Biology and Philosophy **14:** 431–449, 1999.

A Critique of R.D. Alexander's Views on Group Selection

DAVID SLOAN WILSON
Department of Biological Sciences
Binghamton University
State University of New York
Binghamton, New York 13902-6000
U.S.A.
e-mail: dwilson@binghamton.edu

Abstract. Group selection is increasingly being viewed as an important force in human evolution. This paper examines the views of R.D. Alexander, one of the most influential thinkers about human behavior from an evolutionary perspective, on the subject of group selection. Alexander's general conception of evolution is based on the gene-centered approach of G.C. Williams, but he has also emphasized a potential role for group selection in the evolution of individual genomes and in human evolution. Alexander's views are internally inconsistent and underestimate the importance of group selection. Specific themes that Alexander has developed in his account of human evolution are important but are best understood within the framework of multilevel selection theory. From this perspective, Alexander's views on moral systems are not the radical departure from conventional views that he claims, but remain radical in another way more compatible with conventional views.

Key words: altruism, evolutionary ethics, group selection, human behavior, moral systems, multilevel selection, R.D. Alexander, superorganism

In 1966 Williams published a book criticizing what he called "some current evolutionary thought," in which he set out the general argument against "group selection" and chastised biologists for invoking selection uncritically at whatever level seemed convenient. William's book was the first truly general argument that selection is hardly ever effective on anything but the heritable genetic units of "genetic replicators" (Dawkins 1978) contained in the genotypes of individuals. (Alexander 1978: 36)

> In other words, I suggest that human social organization has for a long time been guided by direct intergroup competition, and that this theory provides an adaptive background for increases in group sizes and complexity of social organizations involving a built-in feedback effect of unparalleled explanatory value. (Alexander 1975)

> This beginning from biology poses four principal problems for students of morality. First, the potency of selection at lower levels such as the individual questions the usual view of moral behavior as serving the interests of others, or of the group as a whole . . . (Alexander 1992: 165)

> It is not easy for anyone to believe, from his own thoughts about his personal motivation and that of other humans, that humans are designed by natural selection to seek their own interests, let alone maximize their own genetic representation. (Alexander 1992: 190)

The purpose of this paper is to resolve ambiguities in the writings of R.D. Alexander on the subject of group selection. In general, Alexander identifies strongly with the gene-centered tradition of G.C. Williams (1966) and R. Dawkins (1976, 1982), which treats group selection as a negligible force in nature (e.g., the first passage quoted above). However, Alexander thinks that humans might be an exception to the rule and his emphasis on the importance of competition among human groups certainly suggests that group selection cannot be ignored (e.g., the second passage quoted above). Nevertheless, it is unclear what role group selection plays in the evolution of indirect reciprocity, punishment, reputation and other mechanisms that Alexander has proposed to explain human social behavior. At times he even seems to have abandoned his original conjecture that group selection is important in human evolution (e.g., the third and fourth passages quoted above).

One reason to resolve these ambiguities is a resurgence of interest in group selection, both in general and in relation to human evolution (reviewed by Sober and Wilson 1998; Wilson and Sober 1994; references that are most closely related to human behavior include Boehm 1981, 1997a,b; Boyd and Richerson 1982, 1985, 1988, 1989, 1990; Campbell 1979, 1983, 1991, 1994; Chepko-Sade et al. 1988; Eibl-Eibesfeldt 1982; Findlay 1992; Fix 1985; Gilpin and Taylor 1988; Harpending and Rogers 1987; Knauft 1991; MacDonald 1994; Pollock 1989, 1991; Richards 1987; Rogers 1990; Rushton 1989; Voorzanger 1984; Wilson 1989, 1997; Wilson and Dugatkin 1997). It is almost certain that the extreme rejection of group selection during the 1960's was undeserved and that unique aspects of our own species are relevant to the balance between levels of selection. Alexander's 60's-style rejection of group selection, coupled with the possible exception that he grants for human evolution, need to be related to these more recent developments.

First, I will summarize some of the developments that have restored group selection as a legitimate theory in evolutionary biology. Then I will attempt to describe Alexander's views on group selection as accurately as possible. Finally, I will try to reveal and correct a number of errors that lead Alexander to underestimate the importance of group selection in human evolution. It is not my purpose to belittle the importance of Alexander's contributions to the study of evolution and human behavior. On the contrary, I believe that some of his specific themes will become even more important when they are properly understood within the framework of multilevel selection theory.

In addition to clarifying multilevel selection theory, in which philosophers have taken a lively interest (reviewed by Sober and Wilson 1994), my critique of Alexander has implications for evolutionary ethics (Ruse 1986; Bradie 1994). In the third and fourth passages quoted above, Alexander clearly regards his account of human moral systems as a radical departure from conventional views that are based on promoting the common good. I will argue that Alexander's amended account is indeed radical, but in a way that is more compatible with conventional views.

A summary of multilevel selection theory

Multilevel selection theory envisions biological systems as a nested hierarchy of units. Genes reside within individuals, which reside within groups, which reside within metapopulations. Every unit is a population of subunits within which natural selection can occur. Genes can differ in fitness within individuals, individuals can differ in fitness within groups, and groups can differ in fitness within the metapopulation. When natural selection operates at a given level, it promotes traits that increase the relative fitness of units at that level. However, adaptations that evolve at one level of the hierarchy are not necessarily adaptive at higher levels and can even be highly maladaptive. For example, efficient predators might have the highest relative fitness within groups, while groups of efficient predators have a low relative fitness in the metapopulation because they overexploit their resources. The general rule is: Adaptation at a given level of the hierarchy requires a corresponding process of natural selection at that level.

During the 1960's, a consensus emerged that natural selection above the level of the individual, while theoretically possible, was so unlikely that it could be ignored (Williams 1966; see Sober and Wilson (1998) for a detailed history). The rejection of group selection was treated as a major event, similar to the rejection of Lamarkism, that allowed evolutionary biologists to close the book on one set of theoretical possibilities and concentrate their attention elsewhere. The confidence with which this conclusion was reached can be traced to a number of factors: Group-level views were stated in such a naive and grandiose form prior to the 60's that they were easy to dismiss. The mathematical models of group selection available at that time were not very plausible. And a number of theories were developed during the 60's, including kin selection and selfish gene theory, that seemed to explain apparently "altruistic" behavior in reductionistic terms. However, many evolutionary biologists became so close-minded about group selection that it became difficult for new developments to get a fair hearing.

In fact, new developments were not long in coming (reviewed by Sober and Wilson 1998; see also Hamilton 1996). Plausible mathematical models of group selection were developed in the 70's. Some of the most decisive empirical tests started to weigh in favor of group selection. Acceptance of these developments has been slow and group selection is still often portrayed as a book that does not need to be reopened. Nevertheless, it is virtually certain that the monolithic view of individuals as the only adaptive units in nature is wrong. The world is a complicated place in which adaptations can evolve at all levels of the biological hierarchy. A special supplementary issue of *The American Naturalist* (vol. 150) on multilevel selection provides a sample of the most recent developments.

Viewed in hindsight, many of the arguments against group selection reflect a massive confusion between different processes, that qualify as competing hypotheses, and different perspectives on a single process. Hamilton (1963, 1964a,b) originally developed inclusive fitness theory as an alternative to group selection, but later realized that it merely views multilevel selection from a different perspective (Hamilton 1975, 1987; see the autobiographical essays in Hamilton (1996) for his own account). As another example, Williams (1966) and Dawkins (1976, 1982) developed the idea that genes are the "fundamental" unit of selection because they have the property of persistence (they are replicators). Groups and individuals are too ephemeral to be replicators and therefore are ineffective units of selection. This was widely interpreted as an argument against group selection, as beautifully illustrated by the first Alexander passage quoted above. In retrospect, however, it has become obvious that the replicator concept does not address the group selection controversy. Group selectionists propose that groups are like individuals in the harmony and coordination of their parts. If neither individuals nor groups are replicators, then the replicator concept cannot be used to argue that they are different from each other (Wilson and Sober 1994).

Multilevel selection theory antedates selfish gene theory. Theorists such as Fisher, Wright and Haldane discussed the possibility of group selection without ever mentioning the word "replicator." For them it was obvious that it is *always* genes that evolve; the question was whether genes evolve by virtue of benefiting individuals, relative to other individuals within a population, or by virtue of benefiting whole groups, relative to other groups within a metapopulation. For selfish gene theory to approach these issues, something more than the replicator concept is required. Dawkins (1976) coined the term "vehicle of selection" to explain how individuals can evolve into adaptive units (= organisms) even though they are not replicators. The essence of the vehicle concept is “shared fate”, as illustrated by one of Dawkins’ metaphors in which members of a rowing crew must cooperate with each other to win the race. Similarly, genes within a single individual usually can increase their fitness only by increasing the fitness of the entire collective, which accounts for the organismic quality of individuals.

If the vehicle concept enables selfish gene theory to explain the adaptive organization of individuals, then the adaptedness of groups can be approached by asking whether groups can be vehicles of selection. There is now a broad consensus on this particular point (e.g., Dawkins 1982, 1989; Cronin 1991; Grafen 1984; Williams 1992). Thus, despite the appearances of decades, selfish gene theory is not an argument against group selection, but merely a different perspective on the same evolutionary forces that are examined by multilevel selection theory. Unfortunately, the vehicle concept itself is subject to a number of interpretations that seem to cloud the issue of whether groups can be vehicles of selection. In particular, is a group a vehicle whenever a trait influences the fitness of the group as a unit, or is it required that groups be units of shared fate with respect to most traits (Sterelny 1997)?

Perhaps the simplest way to resolve this issue is to return to the original framework of multilevel selection theory, which offers a straightforward procedure for identifying where the process of natural selection occurs in a nested hierarchy of units. One merely locates the units that differ in fitness within the next higher unit (Wilson and Sober 1994). This is one rendering of the vehicle concept; multilevel selection theory shows that it is the one most relevant to the question of whether groups can evolve into adaptive units, with respect to particular traits.

Against this background, I will now attempt to describe Alexander’s views on group selection.

Alexander on genomic group selection

Some of Alexander’s strongest statements in favor of group selection refer, not to human groups, but to the genes within individual organisms.

> The genes in the genomes of asexual organisms . . . are in fact group selected, and for most practical purposes so are those in sexual organisms . . . The evidence that genes in genomes are group-selected is, first, that they have evolved to co-exist in the same group (genome), and to die within the group in which they initially placed themselves, leaving only their dispersed progeny in sexually produced gametes or their descendants as products of asexual mitosis . . . second, they have evolved to

> share equally in the reproductive opportunities afforded in their respective groups ... As a consequence, once formed, the genome is ... an indivisible unit with a unified function; the interests of all the genes in a genome are identical all the time (asexual organisms) or nearly all the time (sexual organisms). It is an aspect or outcome of this evolved identity that the organism has come to be an entity selected according to a singular principle: the maximization of inclusive fitness ... Recombination is not differential reproduction; during oogenesis no chromosome or gene gains from ending up in a polar body, yet each allele has essentially an equal chance of appearing in the daughter cell destined to become an egg. A minuscule amount of differential reproduction occurs during this crucial less than one-millionth part of the life span, as a result of meiotic drive. To the extent that Mendelian expectations hold in inheritance, however, differential reproduction of alleles occurs because of the differential success of the groups (entire genomes) in which they find themselves ... (Alexander 1992: 166–167; 1987: 69).

Alexander does not mention the term "vehicle" by name, but he is clearly invoking the concept of shared fate and equal fitness of genetic units *within* individuals to explain the organismic properties *of* individuals. Alexander and Borgia (1978) have also developed the thesis that the rules of meiosis promoting equal fitness within the genome are an evolved adaptation – a "parliament" of genes suppressing the actions of "outlaw" genes that benefit themselves at the expense of the collective.

I am in complete agreement with these passages by Alexander and would like to stress one elementary implication. A gene that increases the fitness of the genome increases its own fitness as part of the collective. Indeed, it is hard to imagine how it could be otherwise. Thus, a gene does not have to be *altruistic* (i.e., have low fitness relative to other genes in the genome) to evolve by genomic group selection. It is enough simply to benefit the collective.

Alexander on selection among groups of individuals

The following passage is one of Alexander's most detailed descriptions of selection among alternative groups of individuals. I have inserted numbers in brackets to refer to specific parts of this passage in my analysis.

> [1] It is easy to imagine traits that would be genetically altruistic such as lowered rates of reproduction that help the population survive but reduce the reproductive success of their individual bearers. [2] For such traits to spread by helping the population, differential reproduction of populations

> within which such altruism was more prevalent would have to exceed that of populations within which it was less prevalent. [3] Social groups and populations geographically close enough to replace one another in the event of unilateral extinction, unlike individuals, characteristically lack the integrity to develop large differences that would result in differential reproduction. [4] To support the concept of group selection it is not enough that groups or populations simply become extinct differentially, even if such groups also possess genetic differences, as they almost always will. For differential extinction of groups actually to be selective in nature . . . the differences between groups must be responsible for the differential extinction. [5] This stringent requirement also leaves aside the difficult question of how altruistic traits spread when they first appear so that they can become more frequent in some populations than in others and produce the hypothetical kinds of situations in which group selection seems to have some likelihood of operating . . . [6] For these reasons, any significant amount of evolution by group selection seems to be an exceedingly remote possibility (Alexander 1979: 41).

Leaving aside for the moment Alexander's gloomy prognosis for the likelihood of group selection, his description of the process of group selection is fairly accurate. In particular, traits that benefit whole groups can spread only by causing groups possessing the trait to out-reproduce other groups [2]. If these traits are also disadvantageous within groups (i.e., they are altruistic), then the process of group selection must be correspondingly strong [5]. The differential fitness of groups per se is not sufficient but must be caused by underlying variation in the trait [4].

Other aspects of the passage are less accurate. The focus on unilateral extinction in [3] and [4] is unnecessary. As Alexander himself implies in [2], the key requirement is differential *fitness* of populations. Just at fitness at the individual level includes both survival and fecundity, fitness as the population level includes both extinction and productivity. A trait that causes groups to fission at a greater rate (e.g., Haldane 1932) or to send out more emigrants (e.g., Hamilton 1975) would be favored by group selection, as surely as a trait that decreases extinction rate. I assume that Alexander would agree with this amendment of his passage.

The focus on altruism is also inappropriate. Altruism requires group selection to evolve, but group selection is not confined to altruistic traits. As we have seen, most traits that evolve by genomic group selection are not altruistic, but benefit themselves as part of the collective. Natural selection within genomes is neutral, which allows traits to easily evolve by genomic group selection. Similarly, a trait that benefits the entire group of individuals as a collective would be selectively neutral within groups, and should evolve by group selection more easily than altruistic traits. It is possible that such traits seldom exist, because benefiting the group usually requires individual self-sacrifice. However, if such traits *do* exist, their evolution qualifies as an example of group selection. Alexander should agree with this statement to remain consistent with his views on genomic group selection, but it is not obvious that he does.

Alexander on human group selection

Alexander's view that group selection may have been important in human evolution was first expressed in 1974:

> I began with a denial of any great significance for the phenomenon of group selection. It is appropriate, perhaps, to finish with a caveat. For two reasons human social groups represent an almost ideal model for potent selection at the group level. First, the human species is (and possibly always has been) composed of competing and essentially hostile groups that frequently have not only behaved toward one another in the manner of different species, but also have been quick to develop enormous differences in reproductive and competitive ability because of cultural innovation and its cumulative effects. Second, human groups are uniquely able to plan and act as units, to look ahead and purposely carry out actions designed to sustain the group and improve its competitive position. These features may actually represent an exhaustive list of the precise attributes of a species that would maximize its likelihood of significant group selection, or evolution by differential extinction of groups (Alexander 1974: 376).

I cannot resist commenting that the ability of human groups to act and plan as units seems more like the *product* of group selection than a precondition for group selection! In any case, the importance of between-group competition is a major theme that Alexander emphasizes throughout his writings. In addition, Alexander (1987: 69) has compared human moral systems to the genetic rules of meiosis that, according to Alexander, evolved by genomic group selection. Thus, it seems that he regards group selection as a major force in human evolution. A closer look, however, suggests otherwise. The passage quoted above comes at the *end* of Alexander's (1974) paper on the evolution of social behavior, which means that he found it unnecessary to invoke group selection to develop the major conceptual themes that are continued in his later papers. Also revealing is a taxonomy of altruistic and selfish behaviors that Alexander introduced in his 1974 paper and repeated with modifications in subsequent works. Alexander makes a distinction between "phenotypic" and “genotypic” altruism and selfishness. The modifier “phenotypic” refers to whether a trait appears altruistic or selfish at the behavioral level, while the modifier “genotypic” refers to whether the trait evolved by individual or group selection. For example, a caring attitude towards others appears altruistic at the behavioral level but might still have evolved by within-group selection (see Sober and Wilson (1998) for a detailed analysis of the relationship between evolutionary and psychological altruism). Phenotypic and genotypic altruism and selfishness result in four categories that Alexander presents as a 2×2 table along with lists of specific examples. Starting in 1974, genotypically altruistic traits are marked with an asterisk to indicate that they will not evolve. Yet, this is the kind of altruism that evolves by group selection according to Alexander! If Alexander thought that group selection was important in human evolution, he might have acknowledged the possibility of genotypic altruism in versions of the table that are published in his works on human evolution. He does not (e.g., Alexander 1978: 40). In fact, the most recent versions of the table do not even include genotypic altruism as a category, but only lists of genotypically selfish traits. Thus, despite his emphasis on between-group competition and fitness-levelling within groups, Alexander evidently thinks that he does not need to invoke group selection to explain the aspects of the human psyche that he has explored. His positive statements about group selection are in the form of an abstract possibility, detached from any specific proposals. Even the positive statement is absent from the most recent article included in this critique (Alexander 1992).

Another passage by Alexander (1987: 169) is worth quoting because it evaluates Darwin’s views on group selection. Alexander first provides the following passage from Darwin (1871 p 500; for brevity I do not include the entire quote):

> 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 increase in the number of well-endowed men and advancement in the standard of morality will certainly give an immense advantage to one tribe over another. 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 aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection. At all times throughout the world tribes have supplanted other tribes; and as morality is one important element in their success, the standard of morality and the number of well-endowed men will thus everywhere tend to rise and increase.

Alexander then comments:

> This is a group selection model, but one that depends on confluences of interests within groups and does not deny the existence of countering conflicts of interest within groups. Thus, it is an appropriate model because, despite Darwin's ignorance of the genetic materials, it would operate through the survival of alleles as a result of selection at the group level.

Here, at least, Alexander acknowledges a form of group selection without altruism that is consistent with his views on genomic group selection. Later he cites both himself (Alexander 1974) and my own models (Wilson 1975, 1980) as consistent with Darwin's view. However, Alexander then raises the possibility that high moral standards are individually advantageous because they earn praise and avoid the condemnation of other group members. The final verdict appears to be that group selection is unimportant after all and certainly is not required to explain the traits of praise and condemnation that cause others to maintain high moral standards.

A critique of Alexander's views

Multilevel selection theory can be mathematically complex (as can inclusive fitness theory), but the basic conceptual framework is easily understood. Even if natural selection always results in gene frequency change, the units that become functionally organized depend on where the fitness differences occur in the biological hierarchy. The question of individual vs. group selection concerns whether genes evolve by virtue of increasing the fitness of individuals, relative to other individuals in the same group, or by increasing the fitness of groups, relative to other groups in the metapopulation.

Alexander agrees with this framework in his discussion of genomic group selection and in some of his passages on selection among groups of individuals. In other respects, however, he violates the same framework. In fact, *most* of the major themes that Alexander has emphasized as important in human evolution invoke group selection, even though Alexander thinks they do not.

Evolutionary biologists who reject group selection rely on two major principles to explain helping behaviors; kin selection, which favors helping among genetic relatives, and reciprocity, which favors helping among individuals who return each other's benefits. In their simplest forms, these two principles are unable to explain many forms of helping in human groups, which are directed towards non-relatives and people who are unlikely to reciprocate in the future. Alexander is aware of this problem and has attempted to solve it with a theory of "indirect reciprocity" that relies only on self-interest (Alexander 1987: 94):

> Returns from indirect reciprocity may take at least three major forms: 1) The beneficent individual may later be engaged in profitable reciprocal interactions by individuals who have observed his behavior in directly reciprocal interactions and judged him to be a potentially rewarding interactant (his “reputation” or “status” is enhanced, to his ultimate benefit); 2) the beneficent individual may be rewarded with direct compensation from all or part of the group (such as with money or a medal or social elevation as a hero) which, in turn, increases his likelihood of . . . receiving additional perquisites; or 3) the beneficent individual may be rewarded by simply having the success of the group within which he behaved beneficently contribute to the success of his own descendant and collateral relatives.

Let us examine these explanations in reverse order. The third explanation invokes group selection, pure and simple. Alexander is describing a situation in which a trait benefits the entire group and is selectively neutral within groups. If the lower-level unit was a gene and the higher-level unit was the genome, Alexander would classify it as an example of genomic group selection. Yet, when the lower-level unit is an individual and the higher-level unit is a social group, Alexander regards it as an example of individual self-interest that does not require group selection.

I will shortly argue that the other explanations involve the same kind of error. First, however, it is important to discuss why such an elementary error (from the standpoint of multilevel selection theory) can be committed. Alexander and many other evolutionary biologists who think they have rejected group selection often employ the following rule of thumb to predict which of two alternative behaviors will be favored by natural selection: If an individual performs x, then it will have a fitness of W_x. If the individual performs y,then it will have a fitness of W_y. Behavior x evolves when $W_x > W_y$, and, of course, it evolves by individual selection. Notice that this rule of thumb resembles the reasoning of a psychological egoist who cares only about his own welfare without regard to anyone else. By this reasoning, a behavior that benefits the individual along with the rest of its group appears as an example of self interest.

Unfortunately, this rule of thumb says nothing whatsoever about relative fitness, which, as Williams (1966) stressed, is the criterion for all evolution by natural selection. We must therefore confirm the rule of thumb with a proper model that is based on relative fitness. If a behavior increases *only* the fitness of the actor, without any effects on other members of the group, then increasing absolute individual fitness also increases relative fitness within the group. Group selection is not required to explain these behaviors. However, the behavior that Alexander is considering extends beyond the individual to affect the fitness of the entire group. For this behavior to be more than selectively neutral, all the ingredients of a group selection model are required; a population of groups, that vary with respect to the trait, with corresponding variation in group fitness. *Extreme* variation among groups is not required because group selection is not opposed by selection within groups. In fact, random variation among groups is sufficient, just as it is sufficient for genomic group selection. However, these nuances are lost on those who regard group selection as a dead issue and rely on a rule of thumb that involves thinking like an egoist to predict what evolves by natural selection.

Now let's consider the second explanation in which an individual who helps others is rewarded by other members of the group. The original helping behavior no longer appears altruistic, but we still must explain how the *rewarding* behavior evolves. If I reward someone for promoting the common good, *I* am promoting the common good (economists call this a second-order public goods problem; see Hawkes 1993; Heckathorn 1990, 1993). If my efforts involve time, energy, or risk, then I promote the common good at a cost to myself and I qualify as an altruist in terms of multilevel selection theory. The cost of rewarding others is sometimes very low, but even if it was zero, the rewarding behavior would be selectively neutral within groups and would still require group selection to evolve. Explaining helping behavior in terms of rewards and punishments merely replaces one multilevel selection problem with another (Sober and Wilson 1998).

Alexander's first explanation has been analyzed in detail by Wilson and Dugatkin (1997). Consider a group of individuals that differ in their propensity to help others. If interactions are random, then the least helpful individuals will have the highest relative fitness within the group. However, interactions are not random because each individual acquires a reputation based on their helping behavior. Let's say that the group is composed of 100 individuals and a particular social interaction requires the participation of 10 people. If free choice is possible, then the 10 most helpful individuals will interact with each other, followed by the next 10 most helpful individuals, and so on down to the ten least helpful individuals who interact with each other, not because they want to, but because they are avoided by everyone else. Wilson and Dugatkin (1997) confirm Alexander's intuition that reputation, coupled with free choice in social interaction, is a powerful mechanism for the evolution of helping behavior. However, from the standpoint of multilevel selection theory it is obvious that the mechanism works by turning the group into a metapopulation of smaller groups. Natural selection favors the *least* helpful individual within each group but favors the *most* helpful group within the metapopulation. Once again, explaining helping behavior in terms of reputation merely replaces one multilevel selection problem with another.

Detailed analyses of these topics from the standpoint of multilevel selection theory are available elsewhere (reviewed by Sober and Wilson (1998), who also discuss criteria for defining groups). Collectively, they lead to the following conclusion: Often it is obvious from the biology of the situation that an evolving trait is expressed in a well-defined group and that many such groups exist in a metapopulation. Evaluating fitness differences within and among groups is straightforward, allowing levels of selection to be easily identified in a multilevel selection model. Nevertheless, Alexander routinely classifies traits that are selectively neutral or disadvantageous within groups as examples of individual self-interest that do not require group selection to evolve. This classification is not based on a principled discussion of multilevel selection theory. In fact, Alexander's most detailed statements about multilevel selection make it clear that the traits *should* be classified as examples of group selection. Rather, Alexander unwittingly employs a double standard in which traits are sometimes classified, not in terms of fitness differences within and among groups, but in terms of their absolute fitness or some other description that resonates with psychological egoism.

The double standard that I have described in detail for Alexander is extremely widespread among evolutionary biologists (see Sober and Wilson 1998; Wilson 1998 for additional examples). Understanding how it developed would be a worthy subject for historians and philosophers of science. I do not claim that Alexander originated the double standard, but he has certainly contributed to its influence.

Alexander's ideas from the multilevel perspective

I mentioned earlier that it is not my purpose to belittle the importance of Alexander's ideas. He was among the first to emphasize the role of between-group competition, rewards and punishments, reputation and other factors in the evolution of human behavior. These factors remain important but they must be understood within the framework of multilevel selection theory, rather than as alternatives to group selection.

Even weak group selection can be an important evolutionary force when it is not opposed by selection within groups. Virtually all individual-level adaptations evolve in the form of genes that benefit the collective without any personal cost, a process that Alexander calls genomic group selection. If individuals could routinely benefit their social groups at no personal cost, then social groups would evolve into organismic units by a similar process. One argument against group selection would be to claim that such traits do not exist. There is no free lunch, and benefiting a group usually involves time, energy, or risk on the part of its members. Alexander does not employ this argument, freely speculating about behaviors that benefit groups at little or no individual cost. Furthermore, Alexander is probably right. It is a remarkable fact about human social life that individuals can often greatly reward and punish others at little or no cost to themselves. Behaviors that would be altruistic if they were performed voluntarily can be promoted by rewards and punishments, which themselves require only mild forms of group selection to evolve – a process that Sober and Wilson (1998) call "the amplification of altruism". Rewards, punishments, and other forms of social control probably vastly increase the importance of group selection in human evolution. Alexander was among the first to use the language of human social control to describe genetic interactions – sheriffs, outlaws, parliaments, rules of fairness, and so on – so it is ironic that he has avoided the natural conclusion that human social groups can be like genomes. Multilevel selection theory completes the metaphor by showing that both genomes and human social groups can be products of higher-level selection.

Stronger forms of group selection are required to evolve altruistic traits, which are disfavored within groups. Kin selection is properly understood as a strong form of group selection, as Hamilton realized in 1975, since genetic variation among kin groups is greater than among randomly formed groups. However, relatedness is not the only way to increase genetic variation among groups. Groups of unrelated individuals that form on the basis of reputation can be as favorable for the evolution of altruism as groups of close relatives (Wilson and Dugatkin 1997; see also Hamilton 1975: 141). Reputation is better studied as a factor that alters the balance between levels of selection than as an alternative to group selection.

Within-group selection favors traits that maximize relative fitness within groups. Psychological egoists strive to increase their welfare regardless of their effects on others. The behaviors chosen by a psychological egoist who equates welfare with fitness therefore do not necessarily correspond to the behaviors that evolve by within-group selection, as Alexander and many other evolutionary biologists have tacitly assumed. Simple rules of thumb for predicting what evolves do not substitute for a proper model that compares relative fitnesses within and among groups. As odd as it may seem, group selection is probably required to explain many aspects of psychological egoism in addition to psychological altruism (Sober and Wilson 1998).

The sense in which Alexander's theory of moral systems is radical

In addition to his specific proposals, Alexander's writings are imbued with the metatheme of human nature as selfish to the core. He also regards his views as fundamentally at odds with the conventional view of morality as dedicated to the common good. We must question Alexander's metatheme, in addition to his specific proposals.

Research in human evolutionary biology is remarkable for being mundane and radical at the same time. For example, Buss (1994) and others have shown that men tend to prefer youth and beauty in women while women tend to prefer wealth and status in men. Daly and Wilson (1988) have shown that children are at much greater risk of abuse from step-parents than from natural parents. I know from experience as a teacher that students who encounter these and other studies in human evolutionary biology are profoundly influenced and claim to see the world with new eyes. How is this possible, when the average person in a bar or a supermarket would have correctly predicted the same results based on their folk psychology?

The answer to this question is complex and only two factors will be considered here. First, folk psychology is not based on a coherent conceptual framework that is derived from a few axioms. When a conceptual framework such as evolutionary theory makes predictions on subjects as diverse as mate choice and child abuse, the effect can be breathtaking even if each specific prediction is mundane from the standpoint of folk psychology. Second, folk psychology is not always correct and evolutionary theory can be used to reject some aspects even as it confirms others. For example, the folk psychology of many cultures treats women as mentally inferior, without sexual appetites and innately monogamous. Evolutionary theory makes these claims unlikely as facts and also explains why they should exist as adaptive fictions, a psychological counterpart to the physical methods that men use to control the reproduction of women. In general, folk psychology should be a mixture of valid observations about human nature and adaptive fictions that are useful to the believer even though they are factually incorrect (Wilson 1990, 1995). Evolutionary theory can sort out which is which and can also explain the specific content of adaptive fictions. In any case, since the valid component of folk psychology is the "toughest kid on the block" when it comes to explaining human nature (Symons 1987), we should expect many of the predictions that emerge from human evolutionary biology to be mundane from the standpoint of folk psychology.

Alexander regards his theory of moral systems as radical in a sense that has no counterpart in folk psychology.

> I suspect that nearly all humans believe it is a normal part of the functioning of every human individual now and then to assist someone else in the realization of that person's own interests to the actual net expense of those of the altruist. What this "greatest intellectual revolution of the century" tells us is that, despite our intuitions, there is not a shred of evidence to support this view of beneficence, and a great deal of convincing

> theory suggests that any such view will eventually be judged false. This implies that we will have to start all over again to describe and understand ourselves, in terms alien to our intuitions, and in one way or another different from every discussion of this topic across the whole of human history (Alexander 1987: 3).

It is hard to believe that the same person who wrote this statement also proposes that group selection has been a significant force in human evolution. The rule "help others without expectation of personal gain" is the quintessential group-level strategy. Groups of individuals that follow this rule will possess the harmony and coordination of an organism and will out perform all other groups. Obviously there is a freeloader problem, but human groups are often designed to be freeloader-resistant. Anti-freeloader mechanisms are not perfect, but to the degree that they work the rule "help others without expectation of personal gain" should be a successful evolutionary strategy and part of the repertoire of all normal human beings. Alexander's statement is justified only if group selection played no role whatsoever in human evolution.

When Alexander's ideas are properly related to multilevel selection theory, they cease to be radical in the sense that he thinks and become strikingly similar to elements of folk psychology. The everyday notions of selfish and unselfish, immoral and moral, correspond closely to the behaviors favored by within- and among-group selection, respectively. The idea that moral systems are designed to promote the common welfare of groups can be accepted at face value. At a finer scale, some moral systems can even be interpreted as a detailed set of instructions for how to build a group-level vehicle of selection (see the discussion of Hutterites in Wilson and Sober 1994).

In my opinion, discovering the evolutionary logic of conventional morality is far more exciting than Alexander's individualism, which is, after all, hardly radical within the academic disciplines of evolutionary biology, psychology and economics. It is enough to achieve the same kinds of insights for morality that have been achieved for mate choice and child abuse. The specific themes developed by Alexander have contributed to this goal and will contribute even more when they are properly embedded in a theory of natural selection as a multilevel process.

Acknowledgements

I thank R.D. Alexander, C. Boehm, A.B. Clark, L.A. Dugatkin, G. Pollack, B. Smuts, E. Sober and G.C. Williams for helpful discussion.

References

Alexander, R. and Borgia, G.: 1978, ‘Group Selection, Altruism and the Levels of Organization of Life’, *Annual Review of Ecology and Systematics* **9**, 449–475.

Alexander, R.D.: 1974, ‘The Evolution of Social Behavior’, *Annual Review of Ecology and Systematics* **5**, 325–383.

Alexander, R.D.: 1975, ‘The Search for a General Theory of Behavior’, *Behavioral Science* **20**, 77–100.

Alexander, R.D.: 1979, *Darwinism and Human Affairs*, University of Washington Press, Seattle.

Alexander, R.D.: 1987, *The Biology of Moral Systems*, Aldine de Gruyter, New York.

Alexander, R.D.: 1988, ‘Knowledge, Intent and Morality in Darwin’s World’, *Quarterly Review of Biology* **63**, 441–443.

Alexander, R.D.: 1989, ‘The Evolution of the Human Psyche’, in P. Mellars and C. Stringer (eds.), *The Human Revolution*, University of Edinburgh Press, Edinburgh, pp. 455–513.

Alexander, R.D.: 1992, ‘Biological Considerations in the Analysis of Morality’, in M.H. Nitecki and D.V. Nitecki (eds.), *Evolutionary Ethics*, SUNY Press, Albany, NY, pp. 163–196.

Boehm, C.: 1981, ‘Parasitic Selection and Group Selection: A Study of Conflict Interference in Rhesus and Japanese Macaque Monkeys’, in A.B. Chiarelli and R.S. Corruccini (eds.), *Primate Behavior and Sociobiology*, Springer-Verlag, Berlin, pp. 161–182.

Boehm, C.: 1997a, ‘Emergency Decisions, Cultural Selection Mechanics and Group Selection’, *Current Anthropology*, in press.

Boehm, C.: 1997b, ‘Impact of the Human Egalitarian Syndrome on Darwinian Selection Mechanics’, *American Naturalist* **150**, S100–S121.

Boyd, R. and Richerson, P.J.: 1982, ‘Cultural Transmission and the Evolution of Cooperative Behavior’, *Human Ecology* **10**, 325–351.

Boyd, R. and Richerson, P.J.: 1985, *Culture and the Evolutionary Process*, University of Chicago Press, Chicago.

Boyd, R. and Richerson, P.J.: 1988, ‘The Evolution of Reciprocity in Sizable Groups’, *Journal of Theoretical Biology* **132**, 337–356.

Boyd, R. and Richerson, P.J.: 1989, ‘The Evolution of Indirect Reciprocity’, *Social Networks* **11**, 213–236.

Boyd, R. and Richerson, P.J.: 1990, ‘Group Selection Among Alternative Evolutionarily Stable Strategies’, *Journal of Theoretical Biology* **145**, 331–342.

Boyd, R. and Richerson, P.J.: 1990, ‘Culture and Cooperation’, in J.J. Mansbridge (eds.), *Beyond Self-Interest*, University of Chicago Press, Chicago, pp. 111–132.

Boyd, R. and Richerson, P.J.: 1992, ‘Punishment Allows the Evolution of Cooperation (or Anything Else) in Sizable Groups’, *Ethology and Sociobiology* **13**, 171–195.

Bradie, M.: 1994, *The Secret Chain: Evolution and Ethics*, State University of New York Press, Albany, NY.

Buss, D.: 1994, *The Evolution of Desire*, Basic Books, New York.

Campbell, D.T.: 1979, ‘Comments on the Sociobiology of Ethics and Moralizing’, *Behavioral Science* **24**, 37–45.

Campbell, D.T.: 1983, ‘The Two Distinct Routes Beyond Kin Selection to Ultra-Sociality: Implications for the Humanities and Social Sciences’, in D.L. Bridgeman (ed.), *The Nature of Prosocial Development: Interdisciplinary Theories and Strategies*, Academic Press, New York, pp. 11–41.

Campbell, D.T.: 1991, ‘A Naturalistic Theory of Archaic Moral Orders’, *Zygon* **26**, 91–114.

Campbell, D.T.: 1994, ‘How Individual and Face-to-Face-Group Selection Undermine Firm Selection in Organizational Evolution’, in J.A.C. Baum and J.V. Singh (eds.), *Evolutionary Dynamics of Organizations*, Oxford University Press, New York, pp. 23–38.

Chepko-Sade, B.D., Dow, M.M. and Cheverud, J.M.: 1988, ‘Group Selection Models with Population Substructure Based on Social Interaction Networks’, *American Journal of Physical Anthropology* **77**, 427–433.

Cronin, H.: 1991, *The Ant and the Peacock: Altruism and Sexual Selection from Darwin to Today*, Cambridge University Press, Cambridge.

Daly, M. and Wilson, M.: 1988, *Homicide*, Aldine de Gruyter, New York.

Darwin, C.: 1871, *The Descent of Man and Selection in Relation to Sex*, Appleton, New York.

Dawkins, R.: 1976, *The Selfish Gene* (1st ed.), Oxford University Press, Oxford.

Dawkins, R.: 1978, ‘Replicator Selection and the Extended Phenotype’, *Zeitschrift fur Tierpsychologie* **47**, 61–76.

Dawkins, R.: 1982, *The Extended Phenotype*, Oxford University Press, Oxford.

Dawkins, R.: 1989, *The Selfish Gene* (2nd ed.), Oxford University Press, Oxford.

Eibl-Eibesfeldt, I.: 1982, ‘Warfare, Man’s Indoctinability and Group Selection’, *Zeitschrift fur Tierpsychologie* **60**, 177–198.

Findlay, C.S.: 1992, ‘Phenotypic Evolution Under Gene-Culture Transmission in Structured Populations’, *Journal of Theoretical Biology* **156**, 387–400.

Fix, A.G.: 1985, ‘Evolution of Altruism In Kin-Structured and Random Subdivided Populations’, *Evolution* **39**, 928–939.

Gilpin, M.E. and Taylor, B.L.: 1988, ‘Comment on Harpending and Roger’s Model of Intergroup Selection’, *Journal of Theoretical Biology* **135**, 131–135.

Grafen, A.: 1984, ‘Natural Selection, Kin Selection and Group Selection’, in J. Krebs and N. Davies (eds.), *Behavioural Ecology: An Evolutionary Approach* Blackwell Scientific Publications, Oxford, pp. 62–84.

Haldane, J.B.S.: 1932, *The Causes of Evolution*, Longmans Green and Co., London.

Hamilton, W.D.: 1963, ‘The Evolution of Altruistic Behavior’, *American Naturalist* **97**, 354–356.

Hamilton, W.D.: 1964a, ‘The Genetical Evolution of Social Behavior, I’, *Journal of Theoretical Biology* **7**, 1–16.

Hamilton, W.D.: 1964b, ‘The Genetical Evolution of Social Behavior, II’, *Journal of Theoretical Biology* **7**, 17–52.

Hamilton, W.D.: 1975, ‘Innate Social Aptitudes in Man, an Approach from Evolutionary Genetics’, in R. Fox (eds.), *Biosocial Anthropology*, Malaby Press, London.

Hamilton, W.D.: 1987, ‘Discriminating Nepotism: Expectable, Common, Overlooked’, in D.J.C. Fletcher and C.D. Michener (eds.), *Kin Recognition in Animals*, John Wiley and Sons, New York.

Hamilton, W.D.: 1996, *The Narrow Roads of Gene Land*, W.H. Freeman/Spektrum, Oxford.

Harpending, H.C. and Rogers, A.R.: 1987, ‘On Wright’s Mechanism for Intergroup Selection’, *Journal of Theoretical Biology* **127**, 51–61.

Hawkes, K.: 1993, ‘Why Hunter-Gatherers Work: An Ancient Version of the Problem of Public Goods’, *Current Anthropology* **34**, 341–361.

Heckathorn, D.D.: 1990, ‘Collective Sanctions and Compliance Norms: A Formal Theory of Group-Mediated Social Control’, *American Sociological Review* **55**, 366–384.

Heckathorn, D.D.: 1993, ‘Collective Action and Group Heterogeneity: Voluntary Provision vs. Selective Incentives’, *American Sociological Review* **58**, 329–350.

MacDonald, K.B.: 1994, *A People That Shall Dwell Alone: Judaism as a Group Evolutionary Strategy*, Praeger, Westport, Connecticut.

Pollock, G.: 1989, ‘Population Structure, Spite and the Iterated Prisoner’s Dilemma’, *American Journal of Physical Anthropology* **77**, 459–69.

Pollock, G.B.: 1991, ‘Crossing Malthusian Boundaries: Evolutionary Stability in the Finitely Repeated Prisoner’s Dilemma’, *Journal of Quantitative Anthropology* **3**, 159–180.

Richards, R.J.: 1987, *Darwin and the Emergence of Evolutionary Theories of Mind and Behavior*, University of Chicago, Chicago.

Rogers, A.R.: 1990, ‘Group Selection by Selective Emmigration: The Effects of Migration and Kin Structure’, *American Naturalist* **135**, 398–413.

Ruse, M.: 1986, *Taking Darwin Seriously*, Basil Blackwell, New York.

Rushton, J.P.: 1989, ‘Genetic Similarity, Human Altruism and Group Selection’, *Behavioral and Brain Sciences* **12**, 503–559.

Sober, E. and Wilson, D.S.: 1994, ‘A Critical Review of Philosophical work on the Units of Selection Problem, *Philosophy of Science* **61**, 534–555.

Sober, E. and Wilson, D.S.: 1998, *Unto Others: The Evolution and Psychology of Unselfish Behavior*, Harvard University Press, Cambridge, MA.

Sterelny, K.: 1997, ‘The Return of the Group’, *Philosophy of Science*, in press.

Symons, D.: 1987, ‘If We’re All Darwinians, What’s All the Fuss About?’, in C.B. Crawford, M.F. Smith and D.L. Krebs (eds.), *Sociobiology and Psychology: Ideas, Issues and Applications*, Lawrence Erlbaum Associates, Hillsdale, N.J.

Voorzanger, B.: 1984, ‘Altruism in Sociobiology: A Conceptual Analysis’, **13**, 33–39.

Williams, G.C.: 1966, *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*, Princeton University Press, Princeton.

Williams, G.C.: 1986, ‘A Defence of Reductionism in Evolutionary Biology’, in R.A. and M.R. Dawkins (eds.), *Oxforf Surveys in Evolutionary Biology*, Oxford University Press, Oxford, pp. 1–27.

Williams, G.C.: 1992, *Natural Selection: Domains, Levels and Challenges*, Oxford University Press, Oxford.

Wilson, D.S.: 1975, ‘A Theory of Group Selection’, *Proceedings of the National Academy of Sciences* **72**, 143–146.

Wilson, D.S.: 1980, *The Natural Selection of Populations and Communities*, Benjamin Cummings, Menlo Park.

Wilson, D.S.: 1989, ‘Levels of Selection: An Alternative to Individualism in Biology and the Social Sciences’, *Social Networks* **11**, 257–272.

Wilson, D.S.: 1990, ‘Species of Thought: A Comment on Evolutionary Epistemology’, *Biology and Philosophy* **5**, 37–62.

Wilson, D.S.: 1995, ‘Language as a Community of Interaction Belief Systems: A Case Study Involving Conduct Toward Self and Others’, *Biology and Philosophy* **10**, 77–98.

Wilson, D.S.: 1997, ‘Incorporating Group Selection into the Adaptationist Program: A Case Study Involving Human Decision Making’, in J. Simpson and D. Kendrick (eds.), *Evolutionary Social Psychology*, Erlbaum, Mahwah, NJ, pp. 345–386.

Wilson, D.S. and Dugatkin, L.A.: 1997, ‘Group Selection and Assortative Interactions’, *American Naturalist* **149**, 336–351.

Wilson, D.S., Pollock, G.B. and Dugatkin, L.A.: 1992, ‘Can Altruism Evolve in Purely Viscous Populations?’, *Evolutionary Ecology* **6**, 331–341.

Wilson, D.S. and Sober, E.: 1994, ‘Re-Introducing Group Selection to the Human Behavioral Sciences’, *Behavioral and Brain Sciences* **17**, 585–654.