties can be overcome. Instead, he rejects

it out of hand. Basically, that is on account of his unwillingness to consider alternatives to the gene-and-individual-centred picture of natural selection, to ask what conditions might permit 'the good of the group' to prevail over 'the good of the individual'. Many years before, Haldane and Wright had developed models for group selection (Haldane, 1932; Wright, 1945). Though differing in some respects, both considered a population broken up into groups in which altruists and non-altruists are mixed. Even though the proportion of altruists within any one group always decreases (almost by definition), their presence boosts group growth substantially. So much so, that in the population as a whole, they increase in frequency. In a sense, the genetic makeup of an altruist results in a 'public good'. Dawkins does not mention it. An experimental situation involving bacteria demonstrated later that the scheme worked (Chuang, Rivoire & Leibler, 2009). R. C. Lewontin's celebrated paper "The Units of Selection" (1970), which presents evidence of selection acting simultaneously at the level of the gene, the individual and the group, is not cited either. And while commenting unfavourably on Zahavi's Handicap Principle (Zahavi, 1975), Dawkins does not see that the handicap has to do with a phenotype, and therefore cannot be passed on as such. The same mistake was made by others. However, the Handicap Principle has lately been contested on the grounds of a supposed difference between the original principle and a condition-dependent handicap, though the significance of that is not immediately obvious (Penn & Számadó, 2020).

4. The Language

As much as the science, the language used in *The Selfish Gene* was criticised, and understandably so. Words used to characterise human behaviour carry risks when used to describe the actions of other animals, no matter if they are used metaphorically. Dealing with non-living entities does not eliminate risks.

As suggested, the use of 'selfish' may have been partly an attempt to dramatize the gene-centric picture of evolution. Dawkins carried on in the same style by coming up with other metaphors. They appeared to be useful if exaggerated then, but come across as grossly misleading now, sometimes unintentionally funny. Consider the phrases "a selfish machine, programmed to do what is best for his genes", or "We are survival machines—robot vehicles blindly programmed to preserve the selfish molecules known as genes", used to describe organisms. The words "savage competition, ruthless exploitation and deceit" on the blurb fall in the same category (Dawkins acknowledged having gone overboard in subsequent editions of *The Selfish Gene*, and toned down the rhetoric). The upshot was mixed. The language delighted a fair proportion of non-biologists, science writers, and, by all accounts almost universally, general readers. They admired the vivid imagery, as well as the clarity with which Dawkins explained concepts. The thought of genes as agents that acted for their own benefit, and dragged organisms along with them, in a manner of speaking, struck a chord. It seemed no more outlandish than other esoteric scientific constructs, such as the curvature of space or elasticity of time. Despite coming equipped with a more sophisticated appreciation of the role of genes in heredity and evolution, many biologists felt similarly.

On the other hand, organismal and evolutionary biologists, especially those who worked with animals in the field, pulled him up for two faults. First, there was his associating the word selfishness with molecules of DNA, which seemed absurd (to be accurate, even though DNA was meant, Dawkins only used "selfish gene". "Selfish DNA" came shortly afterwards; Orgel & Crick, 1980). Besides, there was the laughable suggestion that genes as such could direct people's fates; agency no longer resided in men and women (or to their parallels among bees, birds, and seals), but in the genes that they carried. Some thought the vocabulary, combined with the attempt to over¬simplify complex phenomena, reflected wilful neglect of what was really going on. My friend Deepak Dhar thinks Dawkins was being intentionally provocative, and suggests why by quoting his friend Per Bak: "Half-truths are better than full truths, just as half bricks are better to throw than full bricks: they go farther".

5. How Does *The Selfish Gene* look today?

How does *The Selfish Gene* stand up in 2026? That brings me to the last of the three surprises mentioned at the start. The book has aged. Not that the message has exceeded its expiry date, if it had one. Natural selection, working through systematic changes in the genetic makeup of populations, still dominates our

understanding of adaptive evolution; and through the route of kin selection, it remains an attractive explanation for the evolution of cooperation. The ideas fleshed out in *The Selfish Gene* are mainly those of Darwin himself, R. A. Fisher, J.B.S. Haldane, G. C. Williams, W. D. Hamilton and R. Trivers. S. Wright and S. S. Chetverikov are not named, and in what has become standard practice, the discovery of natural selection is attributed to Darwin; Wallace's name is omitted (Lloyd, Wimpenny & Venables, 2010). As we have seen in the way he handles kin and group selection, their presentation is mixed. More than that, the style, which struck me as daring and exciting then, feels wordy and laboured now. It could be that my response to popular science writing is less tolerant than it was 50 years ago. Be that as it may, it is clear that the book's stand on the level at which natural selection operates, poses problems. To an extent my disquiet may be unfair, and I may be faulting Dawkins for not having anticipated major contributions to how we see evolution 50 years down the line. However, as discussed, there is more to it; people had pointed out missteps at the time.

For students of evolution as for others, the book continues to be an entertaining, highly readable, occasionally gripping, account of the essence of Fisher's mathematical explanation for adaptive evolution: namely, that evolution takes place as a consequence of natural selection between individuals whose traits differ, at least in part, because of the additive effect of alleles at several genetic loci. Today, one has a more expansive view of evolution, with important roles assigned to factors besides open-ended natural selection–to the physical properties of living matter, demography, pre-adaptations, self-organisation, stochastic effects, and the environment, to name a few. Ignoring them, and especially ignoring the possibility that 'altruism' may have varied explanations, detracts from the value of the book. I have been teaching the subject of evolution for a great many years, and invariably recommend *The Selfish Gene* as background reading to students. I add that in terms of literary quality and scientific depth, it falls short of two other works by Dawkins: *The Blind Watchmaker* (in respect of the writing and science) and *The Extended Phenotype* (which for me is his best for the science). At the same time, I draw attention to its shortcomings and emphasise that it is a polemical book, very much a book of advocacy. The science as well as the language lend themselves to misuse. Pushed to its extreme (always a temptation), a genetic explanation for cooperation underestimates the role of individual agency—in humans for sure, and additionally in other animals that exhibit traits such as mutual recognition, intentionality, learning and memory (Griffin, 2001).

Implicitly, it devalues the role of culture in social behaviour. I use "culture" in a broad sense, to stand for the same thing as in sociology: the way of life of a group. But here, the definition extends to cover groups of humans as well as non-humans. Gierer has a fascinating essay on how biological evolution can act together with socio-cultural factors to result in cooperation. He traces the antecedents of the hypothesis to the 14th century Arab scholar Ibn Khaldun (Gierer, 2001). For humans, laying excessive stress on the genetic underpinnings of selfishness and the favouring of relatives, e.g. nepotism, endows those traits with an aura of inevitability, and makes it easier to normalize them. With non-humans, there is the risk of closing the mind to alternative hypotheses, on top of unquestioningly accepting the dogma that all living organisms except humans are 'mindless' (Fisher, 1930). It is often asserted that the results of scientific investigation are objectively true and value-free, but the claim needs constant examining. One should anticipate consequences in the age of artificial intelligence and robotics. Boles illustrates how the mathematics behind a class of individual-based models for cooperation can be used, indeed may have been used already, for manipulating behaviour by tugging on psychological ropes from the outside (Boles, 2026).

The use of everyday words in a restricted and specialised sense can be risky. Sometimes a word can convey a wrong impression, as when an electron is said to possess 'spin'. The word calls to mind the image of a spinning top; the mistake is unfortunate, but one learns soon. Elsewhere it can be amusing, as when the behaviour of an amoeba is described as noble. When a word is commonly used in one context, and its use becomes popular in another context where it is interpreted wrongly, and the meaning becomes entrenched, it points to a failure of communication. In the present context, words such as selfish and altruistic are taken from human behaviour, and they are used loosely as descriptions of individuals. When applied to other animals, it tends to be forgotten that – like humans–their behaviour too is strongly influenced by contingencies. A 'cheater' in one context can be a 'cooperator' in another. More, without specifying the

context, it does not make sense to think that a gene, or set of genes, can predispose an organism to behave in a selfish or altruistic manner. That point is lost when the words are used without qualifying their limitations. With organisms that have nervous systems, there is the further danger that such words can be assumed to reflect (supposed) psychological states, whether or not that is the intention of the user. 'Selfish' and 'altruistic' had been employed by G. C. Williams, W. D. Hamilton, E. O. Wilson, and possibly others before them, as descriptors for traits that respectively would, or would not, be favoured by natural selection acting at the individual level; Wilson had already begun running into trouble on that account. Coined by Dawkins, the expression 'selfish gene' might have remained harmless if everyone had used it in a narrow technical sense and kept in mind that it was only a metaphor. What ensued was foreseeable. Understandably, many took 'selfish' and 'altruistic' as an implicit acknowledgement of genes as agents that made their carriers selfish or altruistic. That happened even though Dawkins had been careful to say that he was using them in a behavioural, not subjective, sense, and was 'not concerned here with the psychology of motives'. It led to needless acrimony. *The Selfish Gene* is a good example of the havoc that words can cause when used without reflecting on how they might be interpreted. Dawkins coined another word, meme, to stand for a unit of imitation. With that he was more fortunate. The signifier merged with what it signified, and the word took off as a self-referential term that carved out a life all its own.

Acknowledgements

I thank András Páldi for inviting this submission, Deepak Dhar and Subhash Lakhotia for their comments on an earlier version, which helped me to clarify my thoughts, and Stuart Newman for directing me to Boles's analysis.

References

Berg, LS 1926, *Nomogenesis: Or, Evolution Determined by Law* (JN Rostovtsov, Trans., DW Thompson, Intro.). Constable & Co., London.

Boles D 2026, "The cooperator's dilemma: How Martin Nowak's mathematics of kindness became a blueprint for control", *Bolesblogs*. https://bolesblogs.com/2026/03/06/the-cooperators-dilemma-how-martin-nowaks-mathematics-of-kindness-became-a-blueprint-for-control/

Bonner JT 1965, *Size and Cycle: An Essay on the Structure of Biology*, Princeton University Press, Princeton, NJ.

Chuang JS, Rivoire O & Leibler S 2009, "Simpson's paradox in a synthetic microbial system", *Science*, vol. 323, no. 5911, pp. 272-275.

Darwin, CR 1859, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, John Murray, London.

Dawkins, R 1976, *The Selfish Gene*, Oxford University Press, Oxford.

Fisher, RA 1918, "The correlation between relatives on the supposition of Mendelian inheritance", *Transactions of the Royal Society of Edinburgh*, vol. 52, no. 3, pp. 399–433.

Fisher, RA 1930, *The Genetical Theory of Natural Selection*, Clarendon Press, Oxford.

Gershenson S 1928, "A new sex-ratio abnormality in Drosophila obscura", *Genetics*, vol. 13, pp. 488–507.

Gierer, A 2001, "Ibn Khaldun on solidarity ("Asabiyah")—Modern science on cooperativeness and empathy: A comparison", *Philosophia Naturalis*, vol. 38, no. 2, pp. 91–104.

Griffin DR 2001, *Animal Minds: Beyond Cognition to Consciousness*, University of Chicago Press, Chicago (2nd edition).

Haldane, JBS 1932, *The Causes of Evolution*, Green and Co., Longmans.

Haldane, JBS 1955, "Population genetics", *New Biology*, vol. 18, pp. 34–51.

Haldane, JBS 1964, "A defense of beanbag genetics", *Perspectives in Biology and Medicine*, vol. 7, pp. 343–359.

Hamilton, WD 1964, "The genetical evolution of social behaviour. I", *Journal of Theoretical Biology*, vol. 7, no. 2, pp. 1–16. https://doi.org/10.1016/0022-5193(64)90038-4

Hamilton, WD 1972, "Altruism and related phenomena, mainly in social insects", *Annual Review of Ecology and Systematics*, vol. 3, pp. 193–232.

Lewontin, RC 1970, "The units of selection", *Annual Review of Ecology and Systematics*, vol. 1, pp. 1–18.

Lloyd D, Wimpenny J & Venables A 2010, "Alfred Russel Wallace deserves better", *Journal of Biosciences*, vol. 35, no. 4, pp. 339–349.

McClintock, B 1950, "The origin and behavior of mutable loci in maize", *Proceedings of the National Academy of Sciences of the United States of America*, vol. 36, no. 9, pp. 344–355.

Maynard Smith, J 1964, "Group selection and kin selection", *Nature*, vol. 201, no. 4924, pp. 1145–1147.

Mayr, E 1959, "Where are we?". In: *Genetics and Twentieth Century Darwinism. Cold Spring Harbour Symposium on Quantitative Biology*, vol. 24, pp. 1–14.

Müller, GB 2017, "Why an extended evolutionary synthesis is necessary", *Interface Focus*, vol. 7, no. 6, art. 20170015.

Naito, T, Kusano, K & Kobayashi, I 1995, "Selfish behavior of restriction-modification systems", *Science*, vol. 267, pp. 897–899.

Nanjundiah, V 2020, "Early thoughts on phenotypic plasticity in development and evolution", in: H Levine, MK Jolly, P Kulkarni & V Nanjundiah (eds.) *Phenotypic Switching: Implications in Biology and Medicine*, Academic Press, London, pp. xxi-xxxix.

Nanjundiah, V, Geeta, R & Suslov, VV 2026, "A historical perspective on Vavilov's Law of homologous series", *Biological Theory* [submitted].

Orgel, L & Crick, F 1980, "Selfish DNA: the ultimate parasite", *Nature*, vol. 284, pp. 604–607.

Östergren G 1945, "Parasitic nature of extra fragment chromosomes", *Botaniska Notiser*, vol. 2, pp. 157–163.

Penn, DJ & Számadó, S 2020, "The Handicap Principle: How an erroneous hypothesis became a scientific principle", *Biological Reviews*, vol. 95, pp. 267–290.

Schmalhausen, II 1946, *Factors of Evolution*. Trans. I Dordick, ed. Theodosius Dobzhansky, Blakkiston, Philadelphia.

Simpson, GG 1944, *Tempo and Mode in Evolution*, Columbia University Press, New York.

Spurway, H 1948, "Genetics and cytology of Drosophila subobscura. IV. An extreme example of delay in gene action, causing sterility", *Journal of Genetics*, vol. 49, no. 3, pp. 126–140.

The Hindu 2026, "When you're dishonest to yourself, you are not going to achieve in this world: Kapil", *The Hindu*, 28 May. https://www.thehindu.com/sport/cricket/when-youre-dishonest-to-yourself-you-are-not-going-to-achieve-in-this-world-kapil/article71034720.ece

Thompson, DW 1942 [1917], *On Growth and Form* (2nd and 1st editions). Cambridge: Cambridge University Press.

Trivers, RL 1971, "The evolution of reciprocal altruism", *The Quarterly Review of Biology*, vol. 46, no. 2, pp. 35–57.

Waddington, CH 1953, "Epigenetics and evolution". In: *Symposia of the Society for Experimental Biology*, Cambridge University Press, Cambridge, vol. 7, pp. 186–199.

Whitman, A 1973, "Nurmi, star runner of the '20s, dies", *The New York Times*, 3 October, p. 1. https://www.nytimes.com/1973/10/03/archives/nurmi-star-runner-of-the-20s-dies-set-scores-of-records-paavo-nurmi.html

Wilson, EO 1975, *Sociobiology: The New Synthesis*, Belknap Press of Harvard University Press, Harvard.

Woltereck, R 1909, "Weitere experimentelle Untersuchungen über Artveränderung, speziel über das Wesen quantitativer Artunterschiede bei Daphniden", *Verhandlungen der deutschen zoologischen Gesellschaft*, vol. 19, pp. 110–173.

Wright, S 1945, "Tempo and mode in evolution, a critical review", *Ecology*, vol. 26, pp. 415–419.

Zahavi, A 1975, "Mate selection—A selection for a handicap", *Journal of Theoretical Biology*, vol. 53, no. 2, pp. 205–214.