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Charles Darwin and Group Selection

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Summary
The question of the levels at which natural selection can be said to operate is much
discussed by biologists today and is a key factor in the recent controversy about
sociobiology. It is shown that this problem is one to which Charles Darwin
addressed himself at some length. It is argued that apart from some slight
equivocation over man, Darwin opted firmly for hypotheses supposing selection
always to work at the level of the individual rather than the group. However,
natural selection's co-discoverer, Alfred Russel Wallace, endorsed group selection
hypotheses.

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1. Introduction
In recent years evolutionary biologists have shown much interest in the question
of the levels at which natural selection can be said to operate. Generally speaking,
confining ourselves initially to the non-human world, it is probably true to say that
although V. C. Wynne-Edwards in his *Natural regulation of animal numbers* argued
strongly for the wide-spread efficacy of some form of group selection, most
evolutionists would agree with G. C. Williams' reply, *Adaptation and natural
selection*, in which it was argued that essentially selection must start with the
individual. Nevertheless, a number of studies have been aimed at showing how
under certain circumstances selection could work at the group level. Hence, it is
probably true to say that matters are not yet definitively settled, either theoretically
or empirically.

1 See R. C. Lewontin, 'The units of selection', in *Annual review of ecology and systematics* (ed. R. F.
4 See for instance: R. Levins, 'Extinction', in M. Gerstenhaber (ed.), *Some mathematical questions in
biology* (1970, Providence: American Mathematical Society), 77-107; S. A. Boorman and P. R. Levitt,
'Group selection on the boundary of a stable population', *Proceedings of the National Academy of Sciences*
69 (1972), 2711-2713; their 'Group selection of the boundary of a stable population', *Theoretical
population biology*, 4 (1973), 82-128; and M. J. Wade, 'A critical review of the models of group selection'.
The debate about the levels of selection has been given added zest by the fact that the assumption that selection almost invariably centres on the individual is crucial to the theories and conclusions of the sociobiologists, those biologists interested in animal social behaviour. Indeed, what the sociobiologists claim, as a major distinguishing feature of their work from that of earlier students of the biology of animal behaviour, is that they alone make the right choice of individual over group selection. This in itself would hardly be a matter of great controversy; but since most of the sociobiologists want to apply their theorizings from the animal world directly to the human world, inevitably there has been some rather heated discussion about whether one can properly use the notion of individual selection to explain the evolution and maintenance of all significant human behaviour. The critics of sociobiology feel that such an attempt leads to a reactionary distortion of human sociality, and they argue that other causes of human behaviour must be sought in explanation.

Of course, one does not have to be a supporter of some form of group selection in the non-human world to be a critic of human sociobiology. Nevertheless, some eminent biologists do fall into both categories, and moreover, I suspect they see important ideological links in their overall critique of the all-sufficiency of individual selection. For instance, both Levins and Lewontin have allowed the possibility of group selection in certain special situations, they are both against sociobiology, and by their own admission see the totality of their work as part of an overall Marxist-orientated biology.

Because both the sociobiologists and their critics resort to the familiar tactic of trying to legitimize the present by reference to the past—one finds protagonists on both sides claiming that they alone stand in the true evolutionary tradition—there is therefore some interest in seeing whether the debate about the levels of selection stretches back to the first announcement of the theory of evolution through natural selection, and where precisely the theory’s chief formulator, Charles Darwin, stood

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7 Levins (footnote 4).

8 Lewontin (footnote 1).


10 See, for instance, Barash (footnote 5) and Sahlins (footnote 6).
on the matter. Such an historical inquiry is the aim of this paper. First, I shall consider Darwin's position on the levels of selection in his major work, On the origin of species. Second, I shall see how his ideas developed over the next twelve years. Third, I shall look at his ideas in his major significant work on human beings, The descent of man. For clarity in this paper, because there has been some confusion about terminology by 'individual selection', I shall mean selection which in some sense affects an individual's reproductive interests. This could be directly through the individual, or indirectly in some way: for instance, by kin selection, where an individual's interests are furthered through close relatives; through parental manipulation, where a parent directs an offspring to its own interests; or through reciprocal altruism, where an individual is selected to do favours for others in the hope of returns. By 'group selection' I shall mean selection in some way causing characteristics which help others, including non-relatives, in an individual's group, most probably by the species. There is not necessarily any hope of return for the individual.

2. On the origin of species

The early chapters of the Origin, those in which Darwin introduced his mechanisms for evolution, certainly give the impression of a Darwin who was going to be firmly committed to individual selection. As is well known, he did not just present natural selection without any theoretical backing, as an axiom as it were. Rather, he argued first to a universal struggle for existence, from premises modelled on Malthus's ideas about available food and space. Then, from the struggle, assuming that there was heritable variation of the required amount and kind, Darwin went on to argue that the survivors and reproducers in the struggle will on average be different from the losers: natural selection. Now as he introduced the struggle, Darwin gave strong evidence that he was going to be thinking at the level of the individual. To have some sort of group selection, one has got to minimize the tensions or rivalries within the group. When, for instance, the ethologist Konrad Lorenz invoked group selection, he did so because he was trying to show how it is that animals have mechanisms inhibiting all-out attacks on conspecifics. Darwin, however, saw the struggle (which was going to lead to selection) as acting just as much between conspecifics as between any two organisms: '... as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life'. In fact, he then went on to say that the closer the relationship the more severe the struggle, '... the struggle almost invariably will be most severe between the individuals of the same species'. It should be added, of course, that he was not necessarily thinking of

14 See Ruse (footnote 5).
17 Ibid. (footnote 11), 63.
18 Ibid., 75.
struggle in the sense of hand-to-hand combat, but struggle for resources of various kinds and so forth. Nevertheless, the point remains that he was viewing the crucial biological tensions as much within the group as without.

Coming to selection itself, we find the same emphasis on the individual. For instance, to illustrate how natural selection might work Darwin gave the imaginary example of a group of wolves, hard-pressed for food. He suggested that the swiftest and slimmest will be selected, because it will be they alone who will catch the prey: deer, and so forth. Hence, there will be evolution towards and maintenance of fast, lean wolves. Obviously, the crux of this explanation is that some wolves survive and reproduce, whereas others do not. There is no question here of selection working for a group; rather it is all a matter of individual against individual.

Although an example like this shows that Darwin thought natural selection itself to be individual orientated, his commitment to the individual is perhaps best illustrated by his variant form of selection, sexual selection. This Darwin divided into two forms: sexual selection through male combat, where the males compete between themselves for the females, and sexual selection through female choice where females choose between males displaying in various ways. It is true that Darwin was criticized for this mechanism, particularly on the grounds that female choice anthropomorphically supposes that animals have the same standards of beauty as humans. But this is as it may be. What is important is how clearly sexual selection shows that Darwin was thinking of selection as something that could act between fellow species' members, preserving a characteristic that gives an organism an advantage over conspecifics. There is no place here for the preservation of characteristics of value to conspecifics at the expense of the individuals within a group.

Introducing selection and its foundations, therefore, Darwin gave the impression that he was going to be a fairly rigorous individual selectionist. But was he completely committed to individual selection? Did he feel that there could ever be a case where selection could and would act for the benefit of the group? In the Origin, as we turn from Darwin's introduction of his mechanisms to their applications, we find that, with respect to the levels of selection dilemma, there are two points at which Darwin had to make a decision: when he discussed social insects and when he discussed hybrid sterility. Let us take them in turn.

By 'social insects' is meant insects with sterile castes, all living together in a community. The problem is how one explains the sterility of individuals in some of these castes, and how members of sterile castes could have evolved to be so very different from fertile fellow community members. Surely one must invoke some sort of group selection to explain how the sterile community members, so helpful to the group, so unhelpful to themselves, evolved? About the question of sterility, Darwin wrote as follows:

How the workers have been rendered sterile is a difficulty; but not much greater than that of any other striking modification of structure; for it can be shown that some insects and other articulate animals in a state of nature
occasionally become sterile; and if such insects had been social, and it had been profitable to the community that a number should have been annually born capable of work, but incapable of procreation, I can see no very great difficulty in this being effected by natural selection. 22

In a related fashion he tackled the problem of how the members of some sterile castes can be very different from their parents, and can be different from the members of other castes. Drawing on a favourite analogy of the effects of artificial selection in the domestic world, Darwin pointed out how breeders can work indirectly, raising desired organisms (which are killed without reproducing), because the fertile parents can somehow latently carry the characteristics of these organisms. Similarly, in the wild, fertile parents could have sterile offspring who help the community, and also could pass on to their fertile offspring the potential to have such sterile offspring in turn. And if different kinds of sterile offspring could be used in a community, these too could be formed by selection. 23

There is no group selection here, where 'group selection' is understood in our above-defined sense as involving unreturned aid to non-relatives. The key to Darwin's argument is that the sterile altruists are closely related to the fertile members of the community. The sterility occurs because it is of value to all the related members of the nest, and also Darwin thought in part because, when one has two sterile castes, without sterility one would have interbreeding and less-effective hybrid forms (that is, forms, less effective for the community). But selection is not preserving characteristics exclusively of value to non-relatives.

One should nevertheless add that although Darwin was certainly an individual selectionist at this point, even an individual selectionist sufficiently sophisticated to see how individual selection can work through a closely related community, he did not really bring his argument to the level brought by today's sociobiologists. Some sociobiologists today argue that caste differentiation (in the Hymenoptera at least) is a function of kin selection: because of the haplodiploid method of sex determination in the Hymenoptera, sisters are more closely related to sisters than to daughters, and thus there is a genetic advantage in raising sisters. 24 Other of today's sociobiologists argue that the key is parental manipulation, where parents make some offspring sterile altruists towards siblings. 25 Both of these explanations see that there can be reproductive conflicts between community members, despite the close relationships. Darwin however, saw the community members united in common interests. It would therefore be somewhat anachronistic to say that Darwin was a kin selectionist rather than a parental manipulator, or vice-versa. Because of his ignorance about the proper principles of genetics, his analysis was just not that fine-grained. One might be tempted to say that Darwin was a shade closer to group selection than today's sociobiologists, because he saw no conflict between relatives, despite their lack of genetic identity. Perhaps so—but again I am inclined to think that anachronistically one is reading into Darwin's work something more subtle than is really there.

The other place in the Origin where Darwin might have been tempted towards a group selection mechanism was over the question of sterility: either the sterility

22 Darwin (footnote 11), 236.
23 Ibid., 237–238.
25 Alexander (footnote 5).
between members of different species, or if hybrids were formed, the sterility of these hybrids.\textsuperscript{26} \textit{A priori} one might think that the very usual sterility between species or the sterility of hybrids between members of two different species (for instance, the sterile horse-donkey, the mule) would have been something fashioned by selection. If one has two forms, each adapted to its respective environment, a hybrid would be (literally!) neither fish nor fowl. Hence, it would be of advantage that such a hybrid either be barred altogether or if possible be sterile because it could not then reproduce and give rise to further ill-adapted forms. The problem is, of course, to whom the absence or sterility of the hybrid would be of advantage. If the hybrid is not formed at all, then the parents lose any chance of offspring. If the hybrid is formed, then it would clearly not be of direct advantage to the hybrid itself to be sterile. Nor, differentiating this case from that of the social insects, would it be of advantage to the parents that the hybrid offspring be sterile—there is no question of the hybrid being freed through its sterility to aid its related community. At best the advantage from absence or sterility of hybrids would be to the parent species, who would thus gain better evolutionary prospects because no energies or resources would be going into ill-adapted hybrid offspring.

But to Darwin, apart from the fact that he could not see why in nature one gets so many degrees and forms of sterility (assuming selection does cause sterility), the unambiguous group selection required to cause sterility was apparently just not a live possibility. Although he did not provide a detailed theoretical attack on group selection, Darwin clearly hinted that he could not see how group selection, favouring the group over the individual, could work at all. Further, he went to some pains to show how individuals of different species frequently cannot interbreed at all because of incidentally formed differences, and similarly how hybrid sterility is an incidental fact, brought about by the lack of harmony between the different contributions by the parents to the hybrid's reproductive mechanisms:

On the theory of natural selection the case [of sterile hybrids] is especially important, inasmuch as the sterility of hybrids could not possibly be of any advantage to them, and therefore could not have been acquired by the continued preservation of successive profitable degrees of sterility. I hope, however, to be able to show that sterility is not a specially acquired or endowed quality, but is incidental on other acquired differences.\textsuperscript{27}

3. \textit{Between the \textit{Origin} and the \textit{Descent}}

There are two items of particular interest in the 1860s. First, there is the fact that Darwin himself wrestled at length with possible selective causes of sterility. Second, relatedly, Darwin and natural selection's co-discoverer, Alfred Russel Wallace, debated the individual-group selection problem. By the end of the decade, with respect to the animal and plant worlds, there was nothing implicit about Darwin's commitment to individual selection. He had looked long and hard at group selection and rejected it. Let us take in turn the matters which engaged Darwin in the levels of selection problem.

Almost immediately after the publication of the \textit{Origin}, Darwin's interests turned to botany. Amongst other plants that he studied were members of the


\textsuperscript{27} Darwin (footnote 11), 245.
Fig. 1. Long-styled (left) and short-styled (right).

Fig. 2. Heteromorphic and homomorphic unions.

Figures 1 and 2.

From C. Darwin, 'On the two forms, or dimorphic condition, in the species of Primula, and on their remarkable sexual relations', *Journal of the Proceedings of the Linnaean Society (botany)*, 6 (1862), 77–96.

Members of this kind of species come in one of two different forms. Some have long styles, with the stamens tucked right

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primula family, primroses and cowslips. Members of this kind of species come in one of two different forms. Some have long styles, with the stamens tucked right
away down the tube of the corolla; others have short styles, with the stigma right down the tube and the stamens at the mouth (see Figure 1). Hitherto, these different forms had been considered accidental varieties, but Darwin was able to show that the two forms play important roles in the cross fertilization of the (hemaphroditic) plants. In particular, the crosses between plants of different types are far more fertile than crosses between plants of the same type (see Figure 2).

In the different degrees of fertility between the different kinds of crosses, Darwin thought that he found a clue pointing to the possibility, in some special cases at least, that selection may have had a hand in sterility barriers. Why should a plant be barred from reproducing in a satisfactory way with half of its fellow species' members? Darwin hypothesized that this barrier may be a consequence of a selection acting to prevent something which is known to be positively deleterious, namely self-fertilization (which produces inferior, inbred offspring). Plants, Darwin supposed, get selected for self-sterility, and then somehow accidentally (at least, not through selection) this gets transferred into a sterility with all forms like the plant itself. Furthermore, thought Darwin, if this hypothesis be true, we should find that the kind of plant which stands the greater chance of being self-fertilized has the greater barriers to prevent it. Since the primulae are fertilized by insects, it is obviously the short-styled form which runs this greater risk, and Darwin was happy to be able to confirm that short-short crosses were indeed even less fertile than long-long crosses. He therefore concluded:

Seeing that we thus have a groundwork of variability in sexual power, and seeing that sterility of a peculiar kind has been acquired by the species of Primula to favour intercrossing, those who believe in the slow modification of specific forms will naturally ask themselves whether sterility may not have been slowly acquired for a distinct object, namely, to prevent two forms, whilst being fitted for distinct lines of life, becoming blended by marriage, and thus less well adapted for their new habits of life.29

Judging from this passage alone, one might think that Darwin had now turned, not merely to a selection hypothesis for sterility, but to a group selection hypothesis, at least in partial explanation of sterility in those organisms which are hermaphroditic. (This latter clause about hermaphrodites was not necessarily that great a restriction, because his work on barnacles had convinced him that sexual organisms evolved from hermaphrodites.30) However, looking at his explanation carefully, it is clear that Darwin had turned to nothing of the sort. In as much as selection was supposed to cause sterility, it was for the good of the individual: so that it would not fertilize itself, thus causing only inferior inbred offspring. Insofar as sterility was being generalized from the individual to the group, it was accidental, in the sense of not being of selective value. There was no question of selection for the group, however much Darwin's rather sloppy use of language might hint otherwise.

At the end of the above-quoted passage, where Darwin had speculated that selection might cause sterility, wisely he added reservations: ‘But many great

30 C. Darwin, A monograph of the sub-class cirripedia, with figures of all the species. The lepadidae; or pedunculated cirripedes (1851, London; Ray Society); and his A monograph of the sub-class cirripedia, with figures of all the species. The balanidae (or sessile cirripedes); the verrucidae, &c (1854, London; Ray Society). See also Ghiselin (footnote 20); and M. Ruse, The Darwinian revolution: science red in tooth and claw (1979, Chicago; University of Chicago Press).
difficulties would remain, even if this view could be maintained. It was perhaps just as well that he covered himself here, for it was not that long afterwards that he discovered evidence which destroyed his hypothesis about the selective origin of sterility. The plant Lythrum salicaria has three forms, and they are all involved in cross-fertilization of members of the species. In particular, given any one of the three forms, long-, mid- and short-styled, one needs one of the other forms to effect the most efficient fertilization. If Darwin’s hypothesis was correct, then since the closer the stigma and the stamens the greater the chance of self-fertilization, the closer the stigma and the stamens on two plants being crossed the greater should be the sterility barrier (excluding of course, cases where stigmas and stamens were in exactly the same positions, because this could not happen on a single plant). However, in fact it turned out that sterility was a direct function of the distance between stigmas and stamens: the very opposite to that predicted through the hypothesis. Hence, Darwin was led to reject his short-lived speculations, and to return to his original position: sterility was an accidental by-product of individual selection.

Perhaps as a warning to others, in the 4th edition of the *Origin* (published in 1866), Darwin inserted a somewhat stronger discussion than hitherto as to why selection could not cause sterility, although like most of us, he found it difficult to reject a good idea—even if it was fairly clearly false: witness his reluctance to throw out his marine explanation of the parallel roads of Glen Roy. Hence, in this edition of the *Origin* he did present his hypothesis about sterility in the primulae, but then he concluded that selection could not cause sterility!

In support of his strengthened claim that selection could not cause sterility, Darwin gave three reasons. First, he pointed out that selection could not be a necessary condition for sterility, because there are indisputable cases of species having developed in different geographical regions, and yet, although selection could not possibly have made them inter-sterile, they prove to be so when they are brought together. Second, there are cases where only one of the possible crosses between members of species proves sterile, and where the other cross is quite fertile (that is, male of species A crossed with female of species B is sterile, but male of species B crossed with female of species A is fertile). Darwin could not see how selection could cause this asymmetrical relationship. Third and most importantly, he stated categorically that even if sterility is of value to the group, it is not of value to the individual, and it is at the level of the individual that selection operates. Sterility could not have been caused by natural selection, ‘for it could not have been of any direct advantage to an individual animal to breed poorly with another individual of a different variety, and thus to leave few offspring; consequently such individuals could not have been preserved or selected’. And in the 5th edition of the *Origin*, he

35 Ibid., 444.
added that if hybrids are born and they are less than fully fertile, then selection will act against them too. In short, he showed that he had thought consciously about and rejected group selection.

If indeed, with his full discussion of the reasons why sterility could not be fashioned by selection, it was Darwin's aim to warn others against thinking that selection could fashion sterility or indeed anything of value to the group rather than the individual, his actions had exactly the opposite effect to that which he intended! In particular, his discussion (which he repeated practically verbatim two years later in his *Variation of animals and plants under domestication*[^36]) spurred Wallace to react by embracing whole-heartedly the cause and efficacy of the group selection:

> It appears to me that, given a differentiation of a species into two forms, each of which was adapted to a special sphere of existence, every slight degree of sterility would be a positive advantage, not to the individuals who were sterile, but to each form. If you work it out, and suppose the two incipient species a . . . b to be divided into two groups, one of which contains those which are fertile when the two are crossed, the other being slightly sterile, you will find that the latter will certainly supplant the former in the struggle for existence . . .[^37]

Although Darwin and Wallace each tried as politely as possible to see the viewpoint of the other, the beginning was basically the end of the matter also. Darwin reiterated that he could not see how sterility, so disadvantageous to the individual, could be preserved by selection; Wallace reiterated that he could not see how sterility, so advantageous to the group, could fail to be preserved by selection; and that was that.[^38] It is true that Darwin and Wallace were not entirely apart: they both agreed that a disinclination to cross with members of another species could have been acquired by selection, even though Wallace unlike Darwin wanted to link this disinclination to sterility. Should a cross ever so occur. But of course for Darwin this admission demanded no compromise on the matter of individual selection. Given a choice between hybrid offspring and offspring entirely of one's own species, it would certainly be in an organism's reproductive advantage not to waste effort on producing hybrids, well-adapted to neither parent's ecological niche. Hence, selection could help one avoid producing such hybrids in the first place. The point was, as Darwin saw it, if the coupling had in fact taken place, it would not then be in an individual's advantage to promote sterility. In other words, if an individual had mated with another, it would not then be in its interests to yield less than fully fertile offspring.

And so we find Darwin and Wallace divided. Rather sadly Darwin concluded that: 'We shall, I greatly fear, never agree'.[^39] Wallace gallantly conceded that it was probably he himself who was wrong (although this did not stop him later in the century from repeating his own position in print![^40]). Wallace feared only that the problem of sterility 'will become a formidable weapon in the hands of the enemies of


[^38]: Ibid., 288-297.

[^39]: Ibid., 296.

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Natural Selection'.41 Incidentally, it is interesting to note that in this disagreement there are faint echoes of the other matter which separated Darwin and Wallace at this time: sexual selection through female choice.42 Darwin wanted to argue that the beauty of, say, the peacock as opposed to the peahen, is a function of the females choosing beautiful males. Wallace argued that the difference is essentially a function of the females being more drab than the males, this drabness coming through the female’s need for camouflage from predators as they incubate their eggs and care for their young. In arguing this way, Wallace was certainly not invoking group selection. However, unlike Darwin, who was emphasizing the individual nature of selection by seeing the main competition (at this point) as coming from within the species, Wallace was deemphasizing competition within the group by seeing the threat coming from without.

Concluding this section dealing with the years immediately following the Origin, we see therefore that Darwin continued to think about the problem of the proper level of selection, and that he became even more convinced that in the non-human world selection acts at, and only at, the level of the individual. Let us see now what happened when Darwin turned his attention to human beings.

4. The descent of man

As is well known, what made Darwin’s speculations in the Origin so unpalatable to so many were the obvious implications for man. As the geologist Charles Lyell sadly wrote to Darwin:

It is small comfort or consolation to me, who feels that Lamarck or Darwin have lessened the dignity of their ancestry, making them out to be with souls, to be told, ‘Never mind, you will be succeeded in unbroken lineal descent by angels who, like the Superior Beings spoken of by Pope, “Will show a Newton as we show an ape”’.43

In fact in the Origin itself, Darwin hardly mentioned man. Wisely deciding not to draw more controversy than he need, Darwin deliberately restricted himself to a single final comment: ‘Light will be thrown on the origin of man and his history’.44 And this, surely the most understated claim of the nineteenth century, Darwin added only that he not later be accused of dishonourably concealing his own true beliefs. But his reticence should not be confused with indecision. It is clear, from private notebooks that he kept, that right from the time when he first became an evolutionist in the late 1830s, Darwin considered man as an animal on a par with other animals.45 Indeed, the first hint that we have of him using natural selection as an evolutionary mechanism is a speculation about how selection might have improved human intelligence.46

Through the years, nothing at all changed, and so we find that when Darwin did finally write fully and publicly on man, in 1871 in his Descent of man, he tried as

41 Darwin and Seward (footnote 37), vol. 1, 297.
43 L. Wilson, Sir Charles Lyell’s scientific journals on the species question (1970, New Haven; Yale University press), 382.
44 Darwin (footnote 11), 488.
carefully and thoroughly as he could to show that man evolved from other animals, by the same processes as hold throughout the organic world. For instance, 'in the rudest state of society, the individuals who were the most sagacious, who invented and used the best weapons or traps, and were best able to defend themselves, would rear the greatest number of offspring'. The one thing which is perhaps noteworthy about Darwin's treatment of man, taken generally, is the very significant role which he gave to the action of sexual selection. And even this, to a certain extent, was forced on him by external circumstances, namely the apostasy of Wallace.

In his early years, Wallace had had even less religious belief than Darwin, and in fact after the *Origin* when he first started to write on man Wallace still treated him as a natural object. However, towards the end of the 1860s, chiefly because of a growing involvement with spiritualism, Wallace came to believe that there were aspects of human development which call for a creative power above any natural process of selection. For instance, he argued that only through some kind of supernatural interference could one explain the relative hairlessness of members of the human species. To counter Wallace, although undoubtedly also as a natural development of ideas which he had had previously, Darwin included in the *Descent* a very large general discussion of sexual selection, and then he argued that many of the differences between humans, both between the sexes and between different races, are due to this kind of selection: men struggle for the women they want, women are attracted to the dominant men, and so forth. Thus, something like human hairlessness can be explained as a function of early men finding hairy mates distasteful.

The precise details of Darwin's general explanation of man's evolution are not our concern here. What is important to us is the obvious fact that normally he saw the individual man or woman as being the crucial unit in the selective process. There was no question that, when faced with his own species, he was going to swing round suddenly and start to argue as a general policy that for *Homo sapiens* alone the group, particularly the species, is the key element in the evolutionary mechanism. As we saw in the above quotation about the evolution of intelligence, it is when some individual man is brighter than his fellows that we get the important evolutionary consequences, for then it is that he (not everyone) will have an increased crop of children. Furthermore, whether he was indeed right in giving sexual selection so important a role in human development, the fact that he did emphasize in even greater detail the extent to which he saw evolutionary competition occurring within the human species. As pointed out earlier, by its very definition sexual selection takes place within a species, pitting conspecific against conspecific.

Nevertheless, in dealing with man's evolution there was one point—a point incidentally noted by Wallace as inexplicable through selection—where Darwin for once did quaver in his commitment to individual selection. This was over the evolution of the human moral sense: man's awareness of and actions upon what is right and wrong. Darwin was certainly not about to follow Wallace in concluding

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47 Darwin (footnote 12), vol. 1, 196.
that human morality implies that there must be a supernatural power guiding human morality; but for once he did lose sight of the individual and allow that possibly the unit of selection may have been the group, specifically the tribe. Rhetorically, Darwin asked: ‘...how within the limits of the same tribe did a large number of members first become endowed with [their] social and moral qualities, and how was the standard of excellence raised’.50 And then immediately he expressed his worries about the power of individual selection to bring about such morality:

It is extremely doubtful whether the offspring of the more sympathetic and benevolent parents, or of those which were the most faithful to their comrades, would be reared in greater number than the children of selfish and treacherous parents of the same tribe. He who was ready to sacrifice his life, as many a savage has been, rather than betray his comrades, would often leave no offspring to inherit his noble nature. The bravest men, who were always willing to come to the front in war, and who freely risked their lives for others, would on an average perish in larger number than other men.51

In short, it would seem that natural selection working at the level of the individual could not bring about or preserve a heritable moral sense.

Of course, asking rhetorical questions and setting forth the difficulties do not in themselves imply absolutely that Darwin believed that the only way in which one could explain the human moral sense was through some sort of group selection: that selection preserved a feeling for morality because the moral group was more fit than the immoral group, even though the moral individual may have been less fit than the immoral individual. However, shortly after the just-quoted passages, Darwin did give evidence that this was the way in which he inclined:

It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet that an advancement in the standard of morality and an increase in the number of well-endowed men will certainly give an immense advantage to one tribe over another.52

Moreover, apparently Darwin told one of his young followers that in the case of man's moral sense, he believed that selection had to be acting at the level of the type rather than the individual.53

It would seem therefore that although Darwin resolutely opposed group selection in the non-human world, when it came to our own species, although again for almost everything he was an individual selectionist, in one crucial respect of our culture—our morality—he weakened and allowed that selection must have acted at the level of the population. He could not see how helping our fellows simultaneously helps our own reproduction, save one makes the reference unit of selection the group rather than the individual. Apparently, at the final point of evolution, Darwin became a group selectionist.

50 Ibid., vol. 1, 163.
51 Ibid.
52 Ibid., vol. 1, 166.
53 E. R. Romanes, *Life and letters of George John Romanes* (1893, London: Longmans), 173. It must be noted, however, that Romanes had his own special views on speciation, which might have made him a less-than-reliable reporter; see Kottler (footnote 26).
Nevertheless, whilst one can hardly deny some truth to this conclusion, there are two modifying points which should be made. First, it must be noted that even if Darwin became something of a group selectionist, he was never a group selectionist thinking that the crucial unit of selection is the species. His concern was at most for the tribe, and he was quite explicit that morality as it developed was to benefit fellow tribesmen, to the detriment of other members of the human species: 'There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection'.

It is true indeed that Darwin allowed that as civilization rises, one's moral concerns extend, through the human world and even to animals. But it is probable that at this point he would have thought we would have left the strictly biological, and have entered the realm of what we might anachronistically call 'cultural evolution'. In other words, here Darwin would possibly have thought that the biological individual-group selection debate was irrelevant. Certainly, he thought that modern culture transcends the biological: for instance, he rather lamented the fact that modern medicine allows the infirm to survive and reproduce, because as he pointed out, biologically this leads to the race becoming less fit.

It should also be noted that Darwin saw many of the tribe-members as being related, and he was quite clear that, as in the case of social instincts, human virtues can be spread through relatives, even if an individual does not survive. I am not suggesting that Darwin went so far as to think that the only kind of group selection involved in promoting morality collapsed into an individualistic kin selection. It is fairly definite that his primitive morality was supposed to aid all fellow tribesmen, including non-relatives. But, it does seem fair to say that his group selection was of a rather mild variety.

The second modifying point about Darwin's acceptance of group selection is that, whatever its degree, it was hesitant at best. Indeed, along with his group-selection explanation of human morality, he offered an individual-selection explanation as well! He argued that morality could have come about through what today's sociobiologists call 'reciprocal altruism', namely a form of enlightened self-interest, where being nice to others pays from an evolutionary viewpoint because they in turn are nice to you. Morality, Darwin suggested, may have begun because 'as the reasoning powers and foresight of the members became improved, each man would soon learn from experience that if he aided his fellow-men, he would commonly receive aid in return'. In other words, it would seem that even as Darwin strayed from the pastures of individual selection to those of group selection, he checked himself. Hence, with respect to human morality he ended up sitting firmly on the fence!

54 Darwin (footnote 12), vol. 1, 166.
55 Ibid., 103.
56 Ibid., 168.
57 Ibid., 161.
58 Trivers (footnote 5).
59 Darwin (footnote 12), vol. 1, 163.
5. Conclusion

Let us conclude our discussion by linking things to the contemporary scene. This is worth doing, not to make Darwin seem more modern than he really is, a pseudo-member of the Harvard biology department—he is too great to need this revisionist treatment—but because as we saw earlier, participants on both sides of today's debate about the levels of selection, particularly as they pertain to the evolution of humans, have invoked the past in defence of their own positions and criticism of their opponents'.

In the light of our discussion, one can only suspect that Darwin's sympathies today would lie with those who push individual selection a very long way. In the non-human world Darwin was a firm, even aggressive, individual selectionist. This did not of course stop him from arguing that peculiar phenomena like the social instincts would have evolved through such selection; although, as pointed out, his views on heredity were not sufficiently sophisticated to make worthwhile any attempt to decide which of the various modern hypotheses about the evolution of insect sociality he would have favoured. We cannot, for instance, tell whether Darwin would have supported kin selection or parental manipulation as the true cause of hymenopteran sociality. But queries at this level do not negate the fact that for organisms other than man, he unequivocally invoked individual selection.

Given the facts covered in the last section, it is obvious that at least a slight gap starts to open up between the Darwin of the last century and the total believer in individual selection of this century. For almost all aspects of man, indeed, there would be agreement in principle about the power of the individual selection, even though there might possibly be differences about the specific workings of such selection. However, it must be admitted that with respect to the evolution of morality Darwin seems to have been more sympathetic to group selection than would be a modern extremist like (for instance) R. L. Trivers. Nevertheless, given Darwin's general commitment to individual selection, his acceptance of group selection for morality seems to have been motivated more by the negative cause of being unable exactly to see how individual selection can cause morality, than by the positive cause of thinking that group selection validates itself on its own merits. Thus, were Darwin to have seen modern work like Trivers's explanation of morality through individualistic reciprocal altruism, he might well have responded positively: particularly since he himself gave the rudiments of such a reciprocal altruism argument!

It might be added moreover that, if one is determined to see Darwin in a modern light, even some of the most notorious human sociobiologists seem to allow that not everything is completely typical when we come to morality. Wilson, for instance, concedes that for human culture the genes have 'given away most of their sovereignty', and he certainly thinks we can (and should) act morally in the interests of our group, rather than the individual. Otherwise he could not argue as he does about the need to eliminate the human population explosion. Similarly, R. D. Alexander allows that we now be at the point where individual and group interest coincide, with respect to certain moral questions. In other words, the individual-group selection tension vanishes, because the two modes of selection fuse together.

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60 Wilson (footnote 5), 550.
62 Alexander (footnote 5).
We know that Darwin thought there comes a time when humans (in some respects) escape their biology. Hence, he would undoubtedly feel fairly sympathetic to the general kind of position that these biologists try to sketch out.

Finally, let us offer solace to the opponents of human sociobiology. If one is uncomfortable with a rather extreme individual selectionism, particularly as applied to man, and if one yet wants historical precedent to legitimize one's yearnings, then no less than the sociobiologists can one find the most respectable of intellectual ancestors. One may not be able to claim one of the fathers of evolutionism, but one can claim the other: Alfred Russel Wallace. He was a group selectionist, and moreover he was not prepared to see man treated on a par with other organisms. I certainly do not want to pretend that today's biologists would find convincing the details of Wallace's doubts about the all-sufficiency of individual selection, or that those who criticize human sociobiology grind the same metaphysical axe as did Wallace (although interestingly, politically Wallace was fairly left-wing, as are many of today's critics). But, given Wallace's conclusions, it does seem true to say that the critics of human sociobiology are no less part of the evolutionary tradition than those they criticize!

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63 A. R. Wallace, Studies: scientific and social (1900, London; Macmillan).