**Title page**

**Title**: Did Dawkins Recant His Selfish Gene Argument against Group Selection?

**Short title:** Did Richard Dawkins Recant?

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**Did Dawkins Recant His Selfish Gene Argument against Group Selection?**

**Abstract**

In 2007, David S. Wilson and Edward O. Wilson [27] pointed out that, by 1982, Richard Daw-kins had admitted that, contrary to what he had claimed in his book *The Selfish Gene* (1976) [7], the idea that only the gene is a fundamental unit of selection could not be used as an argu-ment against the notion of group selection. This elicited a sharp denial from Dawkins [30], which was followed by an explanatory reply by Wilson and Wilson [33] and another vehement denial by Dawkins [34]. I analyse the prehistory of this surprisingly complex and convoluted dispute and subsequently disentangle it. My conclusion is that much of it is based on a series of misunderstandings. First, Wilson’s and Wilson’s [27] original interpretation of Dawkins’ sel-fish gene argument was incorrect. Second, in their explanatory reply [33], they distinguished between two kinds of group selection: the idea that groups can be units of selection (theoretical group selection) and the idea that group selection plays a functional role in evolution (functional group selection). They clarified that their claim concerned theoretical group selection, not func-tional group selection. Third, that clarified claim was correct and not correct. It was incorrect because Dawkins has never explicitly acknowledged that he had erred by developing his selfish gene theory as an implicit argument against this kind of group selection. However, the distinc-tion that he made, by 1978, between two kinds of unit of selection, replicators (genes) and vehi-cles (somas), does imply such an acknowledgment since it holds that groups can be units of se-lection (vehicles). In this important sense, Wilson’s and Wilson’s clarified claim [33] was cor-rect. Fourth, Dawkins’ second denial [34] concerned functional group selection, not theoretical group selection.

**1. Introduction**

Science may be a social endeavour, and very much dependent on constructive and collaborative interactions between scientists, but it cannot be denied that antagonistic or even hostile interac-tions also form an important part of the scientific modus operandi. The long-drawn-out dispute between Richard Dawkins and Stephen Jay Gould is a good case in point, as is the new Dawkins feud that started, a few years after Gould passed away in 2002. However, whereas the former debate has been well documented [1], the latter debate remains, to the present day, uncharted territory. In what follows, I will focus on its long prehistory and on the 2007 incident that started it and that revolved around the question whether Dawkins ever recanted his (implicit) selfish gene argument against group selection.

**2. A long prehistory**

Dawkins’ new antagonist, the American entomologist Edward O. Wilson, is himself no strang-er to controversy as he was the central figure in the dispute that erupted after the publication of his *Sociobiology: The New Synthesis* (1975) [2].[[1]](#footnote-1) Ironically, Dawkins and Wilson were allies in that vicious debate. Or should I say forced allies? There certainly always has been a whiff of animosity between the two public fathers of the modern evolutionary study of social behaviour (i.e., sociobiology).[[2]](#footnote-2) It all started innocently enough when, in March 1976, the success of *So-ciobiology* forced Dawkins to change the publication date of *The Selfish Gene* [7]: he was “wor-ried that the question of the social behavior of animals was going to take on ‘bandwagon pro-portions’ and that the proposed spring [1977] publication date [for *The Selfish Gene*] would be too late for [his] book to make the maximum impact.”[[3]](#footnote-3) A few days later, he decided to publish with Oxford University Press, which, from its side, committed itself to publishing his book in a record six months (October 28, 1976).[[4]](#footnote-4)

As it turned out, his worries were unfounded: the sociobiology controversy was still very much raging in 1977. In August of that year, ‘Sociobiology, A New Theory of Behavior’ was even the cover story of *Time Magazine*. *Sociobiology* remained the focal point of the contro-versy but Wilson’s book was nevertheless, in an important way, overshadowed by *The Selfish Gene*: many of Dawkins’ colleagues, including, to his delight, his “intellectual hero” Bill Ha-milton, found his book a better synopsis of the new field than *Sociobiology*.[[5]](#footnote-5) Segerstråle [10] put it as follows: “The core of sociobiology (as we now know it) was articulated in *The Selfish Gene* rather than in Wilson’s *Sociobiology*. Wilson’s book was called ‘the new synthesis,’ but for practicing sociobiologists, the ideas presented in Dawkins’ book became the synthesis-in-use. And the concept that helped delineate and solidify the new sociobiological paradigm was the gene’s eye view” (p. 91).

*Sociobiology* not only forced Dawkins to change the timing of the publication of *The Selfish Gene*, though. He also had trouble accepting that Wilson had given the new science its name. In his eyes, it was the branch of ethology, inspired by Bill Hamilton and particularly by his novel explanation of altruism, kin selection, or, as the latter called it himself, inclusive fitness.[[6]](#footnote-6) In 1977, at the plenary session ‘Sociobiology’ of the 15th International Ethological Conference in Bielefeld, Germany, he [11] spoke of the “irritating pretensions” (p. 61) of Wilson’s term ‘sociobiology’, adding: “but we shall probably have to learn to live with it” (ibid.). Seven years later, he even embraced it when he decided to stand up and be counted as a ‘sociobiologist’ in his review [12] of *Not in Our Genes: Biology, Ideology and Human Nature* (1984) [13], a book by evolutionary geneticist Richard C. Lewontin, neurobiologist Steven P. Rose and psycholo-gist Leon J. Kamin that severely criticized sociobiology.

Dawkins has also always been very touchy at the suggestion that he has been influenced by Wilson. Or, as he [14] put it himself: “my hackles have always risen at the entirely false sug-gestion that [Wilson’s] book influenced mine” (p. 328). *The Selfish Gene* was instead, not sur-prisingly, very much influenced by Hamilton’s theory of inclusive fitness and also by a deep aversion for the traditional explanation of altruism, group selection (see below). The former theory implies that altruistic animals act for the good of genes, which they share with relatives, whereas group selection assumes that they act for the ‘good of the group or species’.[[7]](#footnote-7) In the first volume of his autobiographical memoir, Dawkins [16] points out that one of the aims of *The Selfish Gene* was to persuade his readers “that [group selection] doesn’t work” (p. 261). Ithas even been characterised as “the nail in group selection’s coffin (…).”[[8]](#footnote-8) By sharp contrast, Wilson had, for a number of reasons, serious trouble accepting the idea that ‘his’ new science was based on kin selection instead of group selection.

In 1965, he had become a very reluctant convert to Hamilton’s theory, during a train voyage from Boston to Florida: he thought of himself as the world authority on social insects and could at first not accept that a novice had come up with such an important, innovative idea about his academic specialty. However, by the time he arrived in Miami, he [6] gave up: “I was a convert, and put myself in Hamilton’s hands. I had undergone what historians of science call a paradigm shift” (p. 310). He later conceded that Hamilton beat him to produce “the main idea, the most original, important idea on social insects of this century.”[[9]](#footnote-9) He had to react, he said, like young Huxley reacted when he read *The Origin of Species* [20]: how stupid of me not to have thought of that. “Well, anyway, as a consequence, kin selection, and this basic approach, has become central in the development of the field of sociobiology.”[[10]](#footnote-10) He even played a role in the break-through of Hamilton’s theory: at a 1965 meeting of the Royal Entomological Society in London, he devoted twenty minutes of his one hour long lecture to Hamilton’s ideas about altruism.[[11]](#footnote-11)

Strangely enough, ten years later, his *Sociobiology: The New Synthesis* discussed Hamilton’s theory in a chapter on group selection, entitled ‘Group selection and altruism’.According to Ir-ven DeVore, an anthropologist and evolutionary biologist who also disliked the term ‘sociobi-ology’, Wilson initially didn’t even appreciate the importance of Hamilton’s kin selection the-ory at all. It was his colleague Robert Trivers who “tried to make Ed rewrite the inclusive fitness discussion, particularly since Ed comes up with a very misleading treatment of kin selection and group selection. For Trivers, kin selection and individual fitness were extensions of Darwi-nism. Group selection was opposed to that… Ed finishes the book. *Sociobiology* has a very pro-minent treatment of inclusive fitness theory!”[[12]](#footnote-12) In any case, as time went on, Wilson devel-oped doubts about the relevance of kin selection. He believed that it was limited to explanations of eusocial behaviour within kin groups and “a kind of altruism,” whereas he saw “sophisticated societies that evolved through group selection, where individuals would be altruistic for the sake of their group’s survival” (i.e., truly altruistic?).[[13]](#footnote-13)

Did he see that or did he want to see such a morally elevated picture of nature, “where individuals would be altruistic for the sake of their group’s survival?” He [6] certainly always had “a special regard for altruism and devotion to duty, believing them virtues that exist in-dependent of approval and validation” (p. 25). And: “I have spent a good deal of time during my career as a scientist thinking about the origins of self-sacrifice and heroism, and cannot say I understand them fully in human terms” (p. 26). Or: “I just think people are capable of being a lot better than they have been. (…) We really are a wonderful species, and I think if we can understand who we really are, then we can reach a much better world, and a much better arran-gement than we have now.”[[14]](#footnote-14) That special regard for altruism and the human species may, in its turn, have been inspired by Wilson’s upbringing in a fundamentalist Baptist family in the deep South of the United States. This religious background certainly had an important influence on his life and on his ‘mission’ as a biophilic humanist [23].

Arguably, a Hamiltonian reduction of altruism to genetic selfishness does not square very well with this exalted opinion of man and the main (human) social virtue. As already indicated above, group selection theory certainly offers a more benevolent view of human nature. In a 2008 editorial, the magazine *New Scientist* [25] even spoke, in respect with the revival of group selection, of a ‘counter-revolution’: a return to an evolutionary theory which views nature “through a lens of benevolence: individuals acted for the good of their group, ensuring its sur-vival.” The earlier shift, in the 1960s, from group selection to kin selection had indeed been de-scribed as a revolutionary paradigm-shift (a term which was also used by Wilson). It was also compared with a religious or metaphysical conversion, one which caused a deep rift between two camps, the group selection people and the kin selection people, “particularly in certain Bri-tish departments (...).”[[15]](#footnote-15) Clearly, the question whether and to what extent social beings and hu-man nature have been shaped by group selection as opposed to kin selection, is emotionally laden and far from value-free.

**3. The incident**

Whatever the reasons for Wilson’s apparent preference for group selection, it was, sooner or later, bound to result in a confrontation with Dawkins, the passionate and vocal champion of kin selection and opponent of group selection. In 2005 [26], Wilson published his first explicit revision of his position with respect to group selection in a paper, written with his trusted and long-time collaborator Bert Hölldobler. Two years later, he added insult to injury by claiming, in an article in *New Scientist* [27], written with David S. Wilson and tellingly entitled ‘Evolu-tion: survival of the selfless’, that Dawkins had acknowledged that he made an error by pre-senting the gene’s eye view of evolution as an argument against group selection.[[16]](#footnote-16) The main point of this paper was that the old arguments against group selection have all failed and that, had this “been known in the 1960s, sociobiology would have taken a very different direction. It is this branch point that must be revisited to put sociobiology back on a firm theoretical foun-dation” (p. 45).

The Wilsons pointed out that Hamilton was one of the first to realise that his kin selection mechanism was no alternative to group selection but must, on the contrary, be interpreted as part of multilevel selection. Altruistic traits are almost always selectively disadvantageous with-in kin-groups and can only spread because kin-groups with more altruists contribute more to the gene pool of a species than kin-groups with less altruists. Likewise, Dawkins’ concepts of selfish genes and extended phenotypes were erroneously developed as arguments against group selection.[[17]](#footnote-17) In their opinion, Dawkins’ concept of genes as “replicators” and “the fundamental unit of selection” “averages the fitness of genes across all contexts to predict what evolves in the total population” [27, p. 45] (that was not Dawkins’ argument against group selection, though, as they implicitly acknowledged in a later reply, see below). Their modern theory of group selection or, more broadly, multilevel selection, by contrast, wonders whether genes can evolve on the strength of between-group selection, despite a selective disadvantage within each group. Put differently, the question is “whether the gene favoured by between-group selection is more fit overall than the gene favoured by within-group selection in the total population” (ibid.). And they add: “It is bizarre (in retrospect) to interpret this as an argument against group selection. Both Williams and Dawkins eventually acknowledged their error, but it is still com-mon to find the ‘gene’s-eye view’ of evolution presented as a drop-dead argument against group selection” (ibid.).

The latter understandably reacted as if stung by a bee. Not only did Wilson and Wilson claim that the branch of ethology which, in his opinion, was largely inspired by Bill Hamilton and particularly by his theory of kin selection should be put on a theoretical foundation of group selection, they also argued that the book that established his reputation was based on an error and that, moreover, he had acknowledged that error. He [30] implicitly called David S. Wilson a boor and asked apologies for what he described as “a total, unmitigated, barefaced lie,” rather than “a semantic confusion, exaggeration of a half-truth or a distortion of a quarter-truth (…)”: “D. S. Wilson should apologise. E. O. Wilson, being the gentleman he is, probably will” (p. 18).[[18]](#footnote-18) This was followed by another exchange of arguments in *New Scientist* and picked up and published by the British press under telling headlines such as ‘Evolutionists at war over altru-ism’s origins’ [32].

In their reply, Wilson and Wilson [33] explained that their comment about Dawkins spe-cifically related “to the error of using the replicator concept—genes as the ‘fundamental’ unit of selection—as an argument against group selection” (p. 18). They subsequently referred to a passage in *The Extended Phenotype* (1982) [29] where Dawkins points out that there are two kinds of units, involved in the natural selection process, replicators and vehicles, that the ma-jority of models ordinarily called ‘group selection’ are implicitly treating groups as vehicles, and that the “end result of the selection discussed is a change in gene frequencies, for example, an increase of ‘altruistic genes’ at the expense of ‘selfish genes’. It is still genes that are regarded as the replicators which actually survive (or fail to survive) as a consequence of the (vehicle) selection process” (p. 115). They also apologized in case their article had given the impression that Dawkins had yet acknowledged a second error: his assumption that within-group selection poses an insuperable problem for between-group selection. Put differently: they distinguished between two group selection questions: can groups be units of selection (theoretical group se-lection) and does group selection play a functional role in evolution (i.e., is it strong enough to overcome within-group selection: functional group selection)? They did not claim that Dawkins subscribed to functional group selection but only that he had used his selfish gene idea as an ar-gument against theoretical group selection and that, by 1982, he had recanted this argument by making a distinction between replicators and vehicles.

Dawkins did not accept their apologies, though, nor their argument that the passage in *The Extended Phenotype* they referred to constitutes a recantation of his previous condemnation of group selection. On the contrary, he [34] called it “a ludicrous attempt to justify their lying sta-tement that I ‘eventually’ acknowledged an earlier error” (p. 17) and presented two arguments to support this harsh verdict:

For one thing, *The Extended Phenotype*was published way back in 1982, which makes non-sense of Wilson’s “eventually”. But more importantly, the point I was making in 1982 (and would make again now) was a general one about the important distinction between repli-cators and vehicles. I mentioned group selection only to clarify that distinction. I was ex-plaining that those models of group selection that had been proposed were vehicle models not replicator models. I was not for a moment suggesting that I accepted those models as va-lid. They were (and are) invalid vehicle models, as opposed to invalid replicator models. (ibid.)

Dawkins assumes here that the Wilsons claimed that, in the aforementioned passage in *The Ex-tended Phenotype*, he accepted group selection models “as valid” (i.e., that he accepted group selection as a functional evolutionary mechanism). However, that was not what Wilson and Wilson wrote. They merely pointed out that he had acknowledged, in the aforementioned pas-sage, “the error of using the replicator concept—genes as the ‘fundamental’ unit of selection—as an argument against group selection.” Did he indeed acknowledge that his selfish gene ar-gument against theoretical group selection was mistaken? In the next section, I will first answer that question and subsequently return to the claim that he attacked in his reply (i.e., the claim that he accepted functional group selection in *The Extended Phenotype*).

**4. Who was right?**

Two things are very clear. First, Dawkins has *never clearly denied* that he used, in *The Selfish Gene* [7], the replicator concept or selfish gene idea as an implicit argument against theoretical group selection. It may not have been *explicitly* formulated as an argument (see below) but it was, apparently, indeed intended as such. In the first, introductory chapter, he explains that his book was inspired by the, at the time, widespread use of group selection to explain altruism. The idea was that groups whose individual members were prepared to sacrifice themselves for the welfare of the group, would be more successful than groups whose individual members were selfish. “This is the theory of group selection,” he adds, “long assumed to be true by bio-logists not familiar with the details of evolutionary theory (…)” (p. 7). His purpose was to “ex-plore the consequences of the evolution theory” (p. 1) for the issue of selfishness and altruism.

This exploration had two dimensions, a negative and a positive. The positive dimension in-volved correct or orthodox evolutionary explanations of altruistic behaviour (mainly kin selec-tion) and other social behaviours that were often explained through group selection. As he put it: “It is all very well for me to (…) point to the difficulties of the group-selection theory, but the existence of individual altruism still has to be explained (…) and this is something I am go-ing to face in later chapters” (pp. 10-11). The negative dimension mainly consisted of the argu-ment that within-group selection poses an insuperable problem for between-group selection (i.e., functional group selection is impossible), and of his selfish gene argument (i.e., theoretical group selection is impossible): the main consequence of neo-Darwinism is that it is not the group or the individual that is the fundamental unit of selection. “It is the gene, the unit of he-redity” (p. 11). As he puts it in chapter 3: “Natural selection in its most general form means the differential survival of entities” (p. 33). This means that selected entities must be potentially capable of surviving for a significant period of time. “Small genetic units have these properties: individuals, groups, and species do not” (ibid.). The implication seems clear: (theoretical) group selection is impossible because only genes are fundamental units of selection, not groups.

Second, Dawkins has repeatedly acknowledged that this discussion of the unit of selection question in *The Selfish Gene* was, at best, ‘confused’ because he did not distinguish between two kinds of unit of selection. For example, in the introduction to the third edition of *The Selfish Gene* (2006) [14], he writes that “it was not until 1978 that [he] began to think clearly about this distinction between ‘vehicles’ (usually organisms) and the ‘replicators’ that ride inside them (in practice genes (…))” (p. ix).[[19]](#footnote-19) And:

There are two kinds of unit of natural selection, and there is no dispute between them. The gene is the unit in the sense of replicator. The organism is the unit in the sense of vehicle. Both are important. Neither should be denigrated. They represent two completely distinct kinds of unit and we shall be hopelessly confused unless we recognize the distinction. (ibid.)

In his paper ‘Replicators and vehicles’ (1982) [35], Dawkins also acknowledged that his pre-vious discussion of the question of units of selection had suffered from a “failure to make a clear distinction between replicators and vehicles” (p. 51). ‘Unit of selection’ (i.e., subject of selection) can either refer to an entity that is passed on to following generations (replicator) or to an entity that carries replicators around and strives to pass them on to following generations (vehicle). In *The Extended Phenotype* [29], several passages are dedicated to this crucial dis-tinction. Apart from the passage, referred to by the Wilsons, there is for example also the sta-tement that “Replicators are not, of course, selected directly, but by proxy; they are judged by their phenotypic effects” (p. 4). The debate between individual selection and group selection is a debate over rival vehicles: “There really should be no debate over ‘gene selection’ versus ‘in-dividual (or group) selection’, since in the one case we are talking about replicators, in the other about vehicles. Replicator survival and vehicle selection are two views of the same process. They are not rival theories” (p. 62).

This is unquestionably an implicit acknowledgement that it is not possible to use the idea that the gene is the fundamental or the ultimate unit of selection (replicator selection) as an argument against theoretical group selection (vehicle selection). However, Dawkins did not acknowledge this with so many words: nowhere in his publications can the specific and explicit acknow-ledgment be found that the original selfish gene idea cannot be used as a falsification of group selection. Nevertheless, Wilson and Wilson were basically right: by 1982, Dawkins had impli-citly acknowledged that he made an error by implicitly presenting his selfish gene theory (i.e., the idea that the gene is the fundamental unit of selection) as an argument against (theoretical) group selection.

As to the question whether Dawkins accepted, in the passage from *The Extended Phenotype*, referred to by the Wilsons, group selection models as valid (vehicle) models: that is indeed not the case (although the passage can be interpreted as such). He merely pointed out that the ma-jority of models, ordinarily called ‘group selection’, treat groups as vehicles, not as replicators, and that this kind of group selection results, like individual selection, in a change in gene fre-quencies. However, elsewhere in *The Extended Phenotype* [29], he *did* accept functional group selection, albeit (very) tentatively. For example, in a passage where he presented the group as an alternative ‘vehicle’ unit of selection, next to the individual organism: “either an individual organism or a group could be a serious contender for the title ‘unit of selection’” (p. 60). He still believed, though, that there were reasons for “coming down on the side of the individual organism rather than larger units” (ibid.). Clearly, this is about the question whether groups can be functional units of selection (since he had already accepted them as theoretical units of selec-tion).

Furthermore, he called the claim that group selection “has soaked up more theoretical inge-nuity than its biological interest warrants” a “prejudice,” adding that “it has never been proved to be impossible and never could be” (p. 115). Also, natural selection, caused by a resistance to destruction, “could apply to groups of organisms as well as to single organisms, for if a group is destroyed all the genes inside it are destroyed too” (p. 114). Or: “To the extent that active germ-line replicators benefit from the survival of the group of individuals in which they sit, (…), we may expect to see adaptations for the preservation of the group” (p. 85). Put differently: (negative) group selection is not only theoretically possible, it may even be a functional evo-lutionary mechanism (i.e., play a role in evolution).

Lastly, in a Tanner lecture [36] he gave in 2003 in Harvard, Dawkins spoke of confusion, in the literature, between true group selection “and something else that is called group selection but turns out to be either kin selection of reciprocal altruism. Or there may be confusion of ‘se-lection between groups’ and ‘selection between individuals in the particular circumstances fur-nished by group living’” (p. 258). And he added, surprisingly: “Those of us who object to group selection have always admitted that in principle it can happen. The problem is that, when it is pitted against individual-level selection (…) individual-level selection is likely to be stronger” (ibid.).[[20]](#footnote-20) According to this remarkable statement, he not only again did not completely exclude the possibility of functional group selection (‘likely’), he also claimed that he never had denied the possibility of theoretical group selection, not even in the first edition of *The Selfish Gene*. This can be interpreted as a belated denial that the selfish gene idea was intended as an argument against (theoretical) group selection. However, if it was indeed not intended as such, why then did he insist, in his explicitly anti-group selection book (i.e., *The Selfish Gene*), that the gene (and not the group) is the fundamental unit of selection?

**5. Conclusion**

Key to a correct understanding of the dispute between Dawkins and the two Wilsons is the dis-tinction between theoretical and functional group selection and that between implicit and ex-plicit recantations. Dawkins did never explicitly acknowledge that he had erred when he deve-loped his selfish gene idea as an implicit argument against theoretical and therefore also func-tional group selection. However, his distinction between vehicles and replicators constitutes an implicit acknowledgment of that error (his 2003 statement that he has never claimed that theo-retical group selection is impossible is not credible). In this important sense, Wilson and Wilson were right: after 1976, Dawkins abandoned his selfish gene argument against theoretical group selection. Not only did he now accept that groups can be vehicles, he eventually even tentatively accepted the possibility of functional group selection (albeit not in a consistent way, see note 20).

His vehement reaction against Wilson’s and Wilson’s claim was understandable, though. Not only did he never explicitly acknowledge that his implicit selfish gene argument against theo-retical group selection was wrong, he has also never clearly, consistently and completely en-dorsed functional group selection. Furthermore, his genecentrism, as elaborated in *The Selfish Gene*, the book that made him famous, had been inspired by Hamilton’s kin selection theory and by a strong aversion for, at the time, widespread but not very well thought-out (i.e., naïve) functional group selection explanations. Lastly, to Dawkins, the science that, through Wilson’s monumental and contentious *Sociobiology*, had irritatingly become known as sociobiology, was based on that kin selection theory and excluded (naïve) group selection as a valid evolutionary mechanism. Wilson, by contrast, always preferred group selection because kin selection seemed to him to have serious limitations as an explanans of altruistic behaviour but maybe also because group selection views life “through a lens of benevolence” and because he hadn’t thought of kin selection himself. The dispute between Wilson and Dawkins that first erupted in 2007 is thus the proverbial tip of a complex and heterogeneous iceberg that stretches all the way back to the origin and the foundation of the science of sociobiology and, in the case of Dawkins, to the start of a brilliant career as a writer and public intellectual.

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1. For an analysis of the sociobiology controversy, see, e. g., Michael Ruse [3] or Ullica Segerstråle [4]. [↑](#footnote-ref-1)
2. As Dawkins [5] put it himself: “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 (…)” (p. 571). Dawkins did in-deed only present a synthesis of the work of other biologists. Or, as Wilson [6] writes: “The elements of socio-biological theory came from many sources” (p. 315). Wilson already conceived of the idea of a synthesis of all the available information on social animals, based on population biology, and of the name ‘sociobiology’ in 1956. [↑](#footnote-ref-2)
3. See Soraya de Chadarevian [8], at p. 32. [↑](#footnote-ref-3)
4. The manuscript had first been shown to Tom Maschler, head of Jonathan Cape (which was sold to Random House in 1991). See, in this respect, de Chadarevian [8]. [↑](#footnote-ref-4)
5. See, in this respect, Dawkins [9], at p. 208. [↑](#footnote-ref-5)
6. Kin selection explains altruism (which lowers the fitness of the altruist) between family members through the increased fitness of the beneficiary of the behaviour of the altruist: since (s)he shares many of his or her genes with the altruist (including, often, the altruistic genes), the latter’s behaviour can result in the spreading of the altruistic genes, even though his or her fitness is diminished. [↑](#footnote-ref-6)
7. See Fanelli [15]. [↑](#footnote-ref-7)
8. See Borrello [17], at p. 140. It would probably be more accurate to say that *The Selfish Gene* was the last nail “in naïve group selection’s coffin,” the kind of group selection thinking that assumed that traits would spread in populations, simply because they benefit groups, without taking into account their fitness cost. By the mid-1970s, a new and more sophisticated group selection “school” was already emerging, though. See, e.g., Dugatkin [18]. [↑](#footnote-ref-8)
9. Wilson, quoted in Thomas [19], at p. 158. [↑](#footnote-ref-9)
10. Wilson, quoted in Thomas [19], at p. 158. [↑](#footnote-ref-10)
11. Maynard Smith also played a key role in the breakthrough of what he called kin selection and contrasted with group selection. In a letter to *Nature*, ‘Group selection and kin selection’ (1964) [21], he wrote that it was possible to distinguish two rather different processes, “both of which could cause the evolution of characteristics which favour the survival, not of the individual, but of other members of the species. These processes I will call kin se-lection and group selection, respectively. Kin selection has been treated by Haldane and Hamilton” (p. 1145). [↑](#footnote-ref-11)
12. DeVore (interview in 1982), cited in Segerstråle [4], at p. 82. However, Trivers himself “did not see things that way” (ibid.). In any case, Wilson [6] believes that few learned about Hamilton’s theory until he “highlighted it in the 1970s” (p. 317). [↑](#footnote-ref-12)
13. Wilson, quoted in Claudia Dreifus [22]. [↑](#footnote-ref-13)
14. Wilson, quoted in Susanna Rustin [24]. [↑](#footnote-ref-14)
15. Segerstråle [4], at p. 54. [↑](#footnote-ref-15)
16. This *New Scientist* paper was an edited and abridged version of a paper, previously published in the *Quarterly Review of Biology* [28]. [↑](#footnote-ref-16)
17. Dawkins’ concept of the extended phenotype was of course not developed at all as an argument against group selection. It was, as he put it in *The Extended Phenotype* [29] “addressed to those that already accept the currently fashionable selfish-organism view life, rather than any form of ‘group benefit’ view” (p. 6). The selfish-organism view was “not necessarily wrong” but “looking at the matter the wrong way up” (ibid.) (i.e., wrong after all): the vehicle may be a unit of selection on its own, but it is, on the other hand, only a local concentration in the web of phenotypic extensions of replicators by which they ensure their survival. [↑](#footnote-ref-17)
18. In a later blogpost, David S. Wilson [31] commented: “Gracious! What a hierarchical guy! Dawkins acts as if he is the No. 2 monkey, kowtowing to the No. 1 monkey (Ed) while dishing it out to the No. 3 monkey (me)! As Ed commented to me after reading Dawkins’ comment, ‘What does he think–that you slipped me a Mickey?’” [↑](#footnote-ref-18)
19. He refers to Dawkins [11]. [↑](#footnote-ref-19)
20. In the endnotes to the third edition of *The Selfish Gene* (2006) [14], he suggests that there may exist a kind of higher-level selection after all but he immediately adds: “when I say ‘higher-level’, I do not mean anything to do with ‘group selection’” (p. 269). I suppose that he here refers to functional group selection, not theoretical group selection. [↑](#footnote-ref-20)