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ABSTRACT

In spite of its checkered intellectual history, and in spite of the myriad proposals of alternative models that claim both to account for the range of human behavior and to dispense with the need for selection above the organism level, a multilevel selection framework allowing for biological as well as cultural group selection remains the only coherent means of accounting for the persistence and spread of behavioral inclinations which, at least upon first appearance at low frequency, would have been biologically altruistic. This argument is advanced on three tracks: through a review of experimental and observational evidence inconsistent with a narrow version of rational choice theory, through a critique of models or explanations purporting to account for prosocial behavior through other means, and via elaboration of the mechanisms, plausibility, and intellectual history of biological group selection.

Introduction

A growing body of experimental and observational evidence on the behavior of humans, and, increasingly, that of our close animal relatives, is difficult to square with rational choice models premised on the proposition that we always choose so as efficiently to advance our material welfare. I speak here not of deviations resulting from the cognitive limitations reflected in that by now overused notion of bounded rationality (Simon 1955). Of course our abilities to ratiocinate are limited. My reference is rather to situations in which we know exactly what we're doing yet still act in ways contrary to the prescriptions of a version of rational choice theory and its branch -- game theory -- devoted to the analysis of strategic interaction.

Experimentally, this encompasses behavior in one shot Prisoner's Dilemma, as well as in ultimatum, trust, dictator, and public goods games. Observationally, it includes the more than 120 million people who go to the polls in the United States in national elections, as well as displays of group solidarity in religion, war, politics, and many other collective activities. In all of these cases individuals manage, in one way or another, to overcome free rider problems and make common cause with other conspecifics not closely related.

Some, particularly within economics, continue to question the import of the experimental results on the grounds that subjects simply don't understand, for example, that they are in one shot games, and as a consequence inappropriately apply heuristics developed for repeated interactions in 'real life' to experimental circumstances. The rejection of the experimental results, however, is often asymmetrical: the outcomes of market experiments are viewed as confirming how well the foraging algorithms work, yet behavior inconsistent with their operation is dismissed on the grounds first that it involves an experiment and second that our abilities to think are sufficiently limited that we can’t tell the difference between a one shot and a repeated interaction (see e.g. Binmore 1994, p. 183). The hypothesis that subjects are unable to distinguish between one shot and repeated interactions has, moreover, been recently tested and rejected by Fehr & Fischbacher (2003, pp. 787-88).

The interpretation of the experimental and the observational evidence as reflecting learned rules of thumb applicable to situations of repeated interactions begs the question of how we managed to become involved in an ongoing string of transactions, that is, how such interactions developed from those that might well have ended after a one time encounter. Repeated interaction, a requirement for reputation to be of any relevance, can help us understand how certain types of cooperation and reciprocity are sustained, but not necessarily how they are initiated. For some questions, such as why we vote (Field 2005b), consideration of reputation offers little help at all.

This body of evidence creates a dilemma for those not comfortable with simply dismissing it. For decades, an influential group of social scientists pursued a dream of constructing a predictive science of human behavior based solely on our foraging algorithms. These account for how a hunter-gatherer decides in which patch to search and for how long, how we behave in a crowded parking lot as we search for a space, and why demand curves are downward sloping. Our foraging capabilities and inclinations are central to who we are, have clearly been favored by millions of years of selective pressures, and provide a behavioral foundation for the understanding of economics as the study of the allocation of scarce means among competing material ends.

But the evidence referenced above compels us to reexamine the implicit premise of this project: that these algorithms are *all* we possess. Many are coming to appreciate that much behavior can only be understood if we recognize other behavioral inclinations, often in conflict with the counsel of foraging algorithms, that coexist uneasily within us (Field 2007).

Others nevertheless resist giving up the dream, and in this find comfort in what is seen (incorrectly) as a quintessentially Darwinian argument: natural selection simply could not have allowed the increase in frequency of genetic predisposers favoring behavior inconsistent with our material self interest. This faux Darwinian flag can become a security blanket similar to the one Linus used to carry around in the old Peanuts cartoon. The apparent authority of history's most influential natural scientist seems to provide justification for dismissing a growing body of evidence as either artifactual or misinterpreted. This in turn allows scholars to avoid confronting the possibility that the vision of a comprehensive behavioral science based solely on the foraging algorithms is unrealizable.

My intent here is to show why that security blanket cannot play its intended role. The purpose of this paper is not to reject Darwinism or to attack rational choice theory per se. It is to challenge a particular interpretation of Darwinism, one based on an incomplete understanding of how natural selection can work, and a particular version of rational choice theory which this interpretation of Darwin has been used to support. In doing so I address what has been one of the most contentious debates within the biological sciences: that associated with the principle of group or multilevel selection. I argue, moreover, that it is not enough to allow for the possibility of cultural group selection alone. In reconciling the experimental results with our understanding of evolutionary processes, it is essential to acknowledge an historically prior role for biological group selection in molding behavioral and cognitive predispositions upon which culture has built.

Multilevel selection

Multilevel selection refers to the operation of natural selection – the motor of evolutionary history -- at more than one level. In this paper I will focus discussion primarily on three ‘tiers’: the organism level, below the organism at the gene level, and above it at the level of the group of organisms. These levels are not entirely symmetric in relation to each other. The gene – not its physical embodiment – but the information it carries -- has pride of place. At whatever ‘level’ selection operates in favoring or disfavoring a behavior, it must do so so as to increase or maintain the relative frequency of genes predisposing to such behavior. Discussion of higher level selection therefore refers to the operation of selective pressures on the nested packages within which genes are contained and replicate.

No biologist today disputes the fact that genes are the ultimate units of selection, that organisms can be thought of as vessels containing them, and that natural selection has molded genetically influenced behavior to facilitate the replication over generations of genes predisposing to such behavior. In many spheres of action, the behavior of an organism facilitates its survival, and thus its ability to reproduce. In such cases, the ‘interests’ of gene and organism coincide. This is not, however, always the case, as the willingness of parents to sacrifice their well-being for their offspring reveals.

Since virtually all biologists recognize the distinction between selective forces operating at the organism and the gene level, the basic premise of multilevel selection is not controversial. But selection can also occur above the level of the individual organism, at the level of the group, and here there is less consensus. Most biologists today agree that selective pressures operating at the group level are theoretically possible. But the prevailing opinion – though weakened from its high water mark in the 1980s – remains that the genetic and behavioral legacy of higher level selection throughout evolutionary history has been negligible, and in particular in the line of descent leading to anatomically modern humans.

My argument in this paper is that recognizing the influence of biological, not just cultural, group selection is necessary in a full account of why we behave today as we do. This has important implications for how we conduct research in the social and behavioral sciences. It also has relevance for natural scientists whose understanding of evolutionary theory conditions assumptions commonly made about human nature.

The multilevel selection framework provides a coherent explanation of how the inclinations evidenced in the behavioral data referenced above could have evolved, an explanation consistent with known mechanisms of natural selection. The thesis of this paper is that, in spite of its checkered intellectual history, and in spite of the myriad proposals of alternative models that claim both to account for such data and to dispense with the need for selection above the organism level, a multilevel selection framework remains the only coherent means of accounting for the persistence and spread of behavioral inclinations which, at least upon first appearance at low frequency, would have been biologically altruistic within the group of which the individual actor was a member.

Making this case requires addressing multiple audiences. Some readers (although probably not regular readers of this journal - see Buchanan 2000 or Gifford 2000) don’t know what group selection is or why it might be relevant to social science or how we think about human nature. Others know what group selection is, grant that it is theoretically possible, but are skeptical that it has been of any empirical importance in evolutionary history. A growing minority will be sympathetic at the outset to the arguments I present.

Intellectual environs

If one surveys the social and behavioral sciences, one confronts a complex tapestry of positions regarding the relevance or legitimacy of applying evolutionary history and theory to the study of human behavior. In economics one finds the common use of stripped down and incomplete Darwinian models to buttress a narrow version of rational choice theory, coupled with a widespread lack of awareness of the subtleties involved in acknowledging the operation of multilevel selection. In particular, the distinctions between the selfish gene and the selfish individual are sometimes elided. Assuming that genes are biologically ‘selfish’ does not necessarily require assuming that individual organisms are.[1]

At the same time, although biologists tend to reject the idea that selection above the organism level has had any lasting impacts on behavior, one discovers within economics, among a select group of scholars, a surprisingly favorable assessment of the contrary view. This group includes, most notably, Paul Samuelson, Gary Becker, Jack Hirshleifer, and Friedrich Hayek.

In the past decade a growing number of social scientists have become familiar with the logic of biological group selection, and thus are less prepared to reject it outright. This has, in many instances, regrettably, led to only minor changes in intellectual strategies, as the practice has become to acknowledge its possibility, and then trivialize or remain agnostic about its empirical legacy, sometimes adding that if it is applicable it is so only to cultural group selection. Thus the four individuals discussed here, a group that includes three Nobel Prize winners in economics, are notable in several respects. They understood the empirical possibility of biological group selection, and, as a group, expressed a remarkably favorable evaluation of its likely behavioral legacy. And they did so after the apparent victory within biology of the attack on the empirical legacy of group selection, yet prior to the recent restatements that have made it somewhat respectable again within biological circles.

Samuelson on higher level selection

Samuelson addressed the problem in his 1993 article ‘Altruism as a Problem involving Group vs. Individual Level Selection in Economics and Biology’. Here in part is what he wrote:

> Mesmerized by *Homo economicus*, who acts solely on egoism, economists shy away from altruism almost comically. Caught in a shameful act of heroism, they aver: ‘Shucks, it was only enlightened self interest.’ Sometimes it is. At other times it may be only rationalization … ‘If I rescue somebody’s son, someone will rescue mine.’…I will not waste ink on face-saving tautologies. When the

> governess of infants caught in a burning building reenters it unobserved in a hopeless mission of rescue, casuists may argue; ‘She did it only to get the good feeling of doing it. Because otherwise she wouldn’t have done it.’ Such argumentation … *is not even wrong*…The bottom line is that we face a hierarchy of competition (and cooperation) and there is no a priori presumption that what conduces to victory at one level also conduces at another….An unsupported claim from an economist-Darwinian does not acquire validity from a cited analogy with evolution. Truth must find its own legs to stand on (1993, pp. 143, 144, 146).

Becker on altruism

The case is more nuanced for Gary Becker, who, like a number of other social and natural scientists whose work will be discussed below, developed a model of altruism towards non-kin to demonstrate that ‘models of group selection are unnecessary since altruistic behavior can be selected as a consequence of individual rationality’ (1976, p. 818).

Becker’s model, and many others claiming similar achievements, promise more than they are able to deliver. If one reads his argument carefully, it becomes clear that the behavior he has in mind increases the relative wealth[2] of the ‘altruist’ and is therefore mutualistic, not biologically altruistic which, by definition, must lower the relative fitness of the practitioner. For Becker, as for a number of other scholars, the name of the game is to ‘solve’ the problem of apparently biologically altruistic behavior by reinterpreting it as mutualistic. This can be done in some cases by embedding the behavior within a regime of indefinitely repeated interaction, which, as noted, begs the question of how such a regime originated. In emphasizing the impact on a selfish agent’s behavior of the possible response of ‘altruists’ he provides insights into how certain types of cooperative reciprocal behavior can be sustained, but not how altruistic behavior could be favored in the absence of an established regime of repeated or continuous interaction.

Obviously, if biologically altruistic behavior were an empty set, we would not have to worry about explaining it, and the ‘central problem’ of sociobiology, as E. O. Wilson defined it in 1975, would disappear. But it is not an empty set, as Becker realizes, and as both experimental and observational evidence strongly suggest. To the degree it’s not an empty set, Becker is remarkably respectful of the need for group selectionist arguments to explain its persistence, attributing to sociobiologists a greater tolerance for such argumentation than they or their successors might be willing to admit. For Becker it is self evident that ‘…if altruism lowers fitness …the sociobiologist’s group selection must be used to explain how altruism evolves by selection’ (p. 824).[3]

Since, by definition, biologically altruistic behavior lowers relative fitness, at least within the group of which the individual is a member, the use of the word ‘must’ here represents an endorsement of the proposition that higher level selection is necessary to explain the persistence of biologically altruistic behavior.

Becker is also notable in interpreting kin selection as an instance of group selection (p. 818), a view that I endorse but one resisted by many biologists.[4]

Hirshleifer on evolutionary theory

Jack Hirshleifer (1978) tread lightly, inasmuch as group selection remains the third rail of biological discourse. Granting that group selection for helping is only ‘rarely effective in the biological realm’ (Hirshleifer 1978, p. 242), he nevertheless recognized in his conclusion that ‘group selection under primitive conditions may have led to the evolution of instincts favoring in-group cooperation and out-group hostility among humans.' In spite of various nods in the direction of what was at the time he wrote conventional biological wisdom (he prefaced the last quote with 'Conceivably'), Hirshleifer was clear that 'Man himself, full of love and hate and sheer cussedness, ill fits the model of 'economic man' – but the gene is an 'economic gene.' It has been selected to survive on the basis of successful selfishness. However, depending upon opportunities the interests of the gene may sometimes be served if the organism housing it is programmed to help or to hurt other organisms' (1978, p. 240).

If one adds that this helping or hurting may adversely affect the relative ability of the organism to survive or reproduce, its relative reproductive fitness, one has about as clear a statement as one could ask for of the multilevel selection argument. The adverse effects on organismic welfare are obvious in parental sacrifice for children and other forms of kin selection. They are equally obvious in the group beneficial but individually harmful behaviors among non-kin that group selection arguments are called upon to explain.

The most empirically important form of these is failure to harm. Hirshleifer calls our attention (1978, p. 239) to the fact that economic and biological competition with other conspecifics can take a variety of progressively more rancorous forms: scrambling, interfering, or predating. Scrambling simply means working hard and effectively to extract resources from the remainder of the natural environment while ignoring other conspecifics. Interfering means engaging in active efforts to prevent other conspecifics from exploiting resources, be they food or mates. Acting as a predator means treating conspecifics as potential sources of calories.

We speak of a competitive environment as being a ‘dog eat dog’ world, but dogs rarely eat other dogs, and human cannibalism is the exception, not the rule. Among both humans and other animals, a central challenge is to understand the evolutionary forces that have largely limited intraspecific competition to the first two of these levels, and in some cases to the first alone. We significantly understate the empirical problem of biologically altruistic behavior among humans if we limit attention to affirmative assistance (Field 2001). That is just the tip of an iceberg. The part underwater consists of the benefits we provide to others, at risk to ourselves, by refraining from first strike, and not initiating harmful actions against others within our identified group, as well as those we provide through our willingness to engage in costly punishment of third parties.

A considerable body of experimental and observational evidence is consistent with the proposition that we are genetically inclined, within groups of conspecifics, to refrain from harming others unless provoked. We are also inclined to engage in aggressive and costly punishment of those who do harm, and, at a considerably weaker level that can, along with boundaries of the group, be culturally influenced, provide affirmative assistance to other conspecifics in need. To the degree that such behavior is biologically altruistic, and it must have been upon first appearance, how such restraint originated and persisted remains difficult to explain without appeal to the operation of higher level selection in our evolutionary past. The same is true for our propensities to engage in third party punishment. That is the essence of what Hirshleifer says in the preceding quote.

Hayek on collectivism

Friedrich Hayek, one of the most independent thinkers of the twentieth century, had no difficulty with this argument. Not one who worried much about treading carefully where he saw the truth, he endorsed without qualification the empirical proposition that our ability to make common cause with our compatriots or coreligionists is partly innate, and that in order to explain this, we must appeal to group selection (Hayek 1988; for discussion of Hayek's views on levels of selection, see Rubin and Gick 2004).

My interest is not principally with where Hayek went with this argument – in particular his conclusion that we have to fight strongly and persistently against these inclinations in order to avoid the horrors of totalitarianism. I acknowledge that our ability to make common cause has a dark side: the control of within group conflict sometimes lays the foundation for violent attacks on outgroups. But the inclination is also what brings millions of people to the polls in democratic nations and is as much an underpinning of democracy as it is of dictatorship (Field 2005b).

As was frequently true, Hayek marched here to a different beat than mainstream economists, many of whom simply deny we have this inclination, and therefore find themselves at a loss to account for why we vote or engage in other forms of collective activity. My argument is that with respect to the scientific issue of the components of the human ethogram, and the evolutionary history that produced it, Hayek, along with Samuelson, Becker, and Hirshleifer, were right in acknowledging the possibility or likelihood of higher level selection in the past, and of a significant behavioral legacy as a result of it.

In contrast to economists, traditional sociologists, anthropologists and to a lesser degree political scientists have been almost unremittingly hostile to the exploration of any biological/genetic influences on human behavior. The intellectual and political reasons for this are multiple, but one can get a reminder of the source of this aversion by reflecting on the misuse of biological arguments within the now largely discredited eugenics movement (Black 2003). The problem is that if one accepts the validity of the evidence referred to above – and scholars outside of economics have greater incentives to do so because it affects a wider percentage of what they view as their subject matter -- one can't also accept the economist's argument that Darwin backstops the position that *Homo economicus* is all there is.

It appears that either the evidence or Darwin has to go. For most sociologists and anthropologists, Darwin goes. But this is hardly more satisfactory than the propensity of economists to dismiss the large body of experimental and observational evidence as artifactual. In *The Descent of Man* Darwin forced us to acknowledge that we are animals with an evolutionary heritage, and we share parts of this heritage with every living thing on the planet. Does that heritage mean, however, that we are unremittingly selfish, in a particularly narrow sense of the word?

Biologists, sociobiologists, and evolutionary psychologists form a third group. While receptive to biological/genetic influences on human behavior, they have been predisposed, for reasons discussed below, against acknowledging the prior operation of selection above the level of the individual organism. Some, such as Richerson and Boyd (2004), while embracing the general skepticism about the behavioral or cognitive legacy of biological group selection, have nevertheless made a strong case that it can operate – and quite rapidly – at the cultural level.

Among sophisticated students of these issues, therefore, there has now evolved what I see as the currently fashionable position. First of all, there is universal acknowledgement that group selection is theoretically possible. Secondly, there is the claim that proponents of group selection vastly overemphasize the likelihood that biological group selection has been empirically important to any meaningful degree in human evolutionary history. And finally, there is the suggestion that cultural group evolution has, on the other hand, been an important force.

Many readers from the social sciences, even if receptive to the proposition that a Darwinian approach need not require that we are unremittingly selfish, must now nevertheless be wondering why biologists as a group appear to be so negative about the empirical legacy of group selection.

Some intellectual history

Prior to the 1960s appeals to and acceptance of the operation of group level selection were unexceptional. Biologists and popular writers commonly ‘explained’ morphological or behavioral traits as having ‘evolved’ because they predisposed toward the survival of the group or species. The structural – functional tradition in sociology borrowed its methodology and metaphors from pre-1960s evolutionary biology.

The *locus classicus* of the case for group selection was Wynne-Edwards’ 1962 work which argued that avian species evolved behaviors, in particular the regulation of clutch size which, though sometimes detrimental to the fitness of individual organisms, benefited the deme because it regulated population size in accordance with available food supplies. Wynne-Edwards’ work has continued to serve as a target and symbol of group selectionist thinking.

The initial and most influential attack on such thinking (Williams 1966) was based on demonstrations that some behaviors previously ‘explained’ as having evolved because they favored the group could in fact be satisfactorily explained by selection at the organism level or below. A decade later Richard Dawkins (1976), building on the insights of the late William Hamilton (1964), emphasized the more general methodological point that the ultimate locus of selection was at the gene level, and evolutionary models of behavior had to show how such behavior conduced to the spread of genes so predisposing.

On the empirical side David Lack (1966) demonstrated that birds laying the species typical number of eggs had more offspring than those who laid fewer or more. Far from involving individual level sacrifice, laying the species typical clutch size conferred a reproductive fitness benefit to those individuals so engaging.   In one of his most memorable passages, Williams stressed that the ability of deer to outrun predators had not evolved for the good of the species. Natural selection had favored fast individuals, with the outcome that one had a herd of fleet deer, not a fleet herd of deer.

Williams’s book was entitled *Adaptation and Natural Selection* but its subtitle was ‘A Critique of Some Current Evolutionary Thought.’ Although the rejection of the empirical importance of group selection was a central theme, and the one for which the book is best remembered, it was in fact part of a broader assault. According to Williams, a variety of modes of thinking reflected a failure fully to accept the implications of the Darwinian/Mendelian synthesis as developed in the work of writers such as R. A. Fisher and J. B. S. Haldane.

Williams had no tolerance at all for those who engaged in teleological thinking which viewed evolution as having inexorably proceeded to yield its crowning achievement – humans, or with writers who suggested that natural selection acted *in anticipation* of future environmental challenges. He *barely* tolerated group selectionist arguments in the sense that he did not actually deny that higher level selection was theoretically possible. As far as its possible empirical legacy, however, he minced no words: 'I will argue…that the recognition of mechanisms for group benefit is based on misinterpretation, and that the higher levels of selection are impotent and not an appreciable factor in the production and maintenance of adaptation' and 'It is my position that adaptation need almost never be recognized at any level above that of a pair of parents and associated offspring' (Williams 1966, pp. 8, 19). Stopping short of outright denial of its theoretical possibility, his use of such words as 'almost never' and 'impotent' made clear how insignificant he thought its empirical legacy had been, kin selection, again, excepted.

On page 93, he reduced the behavioral legacy of higher level selection about as far as one can go: to zero: 'Chs. 5-8 will be primarily a defense of the thesis that group related adaptations, do not, in fact, exist. A *group* in this discussion should be understood to mean something other than a family and to be composed of individuals that need not be closely related.'

In rejecting any behavioral or morphological legacy of the operation of group selection based on the implausibility of its operation, Williams had in mind a model put forward by Sewall Wright (1945). Wright imagined a number of small geographically separated populations in some of which 'altruistic' traits arrived at fixation due to genetic drift. These altruistic groups then outcompeted others in warfare or colonization of new territories and so altruistic genes spread even though they possessed a within group fitness disadvantage. Williams maintained that because the 100 percent altruist groups were exceedingly vulnerable to invasion, the conditions necessary to allow biological group selection as described by Wright to emerge were unlikely. If the groups were close enough to compete in warfare or colonizing new territories, they were close enough to suffer invasion. And once one defector managed to insinuate him or herself within one of the 'altruist' groups, it was all over for the altruists.

Wright's model is viewed today as relevant for cultural group selection, in which norms and ostracism can prevent the influx of those who might be more inclined to defect.[5] But we now have more robust models of the operation of higher level biological group selection, the most influential of which has been that developed and popularized by David Sloan Wilson (Wilson and Sober 1994). Wilson's model requires small groups of organisms which separate for one or several generations. Organisms displaying group beneficial behaviors that nevertheless damage their relative fitness within groups are, within the group, biologically altruistic. The share of genes so predisposing will inexorably decline within each group. But if there is a positive covariance between the share of 'altruists' in a particular group and the rate at which it grows, and if the groups periodically recombine before reassorting again into groups, then group beneficial traits can increase in frequency over time within the global population. This is true even though the share of altruists within any group at any moment of time is never increasing and usually declining.

The type of behaviors we are concerned with damage relative fitness within the group, although ultimately, as the result of higher level selection, they do the opposite within the global population. Some critics of Wilson's argument have claimed that if the genes predisposing to such behavior increase in relative frequency in the global population in subsequent periods, the behavior can't be biologically altruistic. This criticism has some bite, but is potentially misleading, and Sober and Wilson (1998) objected to it strongly, calling it the averaging fallacy. If we extend its logic to a less controversial arena for the operation of group selection, a propensity to sacrifice for one's children, it is clear that such sacrifice can benefit the spread of genes so predisposing. But it still makes sense, and it is common practice, to describe such behavior as biologically altruistic from the standpoint of the organism, and we can say the same about behavior that benefits the group but damages the organism's reproductive fitness within it. It will improve the clarity of discussion if proponents of group selection are explicit in maintaining that the criterion for biological altruism is satisfied within the group, and that such behaviors are legitimately referred to as biologically altruistic, even if they eventually lead to an increase in the frequency of genetic predisposers to such behavior within the larger population.

Because Wilson's model does not require fixation of altruist traits within a group, it is not subject to the same criticisms as Wright's. Permeability of the groups, through such human customs as exogamy, for example, becomes part of the machinery for repooling, rather than in the Wright formulation, where it is seen as the approach's Achilles heel.

Williams can’t be criticized for going after what was in 1966 the most carefully formalized account of group selection available at the time. A more significant issue in reflecting on the long run impact of his work is his partial elision of the distinction between selection at the individual organism level and at the gene level. This has not received a great deal of attention, perhaps because it was only subsequently, with the publication of Dawkins (1976), that its significance became more apparent. Williams distinguished principally between biotic (i.e. group) and genic selection and wrote that ‘it is universally conceded by those who have seriously concerned themselves with the problem … that such group related adaptations must be attributed to the natural selection of groups of individuals and that the natural selection of alternate alleles within populations will be opposed to this development’ (1966, p. 92.)

Certainly, no advocate of group selection today would be prepared to concede this. It would be more precise to say that the natural selection of *organisms containing alternate alleles* within populations will be opposed to the force of selection at the group level. To the degree that genes influence behavior, natural selection must operate to cause such genes to increase (or not decrease) in relative frequency in the future, whether selection occurs at the level of the organism or at the level of groups of organisms.

In kin selection, genes predispose parents, for example, to sacrifice for offspring, even to the point of death: the interests of organism and genes are opposed, and the genes win. In D. S. Wilson’s model of group selection, altruistic behavior toward non-kin adversely affects relative fitness of individuals within groups but groups with higher shares of altruists grow more rapidly. When the groups periodically recombine in a general population before reassorting, the share of altruist genes in the general population grows or at least does not decline. Again: the interest of organism is here opposed to the interest of gene, but the outcome is that the genes win.

Williams and others must be partly held to account for the continuing misconception, particularly among social and behavioral scientists, that organism level and gene level selection are pretty much the same thing. In later publications, Williams acknowledged the distinction much more explicitly. Once one acknowledges that there is no conflict between an emphasis on selection at the group level and an insistence that genes are the ultimate loci of selection, it is apparent that advancing a gene centered perspective does not strike a further blow against group selectionist thinking, as Dawkins seemed to think.

Williams has substantially moderated his position on the likely behavioral legacy of higher level selection. In his less frequently referenced 1992 volume, *Natural Selection: Domains, Levels, and Challenges,* he states ‘As I will argue in chapters 3, 4 and 9, it is logically possible for selection to operate at group levels to produce adaptive group organization, and I suggest that certain sorts of group selection are probably important’ (p. 6). This is, to put it mildly, a far more accommodating position with respect to the legacy of group selection than that staked out in 1966.

Why does an understanding of the premise of multilevel selection matter? Because the conventional wisdom in biology, in particular its uncompromising rejection of the empirical possibility of selection above the organism or possibly family level, has served in the social and behavioral sciences to reinforce a narrow version of the rational choice approach. And by reinforcing that version, it continues to have a debilitating effect on scientific progress. Even though some of the pioneers of the attack on group selection, such as Williams, have backed away from the view that the behavioral consequences of higher level selection have been effectively nil, the legacy of the conflict remains an obstacle to developing better explanatory and predictive models of human behavior.

Intellectual hysteresis

For those not trained as biologists it can be difficult to understand the pained expressions and reluctance to proceed sometimes elicited by the suggestion that a prior history of higher level selection has something to do with surviving human behavioral propensities. Is this like suggesting the existence of a perpetual motion machine? The analogy can't be apt, since no one denies the theoretical possibility of higher level selection. Is it because it is a silly issue, having been decisively disposed of decades earlier? Some may hold this view, but I suspect that in most cases the reluctance to reconsider is not because conclusions reached on the matter were easy.

It is because they were hard. Many leading biologists agonized over the question before adopting what became the conventional position. Robert Trivers (1985, pp. 79-84), for example, describes in some detail his struggles in coming to terms with Wynne-Edwards' book before concluding that higher level selection could not have been empirically important..

Reaching this conclusion did, of course, place adherents squarely within what became the biological mainstream, and many went on to build careers premised in part on completing the revolution that Williams and Dawkins believed they had begun. These past commitments, and a reluctance to question what had become foundational assumptions for research, have no doubt also contributed to a certain amount of intellectual hysteresis.

The ability to reconsider the issue dispassionately is complicated by an unusual interaction between two dynamics, both related to intellectual specialization and both driven by limitations in our cognitive abilities. The first has to do with a simple reluctance to revisit tough issues previously considered. There are only so many hours in the day, and so many years in a scientist's productive life. Our capacity to absorb, understand, keep up with, and remember the details of complex literatures is limited. Even within our own areas of specialization, at stages of our intellectual development we focus on a particularly contentious issue, reach a position on it, and put it behind us. Decay rates being what they are, we remember the conclusion, but over time less and less of the supporting argumentation or evidence on the various sides of the issue.

An unavoidable consequence is that when we have extensively scrutinized an issue in the past we are often more reluctant to consider it now than if we had never examined it in the first place. The phenomenon is unavoidable: we simply cannot make progress in our work if we are constantly zero-basing every question, going back every morning to square one. On the other hand, even if we raise the hurdle to reconsidering previously vetted matters, we shouldn't impose a prohibitive tariff.   To modify an old saw, it can sometimes be worse to have considered and erred than never to have considered at all.

What if the matter was, as they say in the judicial business, wrongly decided? We don't always get it right, or completely right the first time, and just as logic and evidence should play critical roles in the positions we initially develop, so too must we be sensitive to their role in precipitating a reconsideration of an issue. In the case under review here, this natural tendency toward hysteresis has been reinforced by another process.

This second dynamic involves specialization not across different stages of own careers, but among different individuals and disciplines. Outside of our own areas we often rely for our positions on trusted specialists who have thought carefully about the matters under consideration. Again, doing so is unavoidable: we cannot hope to develop, ascertain, or verify every premise upon which our work is based. In relying on outside specialists, however, we cannot afford to suspend our critical faculties entirely, any more than we can when seeking medical help for ourselves or our family. We retain ultimate responsibility for the positions we import as well as those we manufacture domestically. Social learning, with its role for imitation and conformity, is an important feature within the scientific as well as other human communities, and we need to be aware that within that community it is possible for scientifically maladapative ideas to take root, just as, more generally, our cultural capabilities open the way to maladaptation as well as adaptation.

The movement within biology toward rejecting the empirical legacy of higher level selection appeared to dovetail nicely with a program within the social sciences aimed at extending the purview of a narrow version of rational choice theory. Economists and rational choice theorists saw biology as an ally in counteracting the ‘fuzzy thinking’ of sociologists, and biologists saw rational choice theory and particularly game theory as an ally in counteracting the ‘fuzzy thinking’ of advocates of higher level selection.

The alliance was not perfect. The assumption of organism level selfishness that pervades much economic and rational choice theory does not correspond exactly with the position adopted by biologists who rejected higher level selection, because the latter group came to emphasize the gene as the ultimate locus for selective pressures. Still, since organism and gene ‘interest’ coincide frequently, the intellectual trends were sufficiently complementary that protagonists within each group often sought each other out as allies, and appealed, explicitly or implicitly, to each others’ work in support of their own.[6]

Biologists, however, have not always appreciated the nuances and explanatory limitations of game theory, and economists/rational choice theorists (with some notable exceptions as described above) have either not been aware of the possibility of group selection, believe that it has been dismissed by biologists as a logical impossibility, or have been unaware of the degree to which biologists such as Williams have backed away from their earlier wholesale dismissal of its possible legacy.

And herein lies the core of the problem. Biologists rejecting higher level selection did so believing that their allies in economics and elsewhere had developed game theoretic models that provided coherent accounts of the origin of such troublesome phenomena as biologically altruistic behavior displayed toward non-kin. At the same time, many rational choice theorists saw biology and evolutionary theory, particularly if higher level selection were ruled out, as providing support from natural science for the first principle that underlay their own models, that of organismic selfishness.

Although these approaches seemed to dovetail, close examination reveals that they were not entirely complementarity. For example, as noted above, assuming that genes are ‘selfish’ is not the same as assuming that organisms are selfish. And if one looks carefully and critically at game theory, it turns out that it is weaker in its predictive powers (and often empirically wrong on those predictions it makes unambiguously) than many enthusiasts seemed to suppose or were prepared to admit. Again, cognitive limitations are only part of the problem. In one shot games the predictions are often flat out wrong, and in indefinitely repeated interactions there are a multiplicity of possible Nash equilibria. The continuing and unresolved problem of equilibrium selection, of 'refining' the set, significantly weakens the predictive achievements of the approach.[7] The problem of multiple equilibria is just as serious in evolutionary game theory.

A dangerous situation can develop when two areas of inquiry appear mutually to reinforce each other in the absence of sufficient internal and external scrutiny. In such circumstances a generally beneficial intellectual specialization can produce an unhealthy symbiosis which if left untreated becomes pathological. Today there remains risk of such an outcome at the point where the social and the natural sciences intersect.

Many rational choice theorists believe that biology provides the underpinnings for the primitives of theory – including basic assumptions about human selfishness. In some cases there has been little thought given to the issues of levels of selection. In still others, reliance is placed on the apparent consensus among biologists and evolutionary theorists that selection above the level of the individual organism has been empirically unimportant. At the same time, many biologists believe that sophisticated game theory provides alternatives to appeals to group selection as explanations for how prosocial inclinations evolved. Each group is relying on critically unexamined work in other disciplines to buttress firmly held positions.

The geneticist Bryan Sykes has opined that 'In all fields of human endeavor where there is a shortage of objective evidence, opinions and people inevitably become polarized into rival camps. Once entrenched, the occupants will not be dislodged; they would rather die than change their minds'(Sykes 2001, p. 115) How applicable is this description to the current controversy over the behavioral legacy of group selection? Partially, although the passage does not adequately credit the degree to which scholars such as Williams have moderated their positions.

There is, moreover, quite a bit of evidence, albeit much of it indirect, relevant to the question. This includes experimental and observational data on human behavior (including that of surviving hunter-gatherer societies) and that of our close animal relatives. It also includes simulation studies, and studies of the successful use of artificial group selection in the poultry industry. As I will argue below, it also includes analysis of a number of other evolutionary transitions that cannot easily be accounted for without appeal to higher level selection.

Those skeptical of the operation of group selection raise objections to each of these evidentiary categories. To the degree that evidence will not persuade, the terrain of discourse must shift to a supporting buttress of the anti-higher level selection position. That is the claim/belief/assertion that alternate individual level selectionist models are or will be available to account for instances of apparent altruism, particularly among non-kin.

So long as the latter belief remains intact, it fuels skepticism about the growing body of evidence inconsistent with an individual level selectionist view. Thus, as noted, one finds among some scholars a generalized dismissal of experimental evidence on human subjects, such as cooperative plays in the one shot PD, as based on an inability of subjects to understand that they are truly in a one shot situation, and the claim that in any event one shot interactions are not and presumably have never been very important (see Bendor & Swistak 1997, Gintis et. al 2003).[8]

I take issue with both of these claims. But there is a more general point. If one looks at models that attempt to dispose of the necessity of appealing to group selection, one finds that in case after case (as in Becker's story), they begin by assuming a large part of what ultimately must be explained: for example, that interactions between agents are *already* indefinitely repeated, or that certain types of behavioral inclinations are *already* at relatively high frequency. Again and again, the attempt is made to reinterpret biologically altruistic behavior as mutualistic, at which point its maintenance can be accounted for using individual level frequency dependent selection, or within the scope of a fairly narrow version of rational choice theory. The mirror image of this approach (as in the theory of reciprocal altruism) is to relabel as altruistic behavior what is in fact mutualistic, and then show that the behavior can be accounted for without appeal to higher level selection. The issues are subtle and complex because for some behaviors, whether behavior is biologically altruistic or biologically mutualistic is not inherent in the nature of the behavior itself: it is frequency dependent (see Field 2001).[9]

A gene centered approach to evolutionary theorizing is here to stay, and has focused research in a way that has provided us with useful insights into many types of animal behavior.[10] But the issue of higher level selection has not been disposed of. Though there has been progress in moving *some* behavior from categories that might previously have relied on indiscriminate appeals to group selection for their explanation, large residual categories remain. And in a number of widely cited analyses intended to dispose of these residual categories, much more has been claimed than close examination reveals is warranted. I develop this point below in analyzing Robert Trivers' model of reciprocal altruism, John Maynard-Smith's concept of frequency dependent selection, Robert

Frank's analysis of altruism in *Passions within Reason*, and Robert Axelrod's treatment of third party punishers of non-punishers.

In 1975 E. O. Wilson declared altruistic behavior to be the central unresolved issue in evolutionary theory (Wilson, 1975, p. 20). This must have reflected skepticism about the empirical significance of higher level selection, since if one allows for that, one has available a perfectly reasonable account of the persistence of biologically altruistic behavior.

In 1983 Wilson concluded that as the result of work by Hamilton, Trivers, and Maynard-Smith, the 'problem' had largely been resolved, without (this was implicit) appeal to group selection (Lumsden and Wilson 1983, p. 49). His interpretation required first, a denial that kin selection was a variant of group or higher level selection (contrary to Becker's view, and my own), and second, a misinterpretation of the import of Trivers' and Maynard-Smith's work for the explanation of the origin of biologically altruistic behavior.

Trivers' theory of recipocal altruism

Trivers' 1971 model was a resetting of the theory of indefinitely repeated games within a biological context. The essence of the argument is this. It pays me to jump in the water to save you if, at small risk to myself, I can confer a large benefit on you and expect the same from you in the future if the tables are turned. If one tacks on to this the idea that payoffs in this game drive reproductive success, one has an apparent evolutionary explanation of reciprocal 'altruism' (it's really mutualism) among non kin.

This model requires, as in Becker, that the interactions be indefinitely repeated. Once we have indefinitely repeated interaction, such a strategy profile, or just about any other, can be sustained. But there are a multiplicity of possible Nash equilibria in such games. Why this one? More tellingly, Trivers' model gives us no insight into how inclinations to cooperate could rise from low to high frequency following initial appearance, or how one could transition from one shot to repeated play PDs.

The first person who jumps in to save another has just revealed to the person drowning that he has some positive probability of being saved even though he has provided no prior benefit: the individual has made no prior deposit to the favor bank. Moreover, it is in the saved individual's best interest to avoid risk to life and limb should the tables be turned several months later. Indeed, it is a strictly dominant strategy to behave in such a manner, just as it is strictly dominant not to attempt a rescue in the first place.

How could such inclinations ever rise from low to high frequency if natural selection took place only at or below the level of the individual organism? How could one ever transition from an environment of one shot interactions to one in which the assumption of indefinitely repeated interaction has some reasonable plausibility? Trivers' model provides no clue.

Even the conclusion that the model offers some insight into how reciprocal relations can be maintained may be too generous. Boyd and Richerson (1988) argue that it would be difficult for 'reciprocal altruism' to be sustained even with indefinitely repeated interaction unless the group size were quite small. Yet textbooks continue to give the theory of reciprocal altruism pride of place as a solution to the 'problem' of altruistic behavior displayed among non-kin (see Barrett, Dunbar & Lycett 2002, ch. 2). The authors of this otherwise insightful text appear to be fully aware of why Trivers' model can in fact tell us nothing about the origin of such behavior yet persist in proceeding as if the difficulties can be (and have been) easily finessed. Perhaps the most telling illustration of this occurs where they suggest that ‘mutualism may be a more appropriate explanation for altruism’ (2002, pp. 30, 34)

If a behavior is biologically mutualistic, it results in a fitness improvement for both parties, and if it results in a relative fitness improvement for the actor, it could evolve by selection at the level of the individual organism. But suggesting that mutualism is an ‘explanation’ for biological altruism is like saying this: since I can’t explain x with the tools I’ve limited myself to, I’ll redefine x as y and then show how I can explain y with them. And then I’ll argue that this explains x.

Frank’s *Passions within Reason* (1988)

Robert Frank’s 1988 book played an important role in putting empirical issues of altruism on the table, and remains frequently cited. He nevertheless chose to develop his analysis entirely within an individual selectionist framework. I believe this was a mistake, because adherence to these conventions leads him to repeated contradictions in his argument.

Frank’s central claim is that under the threat of harm, ‘being predisposed to respond irrationally serves much better … than being guided only by material self interest’ (p. x). A rational choice is one that uses efficient means to pursue ends. A rational choice should therefore *serve you better* than any available alternative. But Frank has just maintained that an *irrational* choice would serve you better. A fundamental principle of logic requires that an action or intention can’t at the same time be deemed both irrational and rational.

Actual retaliation (e.g., rejecting a positive offer in an ultimatum game) is clearly irrational, a violation of the subgame perfect equilibrium concept; if one assumes rationality, people should understand that those who claim or threaten that they will reject or retaliate are engaging in cheap talk. Frank, seems to be saying, however, that we are better off if 'programmed' to act differently, that is, to retaliate.[11]

Yet if this argument (that we are better off if primed to retaliate if attacked) is made in the preface, exactly the opposite claim is made, in discussing feuding among Appalachian clans, early in the main text: 'The McCoys or the Hatfields could have ended the violence at any moment by not retaliating for the most recent attack. At each juncture it was clear that to retaliate would produce still another round of bloodshed' (Frank 1988, p. 2). Being predisposed to retaliate means that, if attacked, one has a low threshold for actually retaliating. But here Frank is saying that the McCoys and the Hatfields would have been better served had they had a very high threshold, had one group at one point been prepared to turn the other cheek. It is incoherent to argue that we are better off if primed both with a low threshold and with a high threshold for retaliation.

Frank's argument is similar to the myriad attempts to explain why it is in one's best interest to play cooperate in a one shot Prisoner's Dilemma game. It cannot be rational to play a strictly dominated strategy, and therefore it cannot be rational to play cooperate in a one shot PD. This is simply a matter of definitions and logic. However one looks at it, one is leaving money on the table, and this is not the type of behavioral predisposition that should have been favored if selection occurred at no higher level than that of the individual organism.

As a matter of practice, of course, people reject positive offers in ultimatum games, play cooperate in one shot PDs, and engage in costly punishment of those who defect in public goods games. And they do so in real life all the time as well. In all of these instances we leave money on the table. Frank provides no coherent explanation of why it would be rational to do any of these things, or how organisms predisposed to such strategies could possible survive and grow in frequency upon first appearance. He can't, because, in agreeing that his presumed evolutionary history had no place for higher level selection, he ruled out the only mechanism capable of accounting for it.

Frank's formal model of how cooperators rose from low to high frequency presumes the preexistence of groups, and within them of indefinitely repeated interaction. This takes as given a great deal of what we need to explain in the first place in terms of the evolution of prosocial inclinations, in particular restraint on harm (See Field 2001, ch. 4, for discussion).

Maynard-Smith's frequency dependent selection

George Price and John Maynard-Smith were jointly responsible for developing the analysis of frequency dependent selection. The important insight here is that the behavioral strategies adopted by other conspecifics represent part of the natural environment that may determine the success of an individual organism's own strategy. Maynard Smith and Price defined an Evolutionary Stable State as a frequency dependent equilibrium in which no strategy could successfully invade.

In 1980 Dawkins claimed this analysis as an alternate to group selection: 'there is a common misconception that cooperation within a group at a given level of organization must come about through selection between groups … ESS theory provides a more parsimonious alternative' (1980, p. 350).

Dawkins' claim is without merit. Maynard-Smith himself notes that ESS theory only explains the stability of an equilibrium, not its origin (1993). George Williams says the same thing: 'The theory in no way accounts for the evolutionary origins of the alternatives it considers. It accepts them as historical legacies and deals with their relative numbers.'[12]

Dawkins' interpretation of ESS theory is an example of the eagerness of those skeptical of the legacy of group selection to accept a new development as 'solving' the problem of higher level selection without subjecting it to sufficient critical scrutiny. ESS is a static concept. It provides explanation for the maintenance of an equilibrium, not the dynamic trajectory that may have led to its establishment in the first place.

Axelrod's third party punishment

Robert Axelrod is most famous for his computer tournaments pitting different strategies for playing repeated Prisoner Dilemma games against each other (see Axelrod 1984, Field 2001, ch. 3). In his 1986 article 'An Evolutionary Approach to Norms' he deals with third party punishment, and third party punishment of non-punishers. Axelrod argues that a powerful mechanism to deter cheating develops when punishment against defectors becomes linked with punishment of nonpunishers. This *metanorm,* he claims, makes the 'norm' against defection 'self-policing.'

My concern is not with the notion that we are inclined to engage in costly aggression against those who violate group norms. There is abundant evidence, both experimental and observational, that we are. The question is whether the origin of such inclinations can be accounted for in a model that dispenses with any higher level selection.

Axelrod’s analysis, which is based on the interaction of self-interested decision makers, simply displaces the multiperson PD to a higher level. Who polices those who defect from their duty to punish those who defect from their duty to punish those who violate social norms? It is a strictly dominant strategy to refrain from punishing those who don’t punish rule violators. It is a strictly dominant strategy to refrain from punishing violators. And it is a strictly dominant strategy to violate the social norm in the first place. How could such a ‘metanorm’ ever have been favored if selection operates only at the level of the individual organism or below? In an evolutionary setting, how could a strategy to punish rule violators, and, with the same ferocity, punish those who don’t punish, ever increase in frequency upon initial appearance?

Axelrod’s simulation results depend on starting his artificial population with a high fraction of those prepared to punish, and punish those who don’t punish. What we need to explain is how such behavior, which upon initial appearance involves leaving money on the table, became established at higher frequency, and on this question the paper is silent. Axelrod admits that his ‘result is dependent on the population’s starting with a sufficiently high level of vengeance. Otherwise the norm still collapses‘ (Axelrod 1986, p. 1102).

The operation of higher level selection

Those of us who grew up learning that the living world was divided between the plant and animal kingdoms may be surprised at how much of biology has been rewritten in the past several decades. This has been the consequence of a great deal of scientific advance, including the analysis of microscopic fossils, the discovery of new forms of life, including extremophiles, and the use of new techniques in molecular biology for cladistic analysis. The taxonomic scheme most widely accepted today separates the living world into two domains – that of the prokaryotes (including the kingdoms of bacteria and archaea) and the eukaryotes (with kingdoms of plants, animals, fungi, and a grab bag known collectively as protists). Prokaryotes are single celled organisms lacking a nucleus or the differentiated organelles that characterize eukaryotic cells. They contain genetic material in the form of DNA, but the DNA is not organized in chromatin or chromosomes within a nucleus. Prokaryotes arose 3.5 billion years ago and had the world to themselves for one and a half billion years, until the first eukaryotes evolved, perhaps 1.5 billion years ago.

In talking about the legacies of group selection on human morphology and behavior, it is important to take a broader historical perspective than the last half million years emphasized by Richerson and Boyd (2004) or the emphasis on the Pleistocene (the roughly 2 million years prior to the Neolithic revolution) that has characterized the work of evolutionary psychologists such as Cosmides and Tooby (1992). We need ultimately to explain the origin of eukaryotic life, the move to multicellular eukaryotic organisms and the rise of sexual reproduction (about 650 million years ago), and a variety of other transitions. It is difficult to see how any of these could have succeeded without the operation at key junctures of higher level selection (see Maynard-Smith & Szathmary 1995).

There is more consensus about conditions of life during the Pleistocene than there is about their implications for the operation of biological group selection. Most agree, based on data from surviving hunter gather societies, scattered archaeological remains, and analyses of genetic variability in current populations, that our ancestors in the Pleistocene are likely to have lived in small groups of 30-100 individuals practicing exogamy.[13] For some, the evidence for exogamy suggests that biological group selection couldn't have been very powerful, while others, such as Hamilton (1975), have reached exactly the opposite conclusion. Where one comes down depends in part on whether one has in mind the older Sewall Wright or the newer D.S. Wilson formulation.

Although I am sympathetic to the Hamilton position, the argument of this paper does not in fact depend on resolution of the debate, because key prosocial inclinations already characterized the common chimpanzee ancestor 6 million years ago. First, as already noted, most animal species display restraint on intraspecific harm. Secondly, the propensity of *pan troglodytes* to mass in groups, and then search out and destroy members of out-groups (Goodall 1986) suggest that the behavioral roots of moralistic aggression also lie deep.[14]

It is very difficult to write a coherent story of the evolutionary history of the common ancestor without appealing to multilevel selection at a number of key junctures. It is almost certain therefore that both its morphology and its behavior bore the imprint of group selection processes. Consider the issue of how mitochondria were integrated into the developing eukaryotic cell. Mitochondria are unusual and distinctive organelles. They contain their own ring of DNA, inherited entirely along the maternal line in species reproducing sexually (the unbroken maternal line of descent is what permitted the recent conclusion that Thomas Jefferson did in fact have a liaison with Sally Hemmings).

Mitochondria function as centers of cellular respiration. They operate a catabolic pathway in which glucose in the presence of oxygen breaks down into water and carbon dioxide. In this exergonic oxidation-reduction (redox) process, free energy is released and phosphorylates (adds a phosphate tail to) adenosine diphosphate, creating adenosine triphosphate (ATP). Most of the cell's ATP is manufactured in mitochondria, and the substance provides energy for the mechanical, transport, and chemical work done elsewhere in the cell. As it 'works,' ATP releases energy as it loses its third phosphate tail and reverts to adenosine diphosphate, which will then be again phosphorylated within a mitochondrion.

Mitochondria are about the same size as bacteria, and reproduce through a process of binary fission similar to that observed in present day bacteria. Its single DNA ring, its ribosomes, and its inner membrane are all similar to those found in surviving rod shaped bacterial prokaryotes. Current evolutionary thinking is that the ancestors of mitochondria were aerobic prokaryotic bacteria that invaded or were engulfed by a developing eukaryotic organism (Margulis 1981, Campbell & Reese 2002, p. 550) at a time when atmospheric oxygen levels were rising.

What would have happened as these ancestral prokaryotes were engulfed? Natural selection within each host would have favored those strains of bacteria that multiplied most rapidly, providing the greatest number of descendants. The genes so predisposing could not, of course, have anticipated the consequence, which was that the host would be quickly consumed and die.[15]

In order for an endosymbiotic relationship to develop, the bacterial forerunners of mitochondria had to evolve to lower virulence. What was in it for the host? The relationship developed at the same time cyanobacteria were increasing the oxygen concentration of the atmosphere, and so there would have been potential benefit for the host to an organelle that could ‘breathe’ oxygen.

Today a mitochondrion cannot survive on its own. Some of the genetic instructions it requires reside in the nuclear DNA. At some stage DNA was probably swapped – a process we observe today among different species of bacteria.

Each host can be considered a group, and each would have been invaded by slightly different ratios of virulent and less virulent bacteria. The virulent forms, which consumed more cellular resources than their less greedy conspecifics, would always have won the intrademic competition, but they would have killed the host too soon. Longer surviving hosts with higher ratios of less virulent bacteria would have contributed more ‘votes’ in determining the frequency composition of subsequent generations. Thus the paradox: within every host the more virulent form of the bacteria would have been increasing in frequency, but the total population was evolving toward lower virulence, allowing the endosymbiotic relationship to develop.

This is an example of Simpson’s paradox. If one divides a population into subpopulations, it is not necessarily the case that the change in the average of the subpopulation averages is the same as the change in the population average (Simpson 1951). A recent example involved admissions to graduate study in Berkeley in the 1970s. Aggregate data showed that women were being rejected at proportionately higher rates than men. When administrators drilled down to find out which departmental committees contained the culprits, they came up empty handed. Within no department were equally qualified men being admitted at higher rates than women. How could these findings be reconciled? By recognizing that women were applying disproportionately to departments that were harder to get into. Because of this covariance, what was true for the population average (disproportionate rejection of women) was not true for any of the subpopulations.

A second biological example of the operation of the Simpson paradox is the case of the Myxoma virus, introduced in Australia in the 1950s to control the burgeoning population of rabbits. That it did, but the consequences of the intervention were not entirely anticipated. When researchers drew blood from surviving animals, they discovered, as might have been expected, that the remaining rabbits had evolved towards greater resistance: those killed off were least resistant to the gene, and the offspring of survivors had greater resistance. What happened to the virus researchers had not anticipated. When they isolated viral samples from these animals and compared them with laboratory stocks of the original, they found that the viral strains in the wild had evolved toward lower virulence.

In this case the hosts (rabbits) were colonized by different mixtures of more and less virulent versions of the virus. Within each deme (host), the more virulent forms were more successful in hijacking the animal's cellular apparatus to secure their own replication. But the rabbits with higher fractions of the more virulent form, ceteris paribus, died sooner, and had less chance to infect others. Again, somewhat paradoxically, the less virulent viral forms were losing out within every host yet increasing their relative share within the global population.

Finally, we have the example of the successful use of group level selection within the poultry industry. One way to increase egg production is to breed those individual hens within the global population that have the highest egg production. But within coops chickens often fight each other over access to food – presumably a trait that has been favored by individual level selection and is exacerbated within the confines of a coop. Groups of chickens that fight more don't lay as many eggs because they often wound or kill each other.

An alternate strategy is to select groups of chickens with the highest average egg yield, and breed them. This strategy, because it reduces mortality from as high as 90 percent to the vicinity of 20 percent, has proved more effective in increasing egg yields than individual level selection (Craig & Muir 1996). This is an example of *artificial* group selection.

Relevance to human behavior

We take the organism for granted as the basic behavioral unit, but there was a time when there were no organisms with differentiated tissues, and before that no multicellular organisms, and before that no eukaryotic organisms. In each of these instances issues of higher level selection come into play. Thus debate about group selection is not just a debate about what happened during the Pleistocene. What occurred during this period was undoubtedly important, and both William Hamilton (1975) and more recently Christopher Boehm (1999) have argued that conditions during that period, particularly life in small bands of 30 – 100 practicing exogamy, created favorable demographic conditions for the operation of higher level selection.

But as living creatures we share with every other form of surviving life and many that no longer exist an ancestral heritage stretching back 3.5 billion years. It's impossible not to appreciate this when one considers the similarities between animal and plant cells.

Plant cells feature chloroplasts, thick cell walls, a central vacuole and plasmodesmata, and lack lysosomes and centrioles.[16] But otherwise animal and plant cells have essentially the same structures, including a nucleus with interior chromatin and nucleolus, rough and smooth endoplasmic reticulum, Golgi apparatus, mitochondria, ribosomes, and a cystoskeleton with microfilaments and microtubules, These homologues, along with the use of identical sequences of base acids to code for the assemblage of proteins, speak of a common evolutionary heritage. They speak also of an evolutionary history of assemblage of organelles from prokaryotic parts that in all likelihood would have required selection above the prokaryotic level.

The evolutionary legacy of higher level selection is not just about what happened in the last two million years, and the task of dismissing its influence is a more formidable project than its critics have been prepared to admit.

That is why the currently fashionable position (biological group selection is possible but its legacy is negligible; cultural group selection has been a major force) represents, in my opinion, a finesse, and one that is not likely ultimately to be effective. By endorsing the conventional biological position, i.e. endorsing Williams 1966, not Williams 1992 - and attributing all of the evidence of prosocial behavior to cultural group selection, one can appear to account for such behavior without raising people's blood pressure by adducing higher level selection.

But the evolution of restraints on attacking other conspecifics, which I have argued is the most empirically important form of biologically altruistic behavior among non-kin, surely took place before the Pleistocene. Outside of humans, cultural learning has been demonstrated in some surviving primates, mammals, and birds, but it is fair to say that most of our ancestors in the last 3.5 billion years lacked the ability to acquire and transmit cultural learning on human scales. The recognition of the significance of culture therefore cannot be a substitute for a comprehensive consideration of the role of biological group selection in evolutionary history, nor of its possible legacy in influencing our behavioral inclinations today.

It is now almost four decades since the systematic attack on higher level selection began, and it is obvious there have been important legacies. Clearly it has had the effect of shutting down a variety of strains of evolutionary thinking. This includes those who suggested that natural selection operated so as to anticipate future environmental challenges, or as if the course of natural history were necessarily one long inevitable teleological progression towards *Homo sapiens.* But Williams overstepped in 1966 when he wrote that the legacy of the operation of biological group selection was effectively nil. His provocative and polemical argument stimulated a great deal of creative work that has enabled us to account for much behavior without the necessity of appealing to higher level selection. But in the zeal to reduce the residual to zero, scholars have often overreached, confusing accounts of how an end-state equilibrium is sustained by individual forces of selection with ones of how it originated.

Williams himself is now more moderate in evaluating the empirical import of higher level selection (see his 1992 book), but the legacy of his earlier evaluation continues to influence thinking within biology, evolutionary psychology, anthropology, and economics.

Samuelson, Hayek, Becker, and Hirsheleifer did not necessarily drink from this well. But dismissal of higher level selection, with the exception of kin selection, which is somehow not viewed as an instance of higher level selection, has found fertile ground among economists and rational choice theorists who continue to operate, as Edgeworth put it, according to the first principle that all individuals are selfish and that, as Robbins argued, this is self evident and not in need of experimental confirmation (Edgeworth 1881, Robbins 1932 [1984], pp. 38-39).

To the contrary, it is not a self evident first principle that humans are, in all spheres of action, selfish in the sense that we operate to efficiently advance our material welfare. And it's not just because we have cognitive limitations that preclude us from doing so. Other behavioral inclinations besides those governing foraging operate, and it is an empirical question how powerful they are, and in what spheres of activity they are likely to be most evident.

Three variants of rational choice theory

There is a large body of work in rational choice theory and a varied and often polemical literature criticizing it. In coming to terms with both constructive and critical arguments, it is helpful to recognize that such theory comes in at least three variants.

Version I simply asserts that individuals act in satisfaction of their desires. Since there is no data that could possibly disprove this premise, this variant is unfalsifiable. It lacks sufficient structure to have any real predictive or explanatory power. As Samuelson put it, *it's not even wrong*.

Version II is based on the premise that individuals choose according to preferences that are stable and transitive. Without some stability over at least the short term, it is hard to conceive of humans engaging in sustained goal oriented activity. Both observation and intuition suggests that we do so engage. Transitivity is justified by appeal to an evolutionary/money pump argument which is ultimately Darwinian. If you did in fact prefer A to B, B to C, and C to A, then, having given you C, I could get you to pay me successively to swap B for C, A for B, and finally C for A – thus inducing you to pay me three times for what I had originally given you for free! Presumably, individuals with such preference structures would have been disfavored over time by evolutionary forces.

At least with respect to decisions of particular individuals, models based on this variant are falsifiable. By presenting an individual with a sequence of binary choices, it is clearly possible for a person to choose B over C, A over B, and then C over A. If such a violation does occur, we must conclude that preferences lack either stability or transitivity.

If we expand the choice set, assume that utility functions are strictly convex and monotonically increasing in goods,[17] and then let people select their most desired bundle under a sequence of budget constraints, we can entertain the possibility of violations of the strong or weak axiom of revealed preference. Such violations presumably call into question one or more of the assumptions underlying the maintained hypothesis.

What is the basis for the assumption of monotonicity: that with respect to marketed goods and services, and assuming zero disposable costs, we prefer more to less? Again, it is presumably Darwinian, representing an appeal to the operation of the foraging algorithms. Like bees to honey, hunter-gatherers were drawn to areas rich in game or edible flora. One can see the same algorithms at work today among college students who flock to events where free pizza is offered, or exploited by recruiters who place chocolate bars on their tables. Such availability clearly triggers something visceral within us.

But the critical question, again, comes down to whether the foraging algorithms exhaust what governs our behavior, or whether we also possess inclinations that sometimes short circuit their counsel, causing us systematically to leave chocolate, or money, on the table. The experimental evidence overwhelmingly indicates that this is so. The play of cooperate in a one shot PD, the rejection of a positive offer in an ultimatum game, or the willingness to engage in costly punishment of defectors in multistage public goods games are simply inconsistent with models based exclusively on the foraging algorithms.[18] We cannot allow allegiance to a mistaken or incomplete understanding of the mechanisms natural selection may employ to blind us to evidence and thereby cripple our ability to build a progressive empirically based behavioral science.

Can version II accommodate these alternate inclinations? In principle, yes. This is evident any time an economist puts a child's utility within an adult's utility function. Becker (1976) provides a coherent and sophisticated implementation of version II, with a very large *but not exclusive* emphasis on self interest: 'Self-interest is assumed to dominate all other motives, with a prominent place also assigned to benevolence toward children (and occasionally others) and with self interest partly dependent on distinction and other aspects of one's position within society' (1976, p. 817). If one is catholic about the arguments of a utility function, and views its structure as an empirical and not axiomatic matter, there is nothing inherently objectionable to this approach. Of course it may or may not work well as a predictive tool, depending on how stable our preferences and how strong our cognitive abilities actually are.

But many economists believe and have argued that the discipline's unique perspective provides stronger priors about what arguments should and should not appear in the utility function. As Francis Edgeworth wrote, ‘the first principle of economics is that every agent is activated *only* by self interest’ (1881, p. 16, my italics). The pursuit of self interest *might* mean that since I am happier the more you consume, acting to benefit you would be selfish. As an empirical matter, however, that’s not what it often *does* mean, or has meant. Lionel Robbins argued that our goals were self evident – so obvious as not to require an evidentiary foundation. .

Version III reflects this style of reasoning, and places the most restrictions on preferences. It assumes, in addition to stability and transitivity, that the long history of natural selection has rendered humans, like other animals, behaviorally predisposed in all spheres of action towards a particular version of selfishness: inclined toward actions that *efficiently advance the material self interest* of the organism undertaking them. As we have seen, when pressed for justification for those unwilling to accept these restrictions as self evident, Darwin is sometimes wheeled in as support. In the next breath, however, adherents to version III are usually prepared to offer a waiver with respect to behavior within the family.

That waiver is the camel’s nose under the tent. In acknowledging the prospect of non-selfish behavior within the family, and the possibility that Darwinian theory might be consistent with it, one has acknowledged an instance of higher level selection, selection above the level of the individual organism. As was obvious to Becker, kin selection is an instance of group selection (a point still heatedly denied by some), although its mechanics and operation are different and far simpler than those associated with selection for biologically altruistic behavior among non-kin.

Once the dam has been breached by acknowledging the operation of kin selection, however, the way is open to consideration of the more complex mechanisms that have selected for biologically altruistic behavior among non-kin. Darwinian theory no more precludes selection for restraint on the initiation of harmful actions within groups, or an inclination to engage in costly punishment of those who are not so restrained, than it does for the more affirmative types of biologically altruistic behavior one observes between parent and child.

Recent developments

The last decade has witnessed a growing awareness within economics and the other social sciences of the issue of multilevel selection and its potential relevance in explaining how prosocial inclinations evolved (see e.g. Gintis 2000). And behavioral economics has continued to be enriched by experimental results documenting these predispositions. Notable has been the work of Ernst Fehr and his collaborators on altruistic punishment. In voluntary provision of public goods experiments, Fehr added a second stage in which subjects could punish others, reducing the payoffs of the free riders at the cost of reducing their own (Fehr & Gächter 2000). Again, the Nash prediction (violated) is that there should be no second round punishment, just as there should have been no voluntary contributions in the first place. Like many of the experimental results mentioned at the start of this paper, it is difficult to explain how such predispositions, presuming that they have some genetic or biological substrate, could have risen from low to high frequency through the operation of selection at levels no higher than that of the individual organism.

Another series of experiments has also attracted considerable attention. Joseph Henrich and his collaborators extended the scope of ultimatum game experiments[19] beyond the typical subject pool of university students, or individuals in developed countries (see Roth et al 1991) to members of fifteen small scale societies who have had only limited contact with Western culture. Their main finding was one of considerable variation in how members of different cultures played the game. A reading of the introduction to Henrich et al (2004) indicates that there remains controversy, even among the scholars who conducted the experiments, over how to interpret the results (see Field 2005a). Nonetheless, Henrich affirms that it is still the case that 'there is no society in which experimental behavior is consistent with the canonical model from economics textbooks' (Henrich et al. 2004, p. 10).

One might conclude from these examples that the battle to 'reintroduce group selection into the behavioral sciences,' as Wilson and Sober proclaimed their objective in 1994, has been won, or at least that the controversies surrounding its legacy have died down. Such declarations would be premature. The situation remains fluid, with many scholars determined to finesse the issue and thereby avoid the toxicity traditionally associated with any sympathetic consideration of the possibility of biological group selection.

An example is Paul Rubin's recent book on *Darwinian Politics* (2002). I share with Rubin the belief that there is an enormous potential for using evolutionary biology to inform our understanding of political behavior. *But not if natural selection is presumed to have operated at levels no higher than the individual organism.* If we adopt that perspective we are forced back within the straightjacket that bedevils much of public choice theory. The discipline was built on the assumption that people try to advance their material self interest by voting, yet no one has yet succeeded in providing an explanation for why an individual interesting in maximizing her material self interest would vote. Rubin's first chapter is quite provocative. But on the critical issue of group selection, he punts – refusing to take a position on its possible behavioral legacy (see also Rubin 2000).[20]

A second case is Peter Richerson and Robert Boyd's approach, the latest version of which can be found in Richerson and Boyd (2004). This is a rigorously argued and compelling book, and I agree with much of it, the main exception being their position on biological group selection. They have staked out an influential[21] position in which the empirical significance of biological group selection's behavioral legacy is trivialized while, they argue, the applicable arena for the operation of multilevel selection has been at the cultural level. The implications of their position, and the difficulties it entails, have not been fully explored.

Over the last two decades the field of behavioral genetics has made remarkable progress. As the result of a number of careful studies of identical and fraternal twins, we now know that many behavioral traits that twenty years ago we would have said were entirely the result of enculturation (see Cavalli-Sforza et al 1982, Table 3), have a heritable genetic component. Some surprising examples include a predisposition to religiosity or spirituality, or political philosophy (conservatism vs liberalism) (Richerson & Boyd 2004, p. 36, see also Alford, Funk, & Hibbing 2005).

It is true of course that twin studies and the calculation of heritability coefficients address the *variability* of such traits within human populations. But if individual differences have a biological substrate, then surely the species typical levels (group averages) must as well. And some of these species typical traits are prosocial: they could not have risen from low to high frequency as the result of the operation of natural selection at levels no higher than the individual organism.

Citing the evidence from the twin studies, Richerson and Boyd argue that while much more of the variance of behavior within populations than we previously thought is genetically based, virtually all of the behavioral differences between groups are cultural. I am sympathetic to these positions. But accepting both of them leaves open the question of how much species typical behavior is genetically mediated, that is how much of the population *average* is genetically mediated.

An emphasis on a behavioral legacy of biological group selection need not be inconsistent with the authors' overarching theme that much behavioral variation between groups is to be explained culturally, rather than as differences in behavior evoked by different environments. I make essentially the same point in Field (1991), in reference to economic and legal institutions, and in Field (1984), in reference to norms. Cultures are not simply epiphenomenal – reflective of more fundamental givens. They influence behavior in their own right, and represent slack in the transmission belt linking environmental variation with behavioral variation. There is plenty of room for careful research such as Landa (1981, 1999), which explores the economic implications of such cultural variation.

But if we view the experimental results in one shot PDs or ultimatum games as revealing species typical features of an innate human psychology, then we are still faced with understanding how such predispositions could have evolved. The fundamental issue here is one of levels, not variance. Any level of cooperation above 0 in a one shot PD, or any level of contribution above 0 in a voluntary contribution to public goods experiment, or any level of punishment above 0 in one of Fehr's two stage games, is a violation of the Nash prediction, just as any rejection of positive offers in a one shot ultimatum game, or any transfer from A to B in a trust game is a violation of the prediction of subgame perfect equilibrium theory.

Richerson and Boyd do not quite come out and say that both the species typical level and group variance around it are cultural phenomenon. But the logic of their argument leads one close to this conclusion. On the one hand, they do acknowledge the existence of 'ancient social instincts' that help explain the 'many social features we share with primate societies' (2004, p. 235), and which are distinguished from tribal social instincts which, they argue, coevolved with culture.[22] By definition these ancient instincts predate the cognitive capabilities that allowed cumulative improvement of cultural forms, a development which the authors set at about half a million years ago. Prior to that point there could have been no cultural group selection, and no gene-culture coevolution, because our ancestors didn't have the capabilities to develop culture as the authors understand it. So how do Richerson and Boyd account for the evolution of these 'ancient social instincts' as well as the other key transitions discussed in Maynard-Smith and Szathmary (1995), if it was not through the operation of biological group selection?

Actually, Richerson, Boyd, & Henrich (2003, p. 365) acknowledge group selection as a mechanism enabling at least one of these transitions: 'Our own bodies are a group-selected community of genes….'[23] With respect to 'ancient social instincts', their position seems to be that the entirety of this category can be explained as the consequences of kin selection. But this is no more a satisfactory assumption to make about animals than it has proven to be for humans. For example, animals, including primates, have evolved cognitive and behavioral restraints on intraspecific harm that extend far beyond what can be accounted for by Hamiltonian kin selection (see Fehr & Henrich 2003, p. 76). And the same hormonal mechanism implicated in human bonding (oxytocin) appears also to play a critical role in the ability of many animals to overcome proximity fear of conspecifics (Fehr, Kosfeld, & Fischbacher 2006). Thus we have evidence of a common biological mechanism in humans and in animals lacking human scale cultural acquisition and transmission capabilities for overcoming the fear of exploitation that otherwise permeates social dilemmas.

Let’s also consider more closely the Richerson-Boyd position on the possible impact of co-evolutionary forces over the last half million years. The authors say that ‘We think cultural evolutionary processes constructed a social environment that caused individual natural selection to favor empathetic altruism’ (p. 238). But do they mean in this passage individual natural selection of cultural variants or individual natural selection of genes predisposing to certain behaviors? If only the former, then prosocial predispositions cannot be part of our innate psychology, and both the variance and levels of prosocial predispositions are purely cultural phenomena.

Suppose it is both the former and the latter. On page 242, the authors state that ‘co-evolution of genes and culture could create innate psychological dispositions that could never evolve by genes alone.’ Richerson and Boyd seem here to be saying that cultural group selection can be sufficiently strong to overcome the negative individual organism level selection that prosocial inclinations face within a group. On page 244, however, they undercut this interpretation, arguing that ‘Selection on genes can’t favor large scale cooperation even if every individual is on average better off if they cooperate. Even taking into account co-evolutionary pressures for more docile genes, selection on genes still tends to favor people who look out for themselves.’[24] If this is true, then cultural group selection could not ever, either before or after the acquisition of our ability to develop and transmit human scale culture, have had an effect on innate prosocial behavioral predisposers comparable to what we might otherwise credit to biological group selection, because it has never been strong enough to overcome selection within groups against such inclinations.

The Richerson and Boyd claim that if we allow for cultural group selection we can remain agnostic about or reject outright an historically prior role for biological group selection leads to several troubling implications and does not stand up to critical scrutiny. If cultural group selection only influences the distribution of cultural variants, and has no influence on gene frequencies, then the experimental literature doesn’t necessarily tell us anything about fundamental features of an innate human psychology. One would have to conclude that both the levels and variance of prosocial predispositions are purely cultural phenomena. If co-evolutionary forces have allowed cultural group selection to affect the evolution of gene frequencies (a position both embraced and then apparently rejected) then cultural group selection might account for the evolution of what Richerson and Boyd call the tribal instincts, *but not for the ancient prosocial instincts*, which preceded our capabilities for evolved culture. Finally, if the co-evolutionary influence on gene selection of cultural group selection has always been too weak to overcome individual organism level biological selection, cultural group selection cannot account for the evolution of innate prosocial inclinations either before or after the acquisition of the ability to acquire and transmit culture. The bottom line is that the authors do not ultimately take a clear position on whether our innate human psychology is basically selfish (with the acknowledged exception of those phenomena explicable through Hamiltonian kin selection), or whether it includes a mixture of genuinely selfish and prosocial inclinations.[25]

The same can be said for Henrich. After praising the importance of experimental research in casting doubt on selfish actor assumptions about human nature, and dismissing Hauser, McCabe, & Smith's (2004) 'Old Guard' dismissal of the possibility of group selection, Henrich rushes to assure readers that he does not intend this as support for the possibility of biological group selection: 'anyone who understands the theoretical and empirical reasons why biologists and anthropologists have been skeptical about the importance of *genetic* group selection for our species (a skepticism I share) will see that what I'm proposing does not suffer from the same criticisms. The standard arguments against genetic group selection do not apply to cultural group selection or selection among multi-stable equilibria' (2004b, p. 134).

This is exactly the same position taken by Richerson and Boyd (Henrich was Boyd's student). The similarity of their positions is reflected in the title of Henrich's target article, responses to which his reply is directed.[26]

Combine this with the Richerson and Boyd 'interpretation' of the D.S. Wilson model as one of cultural group selection (and, by implication, not biological group selection) with the fact that their dismissal of the empirical possibility of group selection is based on an analysis of Wright's 1945 model, and one begins to appreciate that the case for biological group selection is far from closed.

Science, like other human endeavors, is influenced by forces of cultural transmission, including imitation and conformity bias. The Richerson and Boyd position has a number of audiences primed to find its message attractive. Some within the biological community are happy to have biological group selection trivialized yet again. Traditional sociologists and anthropologists, who have never been comfortable with links between genetics and behavior, are happy to have the possibility of such a connection apparently sundered, even as they are encouraged to adopt population thinking and evolutionary modeling. Economists partial to assumptions about innate human psychology consistent with a level III approach to modeling may remain (wrongly) skeptical of the emphasis on culture as an independent influence on behavior. But the Richerson and Boyd position can provide a convenient way to dismiss the troublesome experimental results. If subjects persist in playing cooperate in a one shot PD it must just be a residual reflection of their socialization or cultural upbringing. If that's the case then the experiments are of little relevance in demonstrating features of an innate species typical human psychology. The Richerson and Boyd position, with its denial of any behavioral legacy of biological group selection, can only strengthen these individuals in their beliefs.[27]

Do not be misled: the currently fashionable position has the effect of undercutting most of the argument for biological group selection. Writers such as Richerson and Boyd have simply decreed that the model of group selection developed by D. S. Wilson is one of cultural group selection (Richerson & Boyd 2004, p. 162, fn. 28, but see p. 208, fn.

28), an interpretation that is increasingly common (see, e.g., Barrett et al 2002, p. 380). How anyone could read Wilson and Sober (1994) or the first three chapters of Sober and Wilson (1998) and suggest that they are setting forth models of cultural group selection alone is beyond me.[28]

In sum, with respect to the issue of the possible legacy of biological group selection, what we observe in recent writings is a continuing pattern of avoidance, evasion, and rejection. There are some exceptions. But where biological group selection is discussed, the tendency is to acknowledge its theoretical possibility, and then dismiss its behavioral legacy. This dismissal comes almost as close to trivializing its significance as did Williams' 1966 book, and does not acknowledge the evolution in Williams' own thinking (Williams 1992).

Conclusion

There are strong grounds for believing that humans as a species are predisposed against initiating attacks on other within-group conspecifics, and that this predisposition is partly genetic. The origins of civil law are likely to be found in codifications of rules governing the reciprocal relations enabled by the interactions between this no first strike impulse and our foraging algorithms. There are also strong grounds for believing that we are prepared to engage in costly punishment of those who do initiate attacks, and again, that the predisposition is partly genetic. The origins of criminal law are probably to be found in codifications of that inclination to moralistic aggression (see Hirshleifer 1978).[29]

But unless one begins by assuming that such behavior is already embedded within a regime of indefinitely repeated interaction, neither of these predispositions makes sense from a game theoretic perspective, and neither, upon first appearance, could have been favored if selection operated no higher than at the level of the individual organism. If we believe that Darwin limits us to version III, we are constrained either to reject Darwin or to dismiss the evidence. Traditional sociologists and anthropologists have been inclined toward the former; many economists and rational choice theorists toward the latter. *We are not in fact forced to make this choice.*

A little evolutionary theory can be a dangerous thing. The waters in the biological, social and behavioral sciences, are still muddied as the result of four decades of controversy regarding the empirical legacy of higher level biological selection. Nevertheless, those in the behavioral and social sciences can't make the mistake of dipping toes in the water, in the process absorbing uncritically the view that higher level selection is a logical impossibility or that its empirical legacy has been nil.

These misconceptions continue to contribute to the sociological/anthropological tradition of dismissing evolutionary biology as irrelevant for the study of human behavior, and the equally damaging tradition within economics/rational choice theory of dismissing evidence inconsistent with Edgeworth's or Nash's view of human nature. Neither sets us along the right road to building a progressive empirically based behavioral science.

But we are no better off in understanding the origin of these species typical predispositions if we adopt the currently fashionable position: acknowledge the theoretical possibility of biological group selection, and then trivialize its behavioral legacy. The rejection of the empirical significance of biological group selection is a scientifically maladaptive cultural variant. Human culture is a superstructure built upon certain prosocial human behavioral predispositions, which can be observed uncontaminated by issues of reputation or repetition in the experimentalist’s lab. These traits, which have an ancient evolutionary lineage, required biological group selection to become established within human populations, and help account for certain universal features of human culture. Different groups have developed cultural variations which, at the margin, influence group member’s behavior. These variations can influence group survival and growth, and are heritable in the sense that they can be passed on from one generation to another. But cultural group selection cannot provide an explanation of species typical features of an innate human psychology upon which culture builds.

We cannot hope to make progress in building a comprehensive theory of human behavior, or in bringing the natural and social sciences closer together in furthering that goal, if we do not acknowledge the operation of group selection processes in evolutionary history. Behavior that at low frequency is biologically altruistic requires appeal to higher level selection to explain its persistence. Rational choice theorists must abandon the mistaken belief that evolutionary biology provides a natural scientific foundation for version III. It is also necessary that we continue to carry the message to biologists that game theory, for all its appeal, is powerless to illuminate a number of important behavioral phenomena. If the explanatory powers of game theory continue to be oversold, both within and outside of the social sciences, the current enthusiasm for this mode of inquiry will dissipate, just as it has several times already in the past half century.

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NOTES

[1] See Field (2001), or Whitman (2004), who makes a similar point.

[2] We assume here that changes in relative wealth affect changes in relative fitness.

[3] See also his statement (p. 826) that altruism toward those not closely related is ‘not explained by the kin selection models of sociobiologists (but perhaps can be explained by their other models of group selection)’.

[4] ‘Sociobiologists have tried to solve their central problem with models of group selection; these models can be illustrated with the particular variant known as kin selection’ (Becker 1976, p. 818).

[5] Richerson and Boyd’s analysis of group selection appears to be based on Wright’s 1945 model. As in Wright, there is emphasis on winning groups replacing losing groups (2004, p. 206). Richerson, Boyd, & Henrich (2003, p. 368) actually speak of biological (genetic) group selection ‘requiring’ the physical extinction of groups. There is no acknowledgment that the demographics of D. S. Wilson’s model differ, and might be more robust to the standard critique. Nothing in Wilson’s model requires group extinction, except in the sense that members of groups periodically merge into the general population before again forming groups. More generally, Richerson and Boyd don’t discuss the mechanism reflected in the Price equations: a covariance between group growth rates and the share within each group of prosocial behavioral inclinations.

[6] This was not universal. See E. O. Wilson’s derogatory remarks about economics as a ‘science’ (1998, pp. 212-13).

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[7] In a few cases involving unbounded strategy spaces, such as the all-payer dollar action, the theory breaks down completely.

[8] But contrast this with Fehr and Henrich (2003, p. 61) who argue that one shot encounters are a common feature of the modern world, even though they might not have been in the past.

[9] The same problem is evident in Gifford (2000), who confuses the problem of explaining how altruistic tendencies rise from low to high frequencies with an analysis of how they are sustained, once at sufficiently high levels, by frequency dependent selection.

[10] For example, Belding squirrels give warning calls at the approach of intruders – putting themselves at risk but benefiting other conspecifics. Prior to the 1960s one might simply have said that this behavior was selected for because it benefited the species. Sherman (1977) found that females live in a group of closely related offspring and that males lead solitary existences and almost never give warning calls. So appeal to kin selection may account for much of the behavior. But showing that genetic propinquity affects the probability of warning calls does not dispose of the problem. In a related study, Hoogland found that prairie dogs were more likely to issue warning calls when there were relatives in the home coterie. But even in the absence of close relatives, males would still issue warnings about 16 percent of the time males and females about 26 percent of the time. As Hoogland noted, ‘Factors other than nepotism must also be involved, however, because recent immigrants into the colony, who have no close relatives either in the home coterie or elsewhere in the colony, sometimes call…’ (1983, p. 471).

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[11] We are better off because, if so programmed, we many not actually have to retaliate, because we won't be attacked in the first place. This is the paradox of deterrence, and of a nuclear strategy based on mutual assured deterrence (MAD).

[12] Williams goes on to acknowledge the problem of multiple equilibria, also a feature of the theory of indefinitely repeated games: 'More than one strategy or ratio of strategies may be a stable equilibrium. The one established by selection may depend on the starting ratio, another kind of legacy from the past' (1992, p. 58).

[13] Exogamy means marrying out: women were expected to seek a mate outside of their birth group. Across human populations, variability in mitochondrial DNA (passed down only along the maternal line) is about the same as that on the autosomal chromosomes, and much lower than variability in data on the X chromosome (passed down along male lines), which is consistent with a pattern of outmigration of women. (see Seilstad, M. T., E. Minch, & L. Cavalli-Sforza 1998, pp. 278-280).

[14] One must always provide some caveats in making inferences from the behavior of surviving animal species to the predispositions of ancestors common to them and to us.

[15] Richerson and Boyd (2004, pp. 147, 194) also discuss this development, but, consistent with their minimization of conflicts that might require appeal to biological group selection for their resolution, refer to it as a coevolving mutualism. The relationship may have eventuated in mutualism, but it surely did not start that way, a point emphasized by Maynard- Smith and Szathmary (1995) and even by Richerson and Boyd (p. 153).

[16] Some animal cells, such as spermatozoa, also have flagella, a feature absent in plants.

[17] A montonic series, if decreasing, never increases, or if increasing, never decreases. A monotonically increasing function is one where if y is greater than or equal to x, f(y) is

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greater than or equal to f(x). In this case, the function in question is the utility function, and y and x amounts of a commodity, or vectors of commodity quantities. Thus if money is considered a generalized good, experimental evidence that people leave money on the table poses something of a problem for version II as well as version III theory. See Varian (2002, p. 45).

[18] If genetic predisposers are the ultimate causes of these species typical predispositions, biological mechanisms are the key to proximate cause. A notable confirmation of this is the recent set of experiments conducted by Fehr et al (2005). Subjects were divided into two groups. Group 1 was given a whiff of oxytocin, a hormone released during sexual intercourse or nursing, and thus implicated in human bonding. Group 2 got a placebo, and then both groups played the trust game, in which A is given a sum of money, any amount of which can be given to B. Whatever is transferred is increased by a multiple. B then may, but is not required to, give some back to A. The subgame perfect equilibrium is for A to transfer nothing, although positive transfers are common in the experimental literature. In this experiment, those in the A role receiving oxytocin provided transfers to B which were on average 17 percent higher than the control group. There was no effect on B's behavior in the game, and no effect of oxytocin if subjects were told they were playing against a computer.

[19] Several of the studies also examined behavior in dictator and voluntary provision of public goods games.

[20] 'I take no stand on the existence of group selection, which is quite controversial among biologists.' Rubin 2002, p. 63

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[21] Boyd has been chair, with Gintis, of the MacArthur preference group, played a role in organizing the research reported in Henrich et al (2004), and coauthored with most of the authors mentioned in this section.

[22] This is consistent with D.S. Wilson's latest formulation of the relation between cultural and group selection: 'Human history and current events can be regarded as an ongoing process of cultural multilevel selection, whose dynamics are influenced by psychological traits that evolved by genetic multilevel selection in the distant past' (Wilson 2004, p. 206).

[23] This conference paper is somewhat more circumspect than Richerson and Boyd (2004) in dismissing a behavioral legacy for biological group selection.

[24] Richerson and Boyd must really mean selection on organisms here, since it makes no sense to talk about co-evolutionary forces if there can be no impact of cultural group selection on prosocial gene frequency. The essence of group selection is that it may favor the spread of genes which damage the relative fitness of the gene-containing organisms within the organism's group.

[25] A more qualified position, but one still heavily influenced by Boyd and Richerson, is reflected in Hammerstein (2003, p. 5): '…we know that many cooperative phenotypes cannot evolve *genetically* in a given population because this would require group selection and selection is often too weak at the group level. The same phenotypes might evolve by group selection in *cultural* evolution, however, if some conformist transmission is involved…'

[26] Fehr and Fischbacher (2003), unfortunately, also seem to have signed on to this point of view (see pp. 789-790).

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[27] There is a variant of this view among evolutionary psychologists who interpret results such as those in the ultimatum game as reflecting a maladaptation (see Fehr and Henrich 2003, pp. 68-69).

[28] On the other hand, some of D. S. Wilson's latest writings appear more accommodationist with respect to the Richerson and Boyd position (Wilson 2004).

[29] The specifics of political culture, and in particular variations in its hierarchical character, are also influenced by our propensities to assert dominance and accept subordination, inclinations whose origins and implications are not explored in this paper. See Boehm 1999.