shot encounters can be guaranteed" (i.e. reputation is always a potential issue). Selection for individual selfishness can sometimes lead to cooperative outcomes, so why not cooperative components of psychologies? These will of course be tempered by other parts of our psychology that look out for number one. Still, even a partly cooperative human psychology would be a finding of high importance, though not one inconsistent with either group selection or inclusive fitness.

1. Queller DC (1992) Quantitative genetics, inclusive fitness, and group selection. *Am. Nat.* 139:540-558.
2. Wilson DS, Pollock GB, Dugatkin LA (1992) Can altruism evolve in purely viscous populations? *Evol. Ecol.* 6:331-341.
3. Buss LW (1987) *The Evolution of Individuality* (Princeton University Press, Princeton).

**Daniel C. Dennett**
*Philosopher; Austin B. Fletcher Professor of Philosophy, Co-Director, Center for Cognitive Studies, Tufts University; Author, Breaking the Spell*

Steven Pinker sets out the problems with the current enthusiasm for group selection clearly and fairly, except for what are, in my opinion, two regrettable but easily corrected misplaced emphases.

First, while evolution by natural selection definitively and demonstrably *works* under conditions of utterly random (non-directed) variation, non-random variation does not *prevent* the algorithmic process of natural selection from grinding out its well-tested innovations, or render it superfluous, as Pinker suggests. Non-random variation typically just speeds up the process, a little or a lot. The cognitive brilliance that Steve Pinker mistakenly sees as usurping the role of natural selection in human cultural change is indeed an important factor, but one should never forget Orgel's Second Law: evolution is cleverer than you are. Brainchildren die like flies, thousands or even millions of hopeful ventures extinguished for every innovation that truly"goes viral" and then goes on to fixation in the shared culture we pass on to our descendants. This process of differential adoption, not just by intelligent consumers, but just as much by uncomprehending (or semi-comprehending, or even heedless) hosts is "ordinary causation" in one sense—the same sense in which every birth, death and rejection in the process of genetic natural selection is ordinary causation—but it is also a clear case of natural selection of cultural items—*memes*, unless you find yourself allergic to that term, as some thinkers apparently are.

Fitness-*reducing* memes are just as possible as fitness-enhancing memes, and one of the chief virtues of adopting the meme's eye perspective is correcting the systematic blindness to this possibility in many theorists who can only see the (often imagined) *benefits* of established cultural institutions because they think natural selection would sweep away all toxic variants. If only! Like the common cold, many cultural items persist because they *can*, in spite of not being consciously and rationally accepted or adopted or promoted by the minds they infest, and in spite of having lost any redeeming features they may ever have had. They have their own fitness as replicators, largely independent of their contributions to the fitness of their hosts.

Pete Richerson's comment articulates the details well, but muddies the water by speaking of cultural *group* selection. There are reasons for calling these phenomena a variety of group selection, reasons ably recounted by Boyd and Richerson in many publications, but better reasons—in my opinion—for avoiding the label, precisely because it *seems* to give support to the vague and misguided ideas of group selection that Pinker exposes so effectively. These phenomena consist in the evolution by natural selection (both cultural and genetic) of what might be called groupishness adaptations, dispositions (or traditions) of cooperation and the punishment of defectors, and the like, but not by a process of differential *reproduction of groups*. What differentially reproduce in these phenomena are groupishness memes, not groups. The establishment of these memes may then enable the genetic evolution of enhancements in hosts—like the lactose toleration that evolved in response to the culturally spread tradition of dairying. This is no more group selection than the differential reproduction of the flora in our guts is group selection.

The second misplaced emphasis is Pinker's phrase "the illusion of design in the natural world." Richard Dawkins, in a similar vein, says "the illusion of design conjured by Darwinian natural selection is so breathtakingly

powerful" in *The Ancestors' Tale* (p457), and elsewhere proposes to speak of "designoid" features of the natural world (*eg., Climbing Mount Improbable*, p4). I disagree with this policy, which can backfire badly. I recently overheard a conversation among some young people in a bar about the marvels of the nano-machinery discovered inside all cells. "When you see all those fantastic little robots working away, how can you possibly believe in evolution!" one exclaimed, and another nodded wisely. Somehow these folks had gotten the impression that evolutionary biologists thought that the intricacies and ingenuities of life's processes weren't all that wonderful. These evolution-doubters were not rednecks; they were Harvard Medical students! They hugely underestimated the power of natural selection because they had been told by evolutionary biologists, again and again, that there is no *actual* design in nature, only the *appearance* of design. This episode strongly suggested to me that one of the themes that has been gaining ground in "common knowledge" is that evolutionary biologists are reluctant to "admit" or "acknowledge" the manifest design in nature. I recommend instead the expository policy of calling nature's marvels *design*, as real as any design in the universe, but just not the products of an *intelligent* designer. There could be a good use for "designoid," to refer to the truly only apparent design manifest, for example, in all the complicated chemical apparatus that cartoonists draw when they need to illustrate a laboratory—it looks impressive to the naïve eye, but is just a nonsensical hodgepodge of tubes, bunsen burners, retorts and the like. That is apparent design; the design in nature, in contrast, is typically as good as, or even much better than, the designs we "intelligent" artificers have yet devised. They work really well, which is as good a criterion of design as any, in my opinion.

I note the irony in the apparent tension between my two recommendations: *drop* the term "group" from the label for cultural selection, since it seems to give aid and comfort to the forces of darkness (the proponents of bogus forms of group selection), but *maintain* the word "design" in spite of the fact that it seems to give such aid and comfort to the intelligent design crowd. The situations are only superficially similar, however. The design due to human designers and the design due to natural selection are often responsive to the same reasons and conditions (think airplane wings and birds' wings) to the point that the former are often quite dutiful copies of the latter. It may even be impossible to tell, without direct knowledge of history, whether a design feature found in some organism is due to natural or artificial selection (think cheetah and greyhound). On the other hand to call a phenomenon group selection which seldom if ever involves the differential *replication* (as contrasted with *survival* or *growth*) of groups seems to me to be gratuitously misleading.

**Herbert Gintis**
*Author, A Cooperative Species: Human Reciprocity and Evolution*

**On the Evolution of Human Morality**

Steven Pinker's thoughtful remarks concerning group selection present a useful occasion for clearing some misconceptions surrounding recent developments in the behavioral sciences concerning our understanding of moral vs. self-interested behavior. Initiated in 1966 by George C. Willams' *Adaptation and Natural Selection* and followed a decade later by Richard Dawkins' *The Selfish Gene*, evolutionary biologists in the last quarter of the Twentieth century came to view humans as fundamentally selfish, contributing to society only when socially-imposed rewards and punishment render it in their self-interest to do so. Dawkins, for instance, opines in the opening pages of *The Selfish Gene*, "We are survival machines—robot vehicles blindly programmed to preserve the selfish molecules known as genes.... a predominant quality to be expected in a successful gene is ruthless selfishness. This gene selfishness will usually give rise to selfishness in individual behavior.... Anything that has evolved by natural selection should be selfish."

Of course, it does not appear in our daily life that everyone is selfish, and if we introspect, most of us will agree that we try to behave, however successfully or unsuccessfully, as moral beings willing to sacrifice personal amenities in the pursuit of truth, justice, loyalty and compassion. Dawkins' explanation is that human morality is a cultural facade laid upon our basically selfish human nature. "Be warned," he states, "that if you wish, as I do, to build a society in which individuals cooperate generously and unselfishly towards a common good, you can

Edge

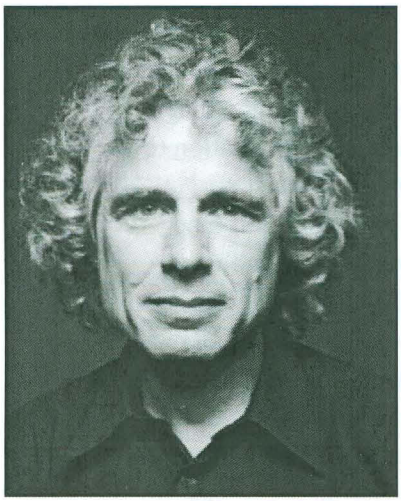
*To arrive at the edge of the world's knowledge, seek out the most complex and sophisticated minds, put them in a room together, and have them ask each other the questions they are asking themselves.*

## THE FALSE ALLURE OF GROUP SELECTION

An Edge Original Essay **Steven Pinker** [6.18.12]

Topic:

**LIFE**



*I am often asked whether I agree with the new group selectionists, and the questioners are always surprised when I say I do not. After all, group selection sounds like a reasonable extension of evolutionary theory and a plausible explanation of the social nature of humans. Also, the group selectionists tend to declare victory, and write as if their theory has already superseded a narrow, reductionist dogma that selection acts only at the level of genes. In this essay, I'll explain why I think that this reasonableness is an illusion. The more carefully you think about group selection, the less sense it makes, and the more poorly it fits the facts of human psychology and history.*

**THE REALITY CLUB: Stewart Brand, Daniel Everett, David C. Queller, Daniel C. Dennett, Herbert Gintis, Harvey Whitehouse & Ryan McKay, Peter J. Richerson, Jerry Coyne, Michael Hochberg, Robert Boyd & Sarah Mathew, Max Krasnow & Andrew Delton,Nicolas Baumard, Jonathan Haidt, David Sloan Wilson, Michael E. Price, Joseph Henrich, Randolph M. Nesse, Richard Dawkins, Helena Cronin, John Tooby.**

**STEVEN PINKER REPLIES**

*Group selection has become a scientific dust bunny, a hairy blob in which anything having to do with "groups" clings to anything having to do with "selection." The problem with scientific dust bunnies is not just that they sow confusion; ... the apparent plausibility of one restricted version of "group selection" often bleeds outwards to a motley collection of other, long-discredited versions. The problem is that it also obfuscates evolutionary theory by blurring genes, individuals, and groups as equivalent levels in a hierarchy of selectional units; ... this is not how natural selection, analyzed as a mechanistic process, really works. Most importantly, it has placed blinkers on psychological understanding by seducing many people into simply equating morality and culture with group selection, oblivious to alternatives that are theoretically deeper and empirically more realistic.*

STEVEN PINKER is a Harvard College Professor and Johnstone Family Professor of Psychology; Harvard University. Author, *The Better Angels Of Our Nature: How Violence Has Declined, The Language Instinct,* and *How the Mind Works.*

**Steven Pinker's *Edge* Bio Page**

[photo credit: Max Gerber]

## THE FALSE ALLURE OF GROUP SELECTION

Human beings live in groups, are affected by the fortunes of their groups, and sometimes make sacrifices that benefit their groups. Does this mean that the human brain has been shaped by natural selection to promote the welfare of the group in competition with other groups, even when it damages the welfare of the person and his or her kin? If so, does the theory of natural selection have to be revamped to designate "groups" as units of selection, analogous to the role played in the theory by genes?

Several scientists whom I greatly respect have said so in prominent places. And they have gone on to use the theory of group selection to make eye-opening claims about the human condition.[1] They have claimed that human morailty, particularly our willingness to engage in acts of altruism, can be explained as an adaptation to group-against-group competition. As E. O. Wilson explains, "In a group, selfish individuals beat altruistic individuals. But, groups of altruistic individuals beat groups of selfish individuals." They have proposed that group selection can explain the mystery of religion, because a shared belief in supernatural beings can foster group cohesion. They suggest that evolution has equipped humans to solve tragedies of the commons (also known as collective action dilemmas and public goods games), in which actions that benefit the individual may harm the community; familiar examples include overfishing, highway congestion, tax evasion, and carbon emissions. And they have drawn normative moral and political conclusions from these scientific beliefs, such as that we should recognize the wisdom behind conservative values, like religiosity, patriotism, and puritanism, and that we should valorize a communitarian loyalty and sacrifice for the good of the group over an every-man-for-himself individualism.

I am often asked whether I agree with the new group selectionists, and the questioners are always surprised when I say I do not. After all, group selection sounds like a reasonable extension of evolutionary theory and a plausible explanation of the social nature of humans. Also, the group selectionists tend to declare victory, and write as if their theory has already superseded a narrow, reductionist dogma that selection acts only at the level of genes. In this essay, I'll explain why I think that this reasonableness is an illusion. The more carefully you think about group selection, the less sense it makes, and the more poorly it fits the facts of human psychology and history.

Why does this matter? I'll try to show that it has everything to do with our best scientific understanding of the evolution of life and the evolution of human nature. And though I won't take up the various moral and political colorings of the debate here (I have discussed them elsewhere), it ultimately matters for understanding how best to deal with the collective action problems facing our species.

The first big problem with group selection is that the term itself sows so much confusion. People invoke it to refer to many distinct phenomena, so casual users may literally not know what they are talking about. I have seen "group selection" used as a loose synonym for the evolution of organisms that live in groups, and for any competition among groups, such as human warfare. Sometimes the term is needlessly used to refer to an individual trait that happens to be shared by the members of a group; as the evolutionary biologist George Williams noted,"a fleet herd of deer" is really just a herd of fleet deer. And sometimes the term is used as a way of redescribing the conventional gene-level theory of natural selection in different words: subsets of genetically related or reciprocally cooperating individuals are dubbed "groups," and changes in the frequencies of their genes over time is dubbed "group selection."[2] To use the term in these senses is positively confusing, and writers

would be better off referring to whichever phenomenon they have in mind.

In this essay I'll concentrate on the sense of "group selection" as a version of natural selection which acts on groups in the same way that it acts on individual organisms, namely, to maximize their inclusive fitness (alternatively, which acts on groups in the same way it acts on genes, namely to increase the number of copies that appear in the next generation; I will treat these formulations as equivalent). Modern advocates of group selection don't deny that selection acts on individual organisms; they only wish to add that it acts on higher-level aggregates, particularly groups of organisms, as well. For this reason, the theory is often called "multilevel selection" rather than "group selection." This all sounds admirably ecumenical and nonreductionist, but my arguments will also apply to multilevel selection. I don't think it makes sense to conceive of groups of organisms (in particular, human societies) as sitting at the top of a fractal hierarchy with genes at the bottom, with natural selection applying to each level in parallel ways.

First I'll examine the idea that group selection is a viable explanation of the traits of human groups such as tribes, religions, cultures, and nations. Then I'll turn to group selection as an explanation of the traits of individual humans, that is, the intuitions and emotions that make it possible for people to learn their culture and coexist in societies. (No one denies that such faculties exist.) Finally I'll examine the empirical phenomena that have been claimed to show that group selection is necessary to explain human altruism.

**1. Group selection as an explanation of the traits of groups.**

Natural selection is a special explanatory concept in the sciences, worthy, in my view, of Daniel Dennett's designation as "the best idea that anyone ever had." That's because it explains one of the greatest mysteries in science, the illusion of design in the natural world. The core of natural selection is that when replicators arise and make copies of themselves, (1) their numbers will tend, under ideal conditions, to increase exponentially; (2) they will necessarily compete for finite resources; (3) some will undergo random copying errors ("random" in the sense that they do not anticipate their effects in the current environment); and (4) whichever copying errors happen to increase the rate of replication will accumulate in a lineage and predominate in the population. After many generations of replication, the replicators will show the appearance of design for effective replication, while in reality they have just accumulated the copying errors that had successful replication as their effect.

What's satisfying about the theory is that it is so mechanistic. The copying errors (mutations) are random (more accurately, blind to their effects). The outcome of interest is the number of copies in a finite population. The surprising outcome is a product of the cumulative effects of many generations of replication. If the copying errors were not random (that is, if Lamarck had been correct that changes in an organism arise in response to a felt need, or if creationists were right that a superior intelligence directed mutations to be beneficial to the organism), then natural selection would be otiose—the design could come from the mutation stage. If the outcome of interest were not the number of copies in a finite population, but some human-centered criterion of success (power, preeminence, influence, beauty), then natural selection would not be mechanistic: the dynamics of change in the population could not be mathematically computed from its prior state. And if it took place in a single generation, then natural selection would be banal, since it would add nothing to ordinary physical cause and effect. When a river erodes the soft rock layers on its bed and leaves behind the harder layers, or when the more volatile compounds in petroleum evaporate faster than the less volatile ones, one hardly needs to invoke the theory of natural selection. One can just say that some things are stronger, or longer-lasting, or more stable than others. Only when selection operates over *multiple generations* of replication, yielding a cumulative result that was not obvious from cause and effect applying to a single event, does the concept of natural selection add anything.

The theory of natural selection applies most readily to genes because they have the right stuff to drive selection, namely making high-fidelity copies of themselves. Granted, it's often convenient to speak about selection at the level of individuals, because it's the fate of individuals (and their kin) in the world of cause and effect which determines the fate of their genes. Nonetheless, it's the genes themselves that are replicated over generations and are thus the targets of selection and the ultimate beneficiaries of adaptations. Sexually reproducing organisms

don't literally replicate themselves, because their offspring are not clones but rather composites of themselves and their mates. Nor can any organism, sexual or asexual, pass onto its offspring the traits it has acquired in its lifetime. Individual bodies are simply not passed down through the generations the way that genes are. As Stephen Jay Gould put it, "You can't take it with you, in this sense above all."

Now, no one "owns" the concept of natural selection, nor can anyone police the use of the term. But its explanatory power, it seems to me, is so distinctive and important that it should not be diluted by metaphorical, poetic, fuzzy, or allusive extensions that only serve to obscure how profound the genuine version of the mechanism really is.

To be sure, some extensions of natural selection to replicators other than genes are rigorous and illuminating, because they preserve the essential features of replicator dynamics. Examples include bits of code in genetic algorithms, the analogs of genes in artificial-life simulations, and, if the physicist Lee Smolin is correct, the laws and constants of entire universes.

But other extensions are so poetical that they shed no light on the phenomenon and only obscure the real power of natural selection. There's no end to the possibilities for pointlessly redescribing ordinary cause-and-effect sequences using the verbiage of natural selection. Cities have more old buildings made of stone than of wood because of the process of edifice selection. Cars today are equipped with steel-belted radials because they outcompeted polyester-belted tires in a process of tire selection. Touch-tone phones have prevailed over dial phones because of their competitive advantages in telephone selection. And so on. Sure, some things last longer or do better in competition than others because they have traits that help them last longer or compete more effectively. But unless the traits arose from multiple iterations of copying of random errors in a finite pool of replicators, the theory of natural selection adds nothing to ordinary cause and effect.

What about groups? Natural selection could legitimately apply to groups if they met certain conditions: the groups made copies of themselves by budding or fissioning, the descendant groups faithfully reproduced traits of the parent group (which cannot be reduced to the traits of their individual members), except for mutations that were blind to their costs and benefits to the group; and groups competed with one another for representation in a meta-population of groups. But everyone agrees that *this is not what happens in so-called "group selection."* In every case I've seen, the three components that make natural selection so indispensable are absent.

> (a) The criterion of success is not the number of copies in a finite population (in this case, the meta-population of groups), but some analogue of success like size, influence, wealth, power, longevity, territory, or preeminence. An example would be the "success" of monotheistic religions. No one claims that monotheistic religions are more fission-prone than polytheistic ones, and that as a consequence there are numerically more monotheistic belief systems among the thousands found on earth. Rather, the "success" consists of monotheistic religions having more people, territory, wealth, might, and influence. These are impressive to a human observer, but they are not what selection, literally interpreted, brings about.
>
> (b) The mutations are not random. Conquerors, leaders, elites, visionaries, social entrepreneurs, and other innovators use their highly nonrandom brains to figure out tactics and institutions and norms and beliefs that are intelligently designed in response to a felt need (for example, to get their group to predominate over their rivals).
>
> (c) The "success" applies to the entity itself, not to an entity at the end of a chain of descendants. It was the Roman Empire that took over most of the ancient world, not a group that splintered off from a group that splintered off from a group that splintered off from the Roman Empire, each baby Roman Empire very much like the parent Roman Empire except for a few random alterations, and the branch of progeny empires eventually outnumbering the others.

On top of these differences, most of the groupwide traits that group selectionists try to explain are cultural rather

than genetic. The trait does not arise from some gene whose effects propagate upward to affect the group as a whole, such as a genetic tendency of individuals to disperse which leads the group to have a widespread geographic distribution, or an ability of individuals to withstand stressful environments which leads the species to survive mass extinction events. Instead, they are traits that are propagated culturally, such as religious beliefs, social norms, and forms of political organization. Modern group selectionists are often explicit that it is cultural traits they are talking about, or even that they are agnostic about whether the traits they are referring to are genetic or cultural.

What all this means is that so-called group selection, as it is invoked by many of its advocates, is not a precise implementation of the theory of natural selection, as it is, say, in genetic algorithms or artificial life simulations. Instead it is a loose metaphor, more like the struggle among kinds of tires or telephones. For this reason the term "group selection" adds little to what we have always called "history." Sure, some cultures have what it takes to become more populous or powerful or widespread, including expansionist ideologies, proselytizing offensives, effective military strategies, lethal weaponry, stable government, social capital, the rule of law, and norms of tribal loyalty. But what does "natural selection" add to the historian's commonplace that some groups have traits that cause them to grow more populous, or wealthier, or more powerful, or to conquer more territory, than others?

**2. Group selection as an explanation of the traits of individuals.**

Let's now turn to the traits of individuals. Is group selection necessary to explain the evolution of psychological traits adapted to group living such as tribalism, bravery, self-sacrifice, xenophobia, religion, empathy, and moralistic emotions? This section looks at theory, the next one at psychological and historical data.

The reproductive success of humans undoubtedly depends in part on the fate of their groups. If a group is annihilated, all the people in it, together with their genes, are annihilated. If a group acquires territory or food or mates, the windfall will benefit some or all of its members. But recall the fleet herd of deer and the herd of fleet deer. If a person has innate traits that encourage him to contribute to the group's welfare and as a result contribute to *his own* welfare, group selection is unnecessary; individual selection in the context of group living is adequate. Individual human traits evolved in an environment that includes other humans, just as they evolved in environments that include day-night cycles, predators, pathogens, and fruiting trees.

Some mathematical models of "group selection" are really just individual selection in the context of groups.[3] The modeler arbitrarily stipulates that the dividend in fitness that accrues to the individual from the fate of the group does not count as "individual fitness." But the tradeoff between "benefiting the self thanks to benefiting the group" and "benefiting the self at the expense of the rest of the group" is just one of many tradeoffs that go into gene-level selection. Others include reproductive versus somatic effort, mating versus parenting, and present versus future offspring. There's no need to complicate the theory of natural selection with a new "level of selection" in every case.

It's only when humans display traits that are *disadvantageous* to themselves while benefiting their group that group selection might have something to add. And this brings us to the familiar problem which led most evolutionary biologists to reject the idea of group selection in the 1960s.[4] Except in the theoretically possible but empirically unlikely circumstance in which groups bud off new groups faster than their members have babies, any genetic tendency to risk life and limb that results in a net decrease in individual inclusive fitness will be relentlessly selected against. A new mutation with this effect would not come to predominate in the population, and even if it did, it would be driven out by any immigrant or mutant that favored itself at the expense of the group.

Let's take the concrete example of collective aggression. Often the benefits to the self and to the group may coincide. A warrior may scare off a party of attackers and save the lives of his fellow villagers together with the lives of himself and his family. In other cases the benefits may diverge: the warrior may stay at the rear, or sneak off to the side, and let everyone else fight. In still others the outcome may be uncertain, but because selection

works on probabilities, he may play the odds, say, taking a one-in-ten chance of getting killed in a raid that promises a one-in-two chance of abducting a few extra wives. We should expect selection to favor traits that maximize the individual's expected reproductive output, given these tradeoffs.

What we *don't* expect to see is the evolution of an innate tendency among individualsto predictably sacrifice their expected interests for the interests of the group—to cheerfully volunteer to serve as a galley slave, a human shield, or cannon fodder. Take the extreme case of a gene that impelled a person to launch a suicide attack that allowed his group to prevail over an enemy. That is hardly a gene that could be selected! (I'll put aside for now the potential benefits to the suicide warrior's kin.) What could evolve, instead, is a tendency to manipulate *others* to become suicide attackers, and more generally, to promulgate norms of morality and self-sacrifice that one intends to apply in full force to everyone in the group but oneself. If one is the unlucky victim of such manipulation or coercion by others, there's no need to call it altruism and search for an evolutionary explanation, any more than we need to explain the "altruism" of a prey animal who benefits a predator by blundering into its sights.

Thus we have a nice set of competing empirical predictions for any examples of group-benefiting self-sacrifice we do observe in humans. If humans were selected to benefit their groups at the expense of themselves, then self-sacrificial acts should be deliberate, spontaneous, and uncompensated, just like other adaptations such as libido, a sweet tooth, or parental love. But if humans were selected to benefit themselves and their kin in the context of group living (perhaps, but not necessarily, by also benefiting their groups), then any guaranteed self-sacrifice should be a product of manipulation by others, such as enslavement, conscription, external incentives, or psychological manipulation.

To be sure, if we go back to group selection as an explanation of *group* traits, particularly cultural ones, then it's easy to see how a group that successfully coerced or manipulated a renewable supply of its own members to launch suicide attacks might expand relative to other groups. But that would have nothing to do with its members' inherited psychology, in this case, their willingness to sacrifice themselves without manipulation. The same is true for less extreme sacrifices.

**3. Do Humans in Fact Have Adaptations that Benefit the Group at the Expense of the Self?**

The recent surge of interest in group selection has been motivated by two empirical phenomena. One is eusociality in insect taxa such as bees, ants, and termites, whose worker or soldier castes forgo their own reproduction and may sacrifice their lives to benefit their fellows, as when a bee dies when stinging an invader. E. O. Wilson notes that a self-sacrificing insect benefits the colony, and concludes that eusociality must be explained by selection among colonies. But most other biologists point out that the sacrificer benefits the queen (her sister or mother), who founds a new colony when she reproduces, so the simplest explanation of eusociality is that the genes promoting self-sacrifice were selected because they benefited copies of themselves inside the queen.[5] The same is true for other collectives of genetic relatives in which only a select few reproduce, such as the individuals making up a colonial organism and the cells making up a body.

The other phenomenon is the existence of altruism and self-sacrifice among humans, such as martyrdom in warfare, costly punishment of free riders, and generosity toward strangers. Group selectionists often analogize self-sacrifice among humans to eusociality in insects, and explain both by group selection. In *The Social Conquest of Earth,* a book whose title alludes to the evolutionary success of humans and social insects, Wilson writes, (p. 56): "An unavoidable and perpetual war exists between honor, virtue, and duty, the products of group selection, on one side, and selfishness, cowardice, and hypocrisy, the products of individual selection, on the other side." In *The Righteous Mind,* Jonathan Haidt agrees, explaining the evolution of moral intuitions such as deference to authority, loyalty to community, and conformity to social norms by proposing that "Humans are 90 percent chimp and 10 percent bee."

Many questionable claims are packed into the clustering of inherent virtue, human moral intuitions, group-benefiting self-sacrifice, and the theory of group selection. One is the normative moral theory in which virtue is

equated with sacrifices that benefit one's own group in competition with other groups. If that's what virtue consisted of, then fascism would be the ultimate virtuous ideology, and a commitment to human rights the ultimate form of selfishness. Of course, that is not what Wilson meant; he apparently wanted to contrast individual selfishness with something more altruistic, and wrote as if the only alternative to benefiting oneself is contributing to the competitive advantage of one's group. But the dichotomy ignores another possibility: that an individual can be virtuous by benefiting *other individuals* (in principle, all humans, or even all sentient creatures), whether or not he enhances the competitive prowess of the group to which he belongs.

Another problem with the bundling of human altruism, insect eusociality, and group selection is that insect eusociality itself is not, according to most biologists other than Wilson, explicable by group selection. But let's provisionally grant one part of the association for the sake of the empirical tests. The gene-centered explanation of eusociality depends on the relatedness of sterile workers and soldiers to a small number of queens who are capable of passing along their genes, and of course that reproductive system is absent from human groups. Nonetheless, according to this argument, humans are like bees in contributing to the welfare of their community. Since the gene-centered theory of insect eusociality cannot apply to humans, perhaps it is unnecessary to explain bees either. In that case, the most parsimonious theory would explain both human altruism and insect eusociality with group selection.

So for the time being we can ask, is human psychology really similar to the psychology of bees? When a bee suicidally stings an invader, presumably she does so as a primary motive, as natural as feeding on nectar or seeking a comfortable temperature. But do humans instinctively volunteer to blow themselves up or advance into machine-gun fire, as they would if they had been selected with group-beneficial adaptations? My reading of the study of cooperation by psychologists and anthropologists, and of the study of group competition by historians and political scientists, suggest that in fact human are nothing like bees.

The huge literature on the evolution of cooperation in humans has done quite well by applying the two gene-level explanations for altruism from evolutionary biology, nepotism and reciprocity, each with a few twists entailed by the complexity of human cognition.

Nepotistic altruism in humans consists of feelings of warmth, solidarity, and tolerance toward those who are likely to be one's kin. It evolved because any genes that encouraged such feelings toward genetic relatives would be benefiting copies of themselves inside those relatives. (This does not, contrary to a common understanding, mean that people love their relatives because of an unconscious desire to perpetuate their genes.) A vast amount of human altruism can be explained in this way. Compared to the way people treat nonrelatives, they are far more likely to feed their relatives, nurture them, do them favors, live near them, take risks to protect them, avoid hurting them, back away from fights with them, donate organs to them, and leave them inheritances.[6]

The cognitive twist is that the recognition of kin among humans depends on environmental cues that other humans can manipulate.[7] Thus people are also altruistic toward their adoptive relatives, and toward a variety of fictive kin such as brothers in arms, fraternities and sororities, occupational and religious brotherhoods, crime families, fatherlands, and mother countries. These faux-families may be created by metaphors, simulacra of family experiences, myths of common descent or common flesh, and other illusions of kinship. None of this wasteful ritualizing and mythologizing would be necessary if "the group" were an elementary cognitive intuition which triggered instinctive loyalty. Instead that loyalty is instinctively triggered by those with whom we are likely to share genes, and extended to others through various manipulations.

The other classic form of altruism is reciprocity: initiating and maintaining relationships in which two agents trade favors, each benefiting the other as long as each protects himself from being exploited. Once again, a vast amount of human cooperation is elegantly explained by this theory.[8] People are "nice," both in the everyday sense and the technical sense from game theory, in that they willingly confer a large benefit to a stranger at a small cost to themselves, because that has some probability of initiating a mutually beneficial long-term relationship. (It's a common misunderstanding that reciprocal altruists never help anyone unless they are soliciting or returning a favor; the theory in fact predicts that they will sympathize with the needy.) People

recognize other individuals and remember how they have treated and been treated by them. They feel gratitude to those who have helped them, anger to those who have exploited them, and contrition to those whom they have exploited if they depend on them for future cooperation.

One cognitive twist on this formula is that humans are language-using creatures who need not discriminate reciprocators from exploiters only by direct personal experience, but can also ask around and find out their reputation for reciprocating with or exploiting others. This in turn creates incentives to establish and exaggerate one's reputation (a feature of human psychology that has been extensively documented by social psychologists), and to attempt to see through such exaggerations in others.[9] And one way to credibly establish one's reputation as an altruist in the probing eyes of skeptics to *be* an altruist, that is, to commit oneself to altruism (and, indirectly, its potential returns in the long run, at the expense of personal sacrifices in the short run).[10] A third twist is that reciprocity, like nepotism, is driven not by infallible knowledge but by probabilistic cues. This means that people may extend favors to other people with whom they will never in fact interact with again, as long as the situation is representative of ones in which they *may* interact with them again.[11] Because of these twists, it's a fallacy to think that the theory of reciprocal altruism implies that generosity is a sham, and that people are nice to one another only when each one cynically calculates what's in it for him.

Group selection, in contrast, fails to predict that human altruism should be driven by moralistic emotions and reputation management, since these may benefit of individuals who inflate their reputations relative to their actual contributions and thus subtract from the welfare of the group. Nor is there any reason to believe that ants, bees, or termites have moralistic emotions such as sympathy, anger, and gratitude, or a motive to monitor the reputations of other bees or manage their own reputations. Group welfare would seem to work according to the rule "From each according to his ability, to each according to his need." Ironically, Wilson himself, before he came out as a group selectionist, rejected the idea that human altruism could be explained by going to the ants, and delivered this verdict on the Marxist maxim: "Wonderful theory; wrong species." Haidt, too, until recently was content to explain the moral emotions with standard theories of nepotistic and reciprocal altruism.[12]

The only empirical phenomenon which has been directly adduced as support for group selection is a set of experimental games in which people seem to sacrifice their interests for those of a group.[13] In a laboratory version of a Public Goods game, participants are allocated a sum of money and invited to contribute as much as they want to a communal pot, which is then multiplied by the experimenter and divided evenly among them. The optimum strategy for the group is for everyone to contribute the maximum; the optimum strategy for the individual is to be a free rider and stint on his public contribution, thereby enjoying both the group dividend andhis private stash. In a typical experiment with repeated rounds of play, free riding takes over and the public contribution dwindles to zero.

A natural conclusion is that this shows that humans are *not* a group-selected adaptation which capitalizes on opportunities to make sacrifices for the common good. But oddly enough, this research has been interpreted as evidence *for* group selection, because of the outcome of one variant of the procedure. When people are given an opportunity to punish free riders by levying a fine on them, then free riding decreases and everyone's profit increases—no surprise there. The surprise is that people will sometimes punish free-riders even if they have to pay for the privilege, and are assured by the experimenters that everyone is anonymous and no one will meet up with their partners again. Since the punishment is costly, and cannot even be rewarded by a reputation for civic-mindedness, it has been described as "altruistic," and has been touted as evidence for group-selected self-sacrifice.

It seems hard to believe that a small effect in one condition of a somewhat contrived psychology experiment would be sufficient reason to revise the modern theory of evolution, and indeed there is no reason to believe it. Subsequent experiments have shown that most of the behavior in these and similar games can be explained by an expectation of reciprocity or a concern with reputation.[14] People punish those that are most likely to exploit them, choose to interact with partners who are least likely to free-ride, and cooperate and punish more, and free-ride less, when their reputations are on the line. Any residue of pure altruism can be explained by the assumption

that people's cooperative intuitions have been shaped in a world in which neither anonymity nor one-shot encounters can be guaranteed. Consider, too, that in real societies the punishment of free riders need not be costly to the punisher. An individual or small group can cheaply injure a social parasite or sabotage his possessions, and they can be rewarded for their troubles in gratitude, esteem, or resources. After all, police, judges, and jailers don't work for nothing.

Finally, let's turn to the role of altruism in the history of group-against-group conflict. Many group selectionists assume that human armed conflict has been a crucible for the evolution of self-sacrifice, like those in insect soldier castes. They write as if suicide missions, kamikaze attacks, charges into the jaws of death, and other kinds of voluntary martyrdom have long been the norm in human conflict. My reading of the history of organized violence is that this is very far from the case.

In tribal warfare among non-state societies, men do not regularly take on high lethal risks for the good of the group. Their pitched battles are noisy spectacles with few casualties, while the real combat is done in sneaky raids and ambushes in which the attackers assume the minimum risks to themselves.[15] When attacks do involve lethal risks, men are apt to desert, stay in the rear, and find excuses to avoid fighting, unless they are mercilessly shamed or physically punished for such cowardice (see, for example, the recent meticulous study of Turkana warfare by Sarah Mathew and Robert Boyd).[16]

What about early states? States and empires are the epitome of large-scale coordinated behavior and are often touted as examples of naturally selected groups. Yet the first complex states depended not on spontaneous cooperation but on brutal coercion. They regularly engaged in slavery, human sacrifice, sadistic punishments for victimless crimes, despotic leadership in which kings and emperors could kill with impunity, and the accumulation of large harems, with the mathematically necessity that large number of men were deprived of wives and families.[17]

Nor has competition among modern states been an impetus for altruistic cooperation. Until the Military Revolution of the 16$^{th}$ century, European states tended to fill their armies with marauding thugs, pardoned criminals, and paid mercenaries, while Islamic states often had military slave castes.[18] The historically recent phenomenon of standing national armies was made possible by the ability of increasingly bureaucratized governments to impose conscription, indoctrination, and brutal discipline on their powerless young men. Even in historical instances in which men enthusiastically volunteered for military service (as they did in World War I), they were usually victims of positive illusions which led them to expect a quick victory and a low risk of dying in combat.[19] Once the illusion of quick victory was shattered, the soldiers were ordered into battle by callous commanders and goaded on by "file closers" (soldiers ordered to shoot any comrade who failed to advance) and by the threat of execution for desertion, carried out by the thousands. In no way did they act like soldier ants, willingly marching off to doom for the benefit of the group.

To be sure, the annals of war contain tales of true heroism—the proverbial soldier falling on the live grenade to save his brothers in arms. But note the metaphor. Studies of the mindset of soldierly duty shows that the psychology is one of fictive kinship and reciprocal obligation within a small coalition of individual men, far more than loyalty to the superordinate group they are nominally fighting for. The writer William Manchester, reminiscing about his service as a Marine in World War II, wrote of his platoonmates, "Those men on the line were my family, my home. ... They had never let me down, and I couldn't do it to them. . . . Men, I now knew, do not fight for flag or country, for the Marine Corps or glory of any other abstraction. They fight for one another."

What about the ultimate in individual sacrifice, suicide attacks? Military history would have unfolded very differently if this was a readily available tactic, and studies of contemporary suicide terrorists have shown that special circumstances have to be engineered to entice men into it. Scott Atran, Larry Sugiyama, Valerie Hudson, Jessica Stern, and Bradley Thayer have documented that suicide terrorists are generally recruited from the ranks of men with poor reproductive prospects, and they are attracted and egged on by some combination of peer pressure, kinship illusions, material and reputational incentives to blood relatives, and indoctrination into the theory of eternal rewards in an afterlife (the proverbial seventy-two virgins).[20] These manipulations are

necessary to overcome a strong inclination *not* to commit suicide for the benefit of the group.

The historical importance of compensation, coercion, and indoctrination in group-against-group competition should not come as a surprise, because the very idea that group combat selects for individual altruism deserves a closer look. Wilson's dictum that groups of altruistic individuals beat groups of selfish individuals is true only if one classifies slaves, serfs, conscripts, and mercenaries as "altruistic." It's more accurate to say that groups of individuals that are *organized* beat groups of selfish individuals. And effective organization for group conflict is more likely to consist of more powerful individuals incentivizing and manipulating the rest of their groups than of spontaneous individual self-sacrifice.

And once again, it won't work to switch levels and say that group selection is really acting on the norms and institutions of successful states. The problem is that this adds nothing to the conventional historian's account in which societies with large tax bases, strong governments, seductive ideologies, and effective military forces expanded at the expense of their neighbors. That's just ordinary causation, enabled by the fruits of human ingenuity, experience, and communication. The truly Darwinian mechanisms of high-fidelity replication, blind mutation, differential contribution of descendants to a population, and iteration over multiple generations have no convincing analogue.

### 4. A Summary of the Trouble with Group Selection

The idea of Group Selection has a superficial appeal because humans are indisputably adapted to group living and because some groups are indisputably larger, longer-lived, and more influential than others. This makes it easy to conclude that properties of human groups, or properties of the human mind, have been shaped by a process that is akin to natural selection acting on genes. Despite this allure, I have argued that the concept of Group Selection has no useful role to play in psychology or social science. It refers to too many things, most of which are not alternatives to the theory of gene-level selection but loose allusions to the importance of groups in human evolution. And when the concept is made more precise, it is torn by a dilemma. If it is meant to explain the cultural traits of successful groups, it adds nothing to conventional history and makes no precise use of the actual mechanism of natural selection. But if it is meant to explain the psychology of individuals, particularly an inclination for unconditional self-sacrifice to benefit a group of nonrelatives, it is dubious both in theory (since it is hard to see how it could evolve given the built-in advantage of protecting the self and one's kin) and in practice (since there is no evidence that humans have such a trait).

None of this prevents us from seeking to understand the evolution of social and moral intuitions, nor the dynamics of populations and networks which turn individual psychology into large-scale societal and historical phenomena. It's just that the notion of "group selection" is far more likely to confuse than to enlighten—especially as we try to understand the ideas and institutions that human cognition has devised to make up for the shortcomings of our evolved adaptations to group living.

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[1] Examples include **E. O. Wilson (2012)**, **Haidt (2012)**, (**Traulsen & Nowak, 2006**). (**Bowles & Gintis, 2011**; **Henrich, 2004**; **Richerson, Boyd, & Henrich, 2003**; **D. S. Wilson & Wilson, 2008**).

[2] See (**West, Griffin, & Gardner, 2007**, **2008**) for extensive discussion.

[3] Again, see **West et al. (2007)**; (**West et al., 2008**) for examples.

[4] (**Williams, 1966**) is the classic reference; see also (**Dawkins, 1976/1989**).

[5] See (**Abbot et al., 2011**; **Boomsma et al., 2011**; **Herre & Wcislo, 2011**; **Nowak, Tarnita, & Wilson, 2010**; **Strassmann, Page, Robinson, & Seeley, 2011**)

[6] See (**Gaulin & McBurney, 2003**).(**Lieberman, Tooby, & Cosmides, 2007**).

[7] See (**Daly, Salmon, & Wilson, 1997**; **Fiske, 1991**; **Lieberman et al., 2007**).

[8] See (**Cosmides & Tooby, 1992**; **McCullough, 2008**), for reviews.

[9] See (**Kurzban, 2011**; **Trivers, 2011**).

[10] See (**Frank, 1988**).

[11] (**Delton, Krasnow, Tooby, & Cosmides, 2011**)

[12] (**Haidt, 2002**).

[13] (**Fehr & Gächter, 2002**)

[14] (**Delton et al., 2011**; **Krasnow, Cosmides, Pedersen, & Tooby, in press**; **Price, 2012**).

[15] (**Gat, 2006**).

[16] (**Mathew & Boyd, 2011**).

[17] (**Betzig, 1986**; **Otterbein, 2004**).

[18] (**Gat, 2006**; **Levy, Walker, & Edwards, 2001**).

[19] (**Johnson, 2004**).

[20] (**Atran, 2003**; **Blackwell & Sugiyama, 2008**; **Thayer & Hudson, 2010**).