

Truth and Reconciliation for Group Selection

David Sloan Wilson

SUNY Distinguished Professor
Departments of Biology and Anthropology
Binghamton University
Binghamton, New York 13902
<http://evolution.binghamton.edu/dswilson/>
dwilson@binghamton.edu

This is a 19-part series of blog posts that is available on my [ScienceBlogs](#) site and combined into a single document here for convenience. The blog format should not mask my serious intent. I regard it as the best introduction to multilevel selection for the beginner or review for those who think they understand the subject. When I publish it in an academic format, hopefully with commentaries by colleagues on both sides of the controversy, it will require very few changes.

I. Why It Is Needed

The phrase "truth and reconciliation" describes a constructive process for coming to terms with a troubled past. It has been used to resolve bitter political conflicts and achieve national unity, starting with South Africa's Truth and Reconciliation Commission in 1995. I would like to initiate a similar process to resolve a bitter scientific conflict.

The idea of comparing a scientific conflict with political conflict is likely to raise hackles from the very beginning. Are not science and politics totally different enterprises? We expect bitter conflicts in politics whereas science is supposed to result in objective truths upon which everyone can agree. Saying that science is like politics appears to sully its reputation.

It is not my purpose to rob science of its dignity. When it comes to science, I'm a true believer. I believe that there is a real world out there that can be apprehended by the human mind--but only if we follow a collection of practices known as the scientific method. The individual mind is too feeble and prone to biases to directly apprehend reality. Even groups of people, left to their own devices, will be prone to biases that depart from reality to serve their collective interests. Science isn't natural. It is a cultural invention that must be carefully maintained to work properly. When science functions as it should, it does indeed result in objective truths upon which everyone can agree. As far as I am concerned, there can be no higher calling than to be a scientist.

While we're at it, let's restore some dignity to politics. Wikipedia, that great populist body of knowledge, defines politics as "the process whereby groups of people make decisions."

Politicians are noble to the extent that they make wise decisions on behalf of everyone in their group. They are ignoble to the extent that they make partisan decisions that benefit some at the expense of others or the long-term welfare of the group as a whole. When politics functions as it should, there can be no higher calling than to be a politician.

Of course, politics rarely functions as it should--hence the low reputation of politicians. It's easy to blame individuals, but we also need to blame whole political systems. Politics isn't natural, any more than science is natural, especially at the large scale at which it must be practiced in modern life. Politics needs a well-designed system of checks and balances, similar to the checks and balances associated with the scientific method. A truth and reconciliation process becomes necessary when politics hasn't been working as it should, which is a droll understatement for the injustices that took place during the apartheid era in South Africa and elsewhere in the world. An essential part of the process is for a society to acknowledge *what happened*, even if all wrongs cannot be righted. Revisionist histories must go. Truth is required for reconciliation. What happens when science doesn't work as it should? Such is the case for the controversy over group selection, which began with Darwin, became prominent during the 1960's, and continues to fester at all levels of scientific discourse, from the pages of scientific journals such as *Nature* to popular science blogs. Thankfully, scientific conflicts no longer result in torture and death, as they once did and as political conflicts still do. Nevertheless, the word heresy appears disturbingly often in the annals of the group selection debate and proponents of group selection have risked scientific death in the form of rejected articles and grant proposals, lost job opportunities, and all-around social exclusion. Most of all, the group selection controversy is still plagued by historical revisionism. There is not even a basic consensus on *what happened*, least of all in textbooks, and many accounts read embarrassingly like patriotic histories, complete with black-and-white villains and heroes.

It is precisely because I am such an idealist about science that I am calling for a truth and reconciliation process for group selection. Something has to change. The controversy didn't need to drag on for decades and it will continue for decades more unless something deliberate is done. The goal is to be constructive--to heal rather than aggravate old wounds. Yet, even healing can be painful, for scientific conflict no less than political conflict.

Another reason to initiate a truth and reconciliation process is because group selection is arguably the single most important concept for understanding the nature of politics from an evolutionary perspective. Recall Wikipedia's definition of politics as "the process whereby groups of people make decisions." Why should people be expected to make decisions "for the good of the group" in the first place? Why should they be expected to act "for the good of the group" after a decision is made? These are the questions that caused Darwin to propose the theory of group selection in the first place. How fitting, that a process for resolving conflict and achieving unity in the political realm can be used to resolve conflict and achieve unity in the scientific realm about the nature of politics from an evolutionary perspective.

II. The Original Problem

Consider some standard examples of design in nature: the aerodynamic wing of the bird, the concealing coloration of the moth, the dense fur of the polar bear. Darwin's insight was to explain these adaptations as products of natural selection: individuals vary, some survive and reproduce better than others, and their properties are inherited by their offspring.

All of these adaptations are *locally advantageous*. Individuals possessing them survive and reproduce better than their immediate neighbors. Now consider some standard examples of social adaptations: the good Samaritan, the soldier who heroically dies in battle, the honest person who cannot tell a lie. We admire these virtues and call them social adaptations because they are good for others and for society as a whole--but they are not locally advantageous. Charitable, heroic, and honest individuals do not necessarily survive and reproduce better than their immediate neighbors who are stingy, cowardly, and deceptive.

How important is this problem? For Darwin, who was formulating the entire theory of evolution, it was one important problem among many. If we restrict our attention to the study of social behavior, however--what E.O. Wilson would later call *Sociobiology*--it is paramount. Most behaviors that we call *prosocial* require time, energy, and risk on the part of the prosocial individual. Most behaviors that we call *antisocial* deliver an immediate benefit to the antisocial individual. If most antisocial behaviors are locally advantageous and most prosocial behaviors are locally disadvantageous, then we have an enormous problem explaining the nature of prosociality, including the nature of human morality, from an evolutionary perspective.

Darwin was aware of this problem and proposed two types of solution. First, he observed that farmers routinely sacrifice some individuals for eating and select their traits by breeding their relatives. Individuals who altruistically sacrifice themselves for their relatives, such as the suicidal sting of the honeybee, might therefore evolve by natural selection. This idea anticipated what later would be called kin selection.

Second, Darwin observed that groups of prosocial individuals will survive and reproduce better than groups of antisocial individuals, even if antisocial individuals have the advantage over prosocial individuals within groups. Here is one of his canonical statements, using human moral virtues as an example (from Chapter 4 of *Descent of Man*).

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

spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection. At all times throughout the world tribes have supplanted other tribes; and as morality is one important element in their success, the standard of morality and the number of well-endowed men will thus everywhere tend to rise and increase.

In this passage, Darwin clearly demonstrates his awareness that a) moral behaviors are locally disadvantageous or at best deliver no advantage, compared to less moral individuals within the same group, and b) moral behaviors expressed within groups can be decisively advantageous in between-group competition. He didn't comment on the irony that within-group morality might well lead to immoral conduct among groups.

I will return to this issue later, but for the moment let's consolidate our gains. The original problem associated with group selection is foundational for the study of social behavior from an evolutionary perspective. Unlike individual-level adaptations such as the polar bear's thick fur, prosocial behaviors are locally disadvantageous. Fortunately, they are advantageous at the larger scale of whole groups. Prosocial behaviors can evolve by a process of between-group selection, as long as this process is stronger than the opposing process of within-group selection.

Is anyone confused yet? I suspect not. You don't need to be an Einstein to get the basics of group selection. All of us can appreciate that doing the right thing makes us vulnerable to exploitation. We can equally appreciate that united we stand, divided we fall. Why should such simple ideas become the basis of endless controversy?

Yet, as we proceed, I guarantee that you will become confused. One reason that a truth and reconciliation process is needed for group selection is to return to the simplicity of the original problem and Darwin's solution. As Ed Wilson and I put it in our recent review article titled "[Rethinking the Theoretical Foundation of Sociobiology](#)": Selfishness beats altruism within groups. Altruistic groups beat selfish groups. Everything else is commentary.

III. Naïve Group Selectionism

In their book *Darwinism Evolving*, David J. Depew and Bruce H. Weber make the interesting point that pre-Darwinian notions did not come to an abrupt halt with the advent of Darwin's theory. Instead, they often became repackaged in superficially Darwinian terms.

That certainly applies to notions of adaptation in nature and human society. Before Darwin, most people regarded nature as the creation of a benign God. *Of course* it must be adaptive, from top to bottom! Human society must also be part of God's plan, however inscrutable. As the Anglican Bishop Joseph Butler (1692-1752) put it, "It is as manifest that we were made for society and to promote the happiness of it, as that we were

intended to take care of our own life and health and private good."

Against this background, the original problem identified by Darwin and his partial solution (see T&R II) must have been disorienting. He was suggesting that adaptations might be restricted to individual organisms and that society might merely reflect their conflicts of interest. His partial solution meant that adaptations *might* exist above the level of individual organisms, but only if special conditions are met. In modern terms, adaptation at level x of the biological hierarchy requires a corresponding process of selection at the same level and tends to be undermined by selection at lower levels.

After Darwin, many biologists continued to assume that adaptations evolve at all levels -- for the good of the individual, group, species, or ecosystem -- without requiring special conditions. Social theorists continued to portray human society as like a single organism in the functional integration of its parts. When the problem identified by Darwin was acknowledged, it was common to assume that higher-level selection easily trumped lower-level selection. Today, these assumptions are labeled naïve group selectionism.

Naïve group selectionism is not dead. If you think that diseases evolve to avoid killing their hosts, that animals evolve to manage their population size, that ecosystems evolve to efficiently recycle nutrients, that nature left undisturbed achieves a harmonious balance, that earth's entire biota qualifies as a single organism (the Gaia hypothesis), or that human society can be compared to a single organism, including technology leading to a single global brain, then you are a naïve group selectionist. You *might* be right, but you are not paying sufficient attention to Darwin's sobering message that special conditions are required.

Everyone who teaches evolution knows that a large fraction of students start out as naïve group selectionists who are likely to utter phrases such as "for the good of the species" unbidden -- even as the wrong answer on the final exam. There is something about adaptation above the level of the individual that just seems *right*, even when your teacher tells you it's *wrong*.

A few biologists who followed in Darwin's footsteps were not naïve, especially the three founders of population genetics theory, Ronald Fisher, J.B.S. Haldane, and Sewall Wright. Like Darwin, they had a lot on their minds. In their effort to place all aspects of evolutionary theory on a mathematical foundation, group selection was just one problem among many. Nevertheless, each clearly recognized that most social adaptations are locally disadvantageous. Either they pass out of existence, or they evolve on the strength of a selective advantage at a larger scale. Fisher, Haldane and Wright sketched a few models to illustrate the point but group selection did not occupy center stage and mathematical models were a foreign language to most biologists in any case.

To illustrate the influence of naïve group selectionism in the middle of the 20th century, here is the final paragraph of the most influential ecology textbook of the period,

Principles of Animal Ecology (1949), authored by W.C. Allee, A.E. Emerson, O. Park, T. Park, and K.T. Schmidt, affectionately known as the great AEPPS.

The probability of survival of individual living things, or of populations, increases with the degree to which they harmoniously adjust themselves to each other and their environment. This principle is basic to the concept of the balance of nature, orders the subject matter of ecology and evolution, underlies organismic and developmental biology, and is the foundation for all sociology.

This passage, and the whole textbook, is suffused with the notion that nature evolves to be adaptive from top to bottom.

Enter George C. Williams, a tall man with the craggy features of Abe Lincoln or the statues on Easter Island. He was not mathematically trained but had learned the lessons of population genetics as a graduate student at the University of California at Berkeley before accepting a postdoctoral position at the University of Chicago in the late 1950's. There he attended a seminar by Alfred Emerson, one of the great AEPPS, a termite biologist who regarded all of nature as like a termite colony. As George recalls the event, "if this was evolutionary biology, then I wanted to do something else -- like car insurance." George left the lecture muttering "Something must be done..."

A great reckoning was about to take place.

IV. The Great Reckoning

By the 1960's, evolutionary theory had settled into a comfortable paradigm called the [Modern Synthesis](#). With other major issues apparently settled (go [here for an update](#) on the Modern Synthesis), the issue of group selection began to occupy center stage. George C. Williams was not the only critic and the great AEPPS were not their only foil (see T&RIII). Across the Atlantic, the Scottish biologist Vero C. Wynne-Edwards published an ambitious volume titled *Animal Dispersion in Relation to Social Behavior* (1962), which claimed that animal populations evolve to avoid overexploiting their resources. Wynne-Edwards was aware that such restraint was "for the good of the group" and might be vulnerable to less prudent behaviors within the group. Nevertheless, he thought that between-group selection easily trumped within-group selection and proceeded to interpret a vast array of social behaviors as adaptations to regulate population size. His book stimulated widespread debate and skepticism from prominent evolutionists such as David Lack and John Maynard Smith.

Another major event in the 1960's was William D. Hamilton's inclusive fitness theory, more widely known as kin selection theory, a term coined by Maynard Smith. Hamilton reasoned that a gene for altruism could evolve if it favored copies of itself in the bodies of other individuals. An identical twin is certain to have the same genes as oneself, a full sibling has a 50% probability, and so on. For an altruistic gene to have a net benefit, the cost to the altruist must be outweighed by the benefit to the recipient multiplied by the

probability of sharing the same gene identical by descent. Here was a way to explain the evolution of altruism -- among genealogical relatives, at least -- without invoking group selection. Indeed, Maynard Smith coined the term "kin selection" to distinguish it from group selection in an article criticizing Wynne-Edwards.

Hamilton's theory had a remarkable corollary. Ants, bees, and wasps (but not termites) have a peculiar genetic system called haplo-diploidy, in which females are produced sexually and have two sets of genes but males are produced asexually and have one set of genes. A consequence of haplo-diploidy is that, when a female mates with a single male, her daughters have a 75% chance of sharing the same genes (because they all get the same genes from their father) rather than a 50% chance for diploid species. Thus, not only did Hamilton's theory explain the general phenomenon of altruism among genealogical relatives, but in the same stroke it seemed to explain the extreme altruism exhibited by ants, bees, and wasps on the basis of their extreme degree of relatedness (termites remained an unexplained exception to this rule).

When Williams published his book *Adaptation and Natural Selection* in 1966, it seemed to provide a synthesis for the subject of group selection, settling the issue in the same way that the modern synthesis settled other major issues in evolutionary theory. Williams attacked naïve group selectionism and forcefully asserted what Darwin, Fisher, Haldane and Wright already knew: Higher-level adaptations require a process of higher-level selection and tend to be undermined by selection at lower levels. Here is one of his canonical statements (p. 92-93):

It is universally conceded by those who have seriously concerned themselves with this problem that...group-related adaptations must be attributed to the natural selection of alternative groups of individuals and that the natural selection of alternative alleles within populations will be opposed to this development. I am in entire agreement with the reasoning behind this conclusion. Only by a theory of between-group selection could we achieve a scientific explanation of group-related adaptations.

Notice that Williams is *affirming* the basic logic of group selection theory, but then he went further in a continuation of the same passage:

However, I would question one of the premises on which the reasoning is based. Chapters 5 to 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 other words, even though group-level adaptations can evolve *in principle*, Williams claimed that in *reality* between-group selection is almost invariably trumped by within-

group selection. This empirical claim became known as the theory of individual selection. The final sentence about families left the door open for kin selection, a point to which we will return.

Adaptation and Natural Selection was widely praised as a resolution to the group selection controversy. For the rest of the 20th century, group selection was taught primarily as a way not to think about evolution. "For the good of the group" thinking was regarded as just plain wrong. Everything that evolved by natural selection was interpreted as a variety of self-interest.

V. The Patriotic History of Individual Selection Theory

One reason that I don't spend a lot of time bashing religion is because there are so many other flagrant departures from factual reality to pick on. Take the patriotic history of nations--the leaders who can do no wrong, the noble "us" and evil "them"--who needs supernatural agents when we can so freely re-arrange the facts of the real world?

Science is supposed to be different. Indeed, science can be idealistically defined as a cultural system designed to hold people accountable for their factual statements. Like religion, however, science as practiced often falls short of science as idealized.

The rejection of group selection and acceptance of the theory of individual selection (see T&R IV) reads disturbingly like a patriotic history. I am aware that this is a serious charge. Basically, I am saying that the theory of individual selection represents a failure of the scientific process and an example of values masquerading as facts, little different than religious, political, and other ideologies. That is why a truth and reconciliation process is needed. Before continuing, however, I want to stress that I remain idealistic about science as a cultural system that--when it works as intended--can indeed hold people accountable for their factual statements. My goal in this series of blogs is to make the scientific process work better for the issues represented by the group selection controversy. Think of me as a scientific reformer.

Consider the following passages written by highly respected evolutionists during the 1970's and 80's.

The economy of nature is competitive from beginning to end...the impulses that lead one animal to sacrifice himself for another turn out to have their ultimate rationale in gaining advantage over a third...Where it is in his own interest, every organism may reasonably be expected to aid his fellows...Yet given a full chance to act in his own interest, nothing but expediency will restrain him from brutalizing, from maiming, from murdering--his brother, his mate, his parent, or his child. Scratch and "altruist," and watch a "hypocrite" bleed (Michael Ghiselin, [The Economy of Nature and the Evolution of Sex](#), 1974 p274).

The intervening years since Darwin have seen an astonishing retreat from his individual-centered stand, a lapse into sloppily unconscious group-selectionism, ably documented by Williams...It is only in recent years, roughly coinciding with the belated rise to fashion of Hamilton's own ideas, that the stampede has been halted and turned. We painfully struggled back, harassed by sniping from a Jesuitically sophisticated and dedicated neo-group-selectionist rearguard, until we finally regained Darwin's ground, the position that I am characterizing by the label 'the selfish organism', the position which, in its modern form, is dominated by the concept of inclusive fitness (Richard Dawkins, [The Extended Phenotype](#), 1982 p6).

I suspect that nearly all humans believe it is a normal part of the functioning of every human individual now and then to assist someone else in the realization of that person's own interests to the actual net expense of the altruist. What this greatest intellectual revolution of the century [i.e., the theory of individual selection] tells us is that, despite our intuitions, there is not a shred of evidence to support this view of beneficence, and a great deal of convincing theory suggests that any such view will eventually be judged false (Richard Alexander, [The Biology of Moral Systems](#), 1987 p3).

According to these authors, evolutionary theory ratifies the concept of *individual self-interest* as a grand explanatory principle. Lest you think that these passages were written for a popular audience, in which case a bit of poetic license might be justified, they are all taken from academic books--scientists writing for other scientists.

Patriotic histories represent conflicts in black-and-white terms and their resolution as definitive. The passages quoted above express complete certainty. Alexander's phrase "a great deal of convincing theory suggests that any such view will eventually be judged false" does not invite continuing inquiry. Richard Dawkins went even further:

As for group selection itself, my prejudice is that it has soaked up more theoretical ingenuity than its biological interest warrants. I am informed by the editor of a leading mathematics journal that he is continually plagued by ingenious papers purporting to have squared the circle. Something about the fact that this has been proved to be impossible is seen as an irresistible challenge by a certain type of intellectual dilettante. Perpetual motion machines have a similar fascination for some amateur inventors. The case of group selection is hardly analogous: it has never been proved to be impossible, and never could be. Nevertheless, I hope I may be forgiven for wondering whether part of group selection's romantic appeal stems from the authoritative hammering the theory has received ever since Wynne-Edwards did us the valuable service of bringing it out into the open ([The Extended Phenotype](#), 1982 p115).

Notice how Dawkins carefully acknowledges that group selection is a theoretical possibility. The basic logic of multilevel selection is impeccable and was *affirmed* by Williams and others, as I recount in T&R IV. The question is whether group-level selection can ever prevail over individual-level selection. According to Dawkins, this question had been answered so authoritatively that doubters could be compared to romantic dreamers and intellectual dilettantes searching for perpetual motion machines.

Given the certainty with which group selection was rejected, it was kept alive in articles and textbooks primarily as a cautionary tale for how not to think. It became almost mandatory for authors to inform their readers that group selection was not being invoked. Just as patriots vilify their opponents and make sure that they are counted on the side of the righteous, invoking group selection became a heresy inviting ridicule and exclusion. Here is how Stephen Jay Gould recalls the period in an introduction to Richard Goldschmidt's [The Material Basis of Evolution](#) (p. xv), which also became the subject of ridicule:

I have witnessed widespread dogma only three times in my career as an evolutionist, and nothing in science has disturbed me more than ignorant ridicule based upon a desire or perceived necessity to follow fashion: the hooting dismissal of Wynne-Edwards and group selection in any form during the late 1960's and most of the 1970's, the belligerence of many cladists today, and the almost ritualistic ridicule of Goldschmidt by students (and teachers) who had not read him.

In future installments of the T&R series, I will show that the certainty expressed by Ghiselin, Dawkins, and Alexander was sheer bravado. The theoretical and empirical case against group selection was never strong and even what there was began to fall apart immediately. That did not alter the patriotic history, however, which is still dutifully reported in text books and transmitted as an oral tradition among graduate students, who warn each other not to invoke group selection in the presence of their faculty advisors. The patriotic history of individual selection theory is a sorry chapter in the history of science. Why did it occur in the first place?

VI. Individualism

Most people are prepared to admit that we are influenced by our cultures in ways that we don't understand. As a proverb puts it, the hardest thing for a fish to see is water. Part of the "water" of Victorian culture was an assumption of European superiority. Darwin was progressive for his time but even he was repelled by the "savages" of Tierra del Fuego. When Victorians attempted to view racial and cultural diversity through the new lens of evolutionary theory, some argued that the different races are different species, with Africans closer to the apes. Others argued that we are all one species but that cultural evolution runs along a single track, from savagery to civilization, so that the humane thing to do was make everyone else more like Europeans. Only in retrospect can we look back and see that not only are these theories wrong, but they don't even follow straightforwardly from evolutionary theory.

What is the water of *our* culture? I would like to nominate individualism. Individualism is the belief that individuals are somehow a privileged level of the biological hierarchy; that explanations framed in terms of individual action are somehow more "fundamental" than explanations framed in terms of social action; that individual self-interest is a grand explanatory principle that can explain all aspects of humanity. For many people, these beliefs seem like common sense. Water always does.

It wasn't always that way. Consider the following passage from the social psychologist Daniel Wegner:

Social commentators once found it very useful to analyze the behavior of groups by the same expedient used in analyzing the behavior of individuals. The group, like the person, was assumed to be sentient, to have a form of mental activity that guides action. [Rousseau \(1767\)](#) and [Hegel \(1807\)](#) were the early architects of this form of analysis, and it became so widely used in the 19th and early 20th centuries that almost every early social theorist we now recognize as a contributor to modern social psychology held a similar view.

Even in Darwin's time, the Russian naturalist and social theorist [Peter Kropotkin](#) accused evolutionary theory of being biased by the individualism of British culture, which made competition seem more commonsensical than mutual aid. Even so, Wegner's passage documents that something happened in the middle of the 20th century that made our culture even more individualistic than it was before. Margaret Thatcher's notorious quip in 1987 that "There is no such thing as society. There are individual men and women, and there are families." would have boggled the minds of the Victorians!

Against this background, when evolutionists rejected group selection in favor of "the theory of individual selection" in the 1960's (see T&R IV), they were just swimming with the other fish. At roughly the same time, a position known as "methodological individualism" became dominant in the social sciences and radical individualism became the dominant position in economics. These parallel events did not take place because scientists were talking to each other across disciplines and changing their views in a coordinated fashion. Much as scientists might like to think otherwise, their formal theories were simply reflecting a larger cultural sea change.

What exactly was this sea change? I would love to know the answer to this question and urge historians of culture and science to study it, or to contact me if they already have. Nazi Germany and the cold war with Communism probably had something to do with it. With Ayn Rand there was a direct connection, since she came from Russia and had a zeal for free-market economics that rivaled religious fundamentalism, as I recount in a chapter of [Evolution for Everyone](#) titled "Ayn Rand: Religious Zealot." Another factor might have been the allure of reductionism; the belief that lower-level explanations are somehow more fundamental than higher-level explanations.

Regardless of the reasons, the hyper-individualism that took hold during the second half of the 20th century became the cultural "water" for the theory of individual selection in evolutionary biology, which portrayed everything that evolves as a variety of self-interest. The zeal associated with hyper-individualism in general might also explain the zeal with which some individual selectionists argued their position, as I documented in T&R V.

Thinking about science as a culturally influenced activity is a tricky business. On one hand, everyone is prepared to admit the abstract possibility and to see it clearly for past examples, such evolutionary theories of racial and cultural diversity in Darwin's day. On the other hand, most scientists don't like to admit the possibility for their own theories. To make matters worse, some scholars who study science as a culturally influenced activity conclude that science therefore has no more truth value than any other cultural belief system, such as astrology.

The hardest ground to capture, it seems, is the middle ground. Science remains the best cultural system we have for holding each other accountable for our factual statements--vastly better than astrology, for example. But scientists are full of biases, many beneath their conscious awareness, just like everyone else. That's why a cultural system is required to overcome individual biases. The cultural system does a pretty good job but is especially prone to failure when everyone shares the same biases. Then there is nobody around to propose and defend an alternative hypothesis. The best solution would be to make sure that scientists are as culturally diverse as possible and to employ an army of scholars to scrutinize current scientific theories for cultural bias in a constructive way, sharing the belief that at the end of the day there can be an accumulation of knowledge that deserves to be called factual.

Factual matters are definitely at stake for the issues associated with group selection. What I called "the original problem" in T&R II remains a fact. It is simply the case that "for the good of the group" traits are often locally disadvantageous. If they are to evolve at all, a selective advantage must exist at a larger scale. If group-level selection is sufficiently strong, then "for the good of the group" traits can evolve in the total population, despite their selective disadvantage within groups. Determining the relative importance of within- vs. between-group selection is a straightforward matter of theoretical and empirical research. Even though hard work might be involved, it should be possible to determine the facts of the matter.

What I called The Great Reckoning in T&R IV appeared to deliver a verdict: group-level selection is almost invariably weak compared to individual-level selection. As George C. Williams put it, "group-level adaptations do not, in fact, exist." Despite the appearances of decades, he was massively wrong.

VII. If You Make A Mess, Should You Clean It Up?

One memorable Christmas morning, as our kids were gathering around the tree, I was on my way upstairs to get a sweater when I smelled something really bad. I knew that smell.

Our cat had diarrhea and had deposited a wet one somewhere. I walked all over the house trying to find it before realizing that I had stepped in it the moment that I smelled it and now had tracked it all over the house.

Did I clean it up? Of course I did. Anyone would.

Here's another example of a mess: Imagine a man who has made a mess of his life. He has taken advantage of those who loved him and piled lies upon lies until he can't keep them straight anymore. Now he has been abandoned and has only himself to blame. If only he could go back to the beginning!

Should this man clean up his mess? Of course he *should*, and would be much better off if he *did*, but we wouldn't be surprised if he *didn't*. It would require great courage. Twelve-step programs are designed for people like him and include acknowledging one's faults and apologizing to others.

Here's a third example of a mess: Imagine that an entire scientific community has made a decision that turns out to be a mistake. The decision was momentous. It was regarded as a watershed event for the field. Its architects were celebrated as heroes. It was enshrined in textbooks. Nevertheless, subsequent events had proven it to be incorrect. If the current information was known back then, a different decision would have been made and the entire field would have taken a different path.

Should the field clean up its mess? It *should*, but the likelihood that it *will* is even less than for the individual who messed up his life. After all, "the field" is not even a corporate unit capable of making a decision like an individual. Instead of a collective decision, a cacophony of responses can be expected, including acceptance, denial, and halfway positions that attempt to acknowledge change while still clinging to the patriotic history.

That is what has happened with the group selection controversy. The categorical rejection of group selection in the 1960's was wrong, plain and simple. If they knew then what we know now, it would never have happened. Some evolutionists are perfectly comfortable with this conclusion. Others act as if nothing has changed since the 1960's. Others say that the original rejection of group selection remains valid and what passes for group selection today is different. Others claim that group selection and its alternatives are equivalent, making it a matter of preference which to employ. Others construct models and perform experiments that anyone would have identified as group selection in the 1960's, but just don't use the G-word. In short, the field as a whole is a big mess.

To see what I mean, consider a four-page news feature on group selection that appeared in the November 20, 2008 issue of Nature magazine. The author is a science writer named Marek Kohn who did a thorough job researching the subject. The article begins this way:

If biologists have learned one thing about evolution over the past 40 years, it is that natural selection does not work for the good of the group. The defining insight of modern Darwinism is that selection 'sees' individuals and acts on them through the genes they embody. To imagine otherwise, generations of students have been warned, is to fall into a naïve error definitively exposed as such in the 1960's.

So far so good. But then we learn that the two sides actually agree on a great deal. For example, everyone today supposedly agrees that group selection occurs and that group selection and kin selection are formally equivalent to each other. Evidently, the debate about group selection is largely semantic and choosing between one and the other is a matter of preference.

I will untangle some of these issues in future posts. The point I wish to make here is that the positions reported in the Nature article bear almost no resemblance to the issues at stake in the 1960's. Back then, the center of the debate was what I have called "The Original Problem (see T&R II)", almost everyone agreed that group selection did not occur (although they agreed it was possible in principle), and kin selection was regarded as a theory that succeeded where group selection had failed. Does anyone seriously think that the "defining insight of modern Darwinism" was merely *semantic*? Somehow, the issues at stake in the 1960's have been permuted into a different set of issues, while everyone pretends that it is the same controversy. I do not fault the author of the article. As a science writer, the best that Kohn could do was report the views of the experts. The problem is that he had to report a mess.

As for everyone today agreeing that group selection occurs, I wish that someone would tell [John Alcock](#), author of [Animal Behavior](#), the most widely used textbook in the field. Alcock truly believes that nothing has changed since the 1960's. So great is his loathing of group selection that he calls it "non-Darwinian"--an irony, since Darwin clearly originated the concept (see T&R II). Regardless of what the Master thought, Alcock can't even bring himself to say that group selection is a form of natural selection that results in adaptations at the group level, when and if it occurs. Legions of college students have been taught by Alcock that "the overwhelming majority of scientists studying the evolution of animal behavior employ Darwinian theory, rather than group selection theory in any of its forms (7th edition, published in 2001)."

Or how about my colleague, Dr. X, who has been harassed throughout his career for writing about subject Y from a group selection perspective? For example, colleagues refused to publish articles with him unless he removed all references to group selection. Dr. X is a real person but--I'm not kidding--he does not want his identity revealed to avoid further harassment. He recently sent me the following message about a newly published article on subject Y:

It just gives you an idea of what people like me are always up against. The argument in this paper is completely group selectionist but neither the

term nor the concept is invoked. Instead, the buzz terms become "coalition building", the formation of "alliances", etc. etc. It's fashionable among the cooperation bunch to talk about coalitions and alliances, but they never come to grips with the levels-of-selection issue... So, things are just as they have been all along.

The problem of packaging old wine in new bottles--ideas that anyone would have associated with group selection in the 1960's, but without using the G-word--pervades the modern literature, as I will show in future posts.

I don't want to *overstate* the degree of censorship and persecution that people have suffered by daring to invoke group selection. My career has not suffered, for example, and believe it or not I count George C. Williams as a good friend. Moreover, the biggest tragedy is not injustices to individuals but the fog of confusion that descends over an entire field when major mistakes are not acknowledged.

At the end of T&R II, I stressed that there is an underlying simplicity to the group selection controversy. The only way to recover the simplicity is by cleaning up the mess that was made by falsely rejecting group selection in the 1960's. That is my next task, but I warn you: It smells really bad.

XIII. Anatomy of a Model

Group selection was decisively rejected on theoretical grounds, according to the patriotic history of individual selection theory. Richard Dawkins declared in 1982 that group selection had "soaked up more theoretical ingenuity than its biological interest warrants" and compared further inquiry to the futile search for a perpetual motion machine. Richard Alexander stated in 1987 that "a great deal of convincing theory suggests that any such view [the beneficence that evolves by group selection] will eventually be judged false" (see T&R V for more).

Blustery statements like these have a bad smell about them. In truth, the models that led to the rejection of group selection were little more than sketches on the backs of napkins. Models supporting the plausibility of group selection began to appear as early as the 1970's, but that did not stop the patriotic propaganda machine from rolling onward.

Before I support my claim, a word about theoretical modeling is in order. Some models attempt to approximate reality in as much detail as possible, but most evolutionary models are more like caricatures. Just as a good artist can capture the likeness of a person with a few lines, a good modeler attempts to capture the essence of a problem such as group selection with the fewest possible assumptions. This kind of model tells us what can happen, given the assumptions of the model. It says nothing about what might happen, given other assumptions. Many models are required to support the sweeping claim that "between-group selection is invariably weak, compared to within-group selection."

Against this background, let's take a look at the most influential model that led to the rejection of group selection, which is affectionately known as the haystack model. The year was 1964. Two years earlier, V.C. Wynne-Edwards had published his book *Animal Dispersion in Relation to Social Behavior*, which made sweeping claims about group selection (see T&R III). One year earlier, a British graduate student named William D. Hamilton published a note in the journal *American Naturalist* outlining how altruism can evolve among individuals that share the same genes. John Maynard Smith, one of the top evolutionists in the UK, was familiar with Hamilton's work and thought that it provided an alternative to group selection. He therefore wrote a critique of Wynne-Edwards in a letter to the prestigious journal *Nature* titled "Group Selection and Kin Selection". The letter was only three pages long and included a brief model, which was truly little more than a sketch on the back of a napkin.

Like Dr. Seuss, Maynard Smith asked the reader to imagine a cartoon world in which a species of mouse lives entirely in haystacks. Each haystack is colonized by a single fertilized female, whose progeny reproduce for a number of generations. At some point, all of the mice from all of the haystacks disperse, mate on a population-wide basis, and the cycle is repeated for a new set of haystacks. There are two genes in the population, one coding for aggressive behavior and the other coding for docile behavior. Aggressive mice outcompete docile mice within each haystack, but they also decrease the growth rate of the group. Specifically, every haystack is colonized by four genes; two from the female and two from the male who fertilized her. Maynard Smith assumed that if one or more of these genes is the aggressive gene, then the aggressive gene completely replaces the docile gene by the time dispersal from the haystack occurs. When a haystack is colonized by four docile genes, however, more mice are produced by the time dispersal occurs than from the other haystacks. Imagine those docile mice streaming away from their haystacks singing "Kumbaya", while the aggressive mice limp forth from their haystacks nursing their wounds!

Let me praise the haystack model before presenting and critiquing the results. The essence of the group selection controversy -- what I called "the original problem" in T&R II -- is whether a trait that is "for the good of the group" can evolve in the total population, despite being selectively disadvantageous within groups. The haystack model elegantly captures the essence of the original problem. In this sense, it is a *good* cartoon. Docility is for the good of the group. Aggressiveness is selectively advantageous within each group. Which level of selection prevails?

Maynard Smith concluded on the basis of his model that aggressiveness almost always wins. Group selection *is* an evolutionary force, but it just can't prevail against the opposing force of selection within groups. In contrast, Maynard Smith felt that Hamilton's theory provided a more plausible explanation for the evolution of altruism. It was Maynard Smith, not Hamilton, who coined the term "kin selection" to contrast it with "group selection".

The haystack model had an enormous impact on the rejection of group selection and the conceptualization of kin selection as an alternative to group selection. Nevertheless, at least one of its many assumptions is fatally biased. Nobody noticed at the time. Can you figure it out in hindsight?

XI. Anatomy of a Model (Continued)

The haystack model (see T&R VIII) includes many assumptions but one was especially biased. Recall that each haystack is colonized by a single fertilized female bearing four genes coding for docility or aggressiveness--two of her own and two from her mate. Maynard Smith assumed that if even one of these genes codes for aggressiveness, then the aggressive gene entirely replaces the docile gene by the time the mice disperse from the haystack. The docile gene is not just at a selective disadvantage within groups. It is as disadvantageous as it can possibly be.

Hamilton's theory, which Maynard Smith dubbed kin selection, made a different set of assumptions. Hamilton modeled altruism as an interaction between two individuals. Like the good Samaritan helping someone in need, an altruist increases the fitness of the recipient by an amount b and decreases its own fitness by an amount c . Selfish individuals happily receive but do not give.

Since Maynard Smith was trying to compare kin selection with group selection, it seems only fair to use Hamilton's definition of altruism in the haystack model. This can be easily done. As before, we assume that haystacks are colonized by a single fertilized female, only now the genes code for altruism and selfishness as defined by Hamilton. Within each group containing both genes, the selfish gene has the advantage and starts to replace the altruistic gene. The *rate* that this happens depends upon the particular values of the b and c terms. For example, if a group is initiated by one altruistic and three selfish genes, and if the mice disperse after ten generations, then the altruistic gene might decline from an initial frequency of 25% to a frequency of 8%, but there is no reason why it must necessarily decline to zero.

Similarly, groups that start with more altruistic genes grow faster than groups starting with more selfish genes, and the *rate* that this happens depends upon the particular values of the b and c terms. For example, after ten generations, groups initiated by one altruistic and three selfish genes might be 40% more productive than groups initiated by four selfish genes.

The modified haystack model captures the essence of what I call the original problem (see T&R II), just like the original haystack model. In both cases, the trait that is "for the good of the group" is selectively disadvantageous within groups and requires a process of between-group selection to evolve. In the modified model, however, the b 's and c 's are allowed to determine the relative importance of within- and between-group selection, rather than arbitrarily assuming that within-group selection is as strong as it can possibly be.

What is the result of the modified haystack model? It turns out that altruism can evolve by group selection, using reasonable values of b and c , even when the altruistic gene is initially rare in the total population. The model that led to the rejection of group selection is favorable for group selection after all.

What was the impact of the modified model? Did it cause the entire field to reconsider the rejection of group selection? Not in the least. Nobody even thought to modify the original model until 1986, when I published an article titled "The haystack model revisited" in the journal *Evolution*. By then, group selection was thoroughly taboo and the article had no noticeable impact.

It gets worse. In 1970, George Price published a model that divided evolution into within- and between-group components and clearly indicated a role for between-group selection. The Price equation is regarded as a thing of beauty by theoretical biologists today, but at the time it had virtually no impact on the triumphant march of individual selection theory that had begun only a few years earlier. In 1975, Hamilton reformulated his theory on the basis of the Price equation, as I will recount in a future installment. According to Hamilton's new interpretation, kin selection is *a kind of group selection* rather than an *alternative* to group selection. During the same year, I published my first model demonstrating the plausibility of group selection--but the individual selection bandwagon rolled on.

So much for blustery claims by Dawkins in 1982 and Alexander in 1987 that the search for plausible models of group selection had been exhausted. When we focus on the original problem, there is near universal agreement among theoretical biologists that between-group selection can successfully counter within-group selection. The recent *Nature* article on group selection (see T&R VII) quotes the theoretical biologist Andy Gardner as saying "Everyone agrees that group selection occurs."

The fact that Gardner remains one of the most severe *critics* of multilevel selection theory will be explained in a future installment. Moreover, his statement accurately applies only to theoretical biologists knowledgeable about the subject. The vast majority of evolutionists receive their knowledge of theory secondhand, starting from textbooks when they are students. For them, the claim that group selection remains theoretically unsupported *still* rolls on. The situation is even worse for people from other fields interested in evolution and for the general public, who receive their knowledge of theory third, fourth and fifth hand.

The events that I have recounted provide a fascinating example of stasis in science, whereby a major decision becomes set in stone and is not easily revised, even when it richly deserves to be. If they knew then what we know now, group selection would never have been rejected as theoretically implausible. Yet, the field as a whole does not spontaneously clean up its mess after the fact. That is why a deliberate effort is required. Andy Gardner and I might disagree at some level, but I think I speak for both of us when I say that *group selection is theoretically well supported*. That should be the new

consensus view. Those who disagree should familiarize themselves with the current literature before repeating the formulaic statements of the past.

X. Naïve Gene Selectionism

Naïve group selectionism (see T&R III) is the unquestioning belief that adaptations can evolve at all levels of the biological hierarchy--for the good of individuals, groups, species and even ecosystems--without requiring special conditions. Many people are prone to naïve group selectionism, today no less than in the past. That is why I always caution against it and featured it early in this series. If multilevel selection theory tells us anything, it is that adaptations at level X of the biological hierarchy require a corresponding process of natural selection at the same level and tend to be undermined by selection at lower levels.

Another form of naivete is just as common but less well publicized--the unquestioning belief that natural selection operates at the level of the gene and that this constitutes an argument against group selection. Call it naïve gene selectionism.

Ever since the rediscovery of Mendel and his peas, evolution has been conceptualized in terms of gene frequency change. Genes codes for traits that are expressed in individual organisms, such as wrinkly and smooth seeds. When a trait increases the relative fitness of the individual bearing the trait, then the frequency of the gene(s) coding for the trait increases in the population.

Group selection is a straightforward extension of this scheme. Genes still code for traits that are expressed in individuals, such as altruism and selfishness as defined by Hamilton (see T&R IX). The main twist to the story is that a trait such as altruism does not increase the fitness of the individual, compared to selfish individuals in the same group. Group selection is required to explain how altruism can evolve despite its local disadvantage, as we saw in the case of the haystack model. When altruism *does* evolve by group selection, however, the frequency of the gene(s) coding for altruism increases is the total population. How could it be otherwise?

In sexually reproducing species, each individual is a unique collection of genes that will never occur again, no matter how well it survives and reproduces. George Williams made this point in *Adaptation and Natural Selection* (see T&R IV) and used it to argue that genes are "units of selection" in a way that individuals are not. After all, an entity must persist across generations to be operated upon by natural selection. Genes replicate with high fidelity and persist across generations, whereas sexually reproducing individuals do not.

If sexually reproducing individuals are not "replicators" and "units of selection," then what are they? Depending upon the author, they became variously known as "interactors," "vehicles," and "targets" of selection. These terms reflect the fact that individuals are the entities that actually interact with the environment and each other.

Genes differentially survive and reproduce only insofar as they cause *individuals* to differentially survive and reproduce.

Notice that these distinctions apply to all the standard examples of evolution, such as Mendel selecting his peas, moths adapting to trees darkened by soot, and the beaks of the finches on the Galapagos Islands. Calling genes "replicators" and individuals "targets" doesn't add anything new. As George has told me on numerous occasions, he wrote *Adaptation and Natural Selection* largely to explain the basic concepts of population genetics to a wider biological audience, not to propose a radical new theory of his own.

So, what's wrong with the "gene's eye view" of evolution if it merely popularizes the standard story of genetic evolution? The error is to suppose that it constitutes an argument against group selection. As I have already shown, what I call "the original problem" (see T&R II) is the standard story of genetic evolution with a single twist. Genes code for traits that are expressed in individuals, but the traits are locally disadvantageous and require between-group selection to evolve. We might need to use terms such as "interactor," "vehicle," or "target" to describe groups in this case, but we don't need to tinker with the concept of genes as "replicators."

Nevertheless, as group selection entered its dark age, the concept of genes as "replicators" and "the fundamental unit of selection" became regarded as a drop-dead argument against group selection. Here is one of hundreds of examples that could be cited, from Richard Alexander in 1979:

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

In this passage, Alexander properly cautions against naïve group selectionism but then unknowingly commits naïve gene selectionism. Williams didn't reject group selection because only genes are replicators, but because (according to his assessment) within-group selection invariably trumps between-group selection. Genes are the replicators regardless of which level of selection prevails!

Richard Dawkins' role in establishing naïve gene selectionism will be the subject of my next installment. Also, a word about the word "naïve" is in order. When an idea proves to be wrong, early adherents are often portrayed as naïve, as if any smart and well-informed person should have known better. That is a naïve rendering of scientific and intellectual discourse. Typically, ideas emerge as wrong only after protracted interactions among smart and well-informed people. It is only in retrospect that the idea becomes "obviously" wrong and continuing adherence can be called naïve.

Speaking of wrong ideas, George Williams made a wrong move when he used the uniqueness of sexually reproducing individuals to conclude that only genes have the persistence to qualify as "units of selection." As Elliott Sober pointed out in his 1984 book [The Nature of Selection](#), phenotypic traits have the persistence that George was looking for, regardless of their genetic (or non genetic) basis. Imagine selecting for a trait such as wing length in a laboratory population of fruit flies. Before you begin the selection experiment, you measure wing length for a number of generations and get the same bell-shaped curve. *The bell-shaped curve persists across generations*, even though each fruit fly is a unique collection of genes that will never recur. Now you begin the selection experiment by allowing only the flies with the longest wings to reproduce. If the trait is heritable, then there will be a response to selection and the bell-shaped curve will shift in the direction of longer wings.

The fact that each fly is a unique combination of genes is beside the point. Moreover, the very existence of genes is beside the point. If phenotypic distributions can recreate themselves generation after generation and respond to selection without the existence of genes, then so much the worse for genes.

This is not just idle speculation. It is likely that stable gene-like entities are the *product* of evolution, not a *pre-condition* for evolution. Biological evolution preceded genes and some forms of biological and cultural evolution might still proceed without genes or gene-like entities.

The concept of evolution without replicators is fascinating but shouldn't obscure the simpler and more basic point that I am making in this installment of the T&R series. Even when genes *do* function as replicators, they have no bearing upon the group selection controversy because they function as replicators *regardless* of which level of selection prevails. We need to guard against naïve gene selectionism in the same way that we guard against naïve group selectionism.

XI. Dawkins Protests (Too Much)

Richard Dawkins did not invent naïve gene selectionism (see T&R X) but he spread it far and wide with the publication of *The Selfish Gene*. Let's follow his logic, beginning on page 6 of the 1989 paperback edition:

This book will show how both individual selfishness and individual altruism are explained by the fundamental law that I am calling gene selfishness. But first I must deal with a particular erroneous explanation for altruism, because it is widely known, and even widely taught in schools. This explanation is based on the misconception that I have already mentioned, that living creatures evolve to do things 'for the good of the species' or 'for the good of the group'.

There's the caution against naïve group selectionism. Good for you, Richard! Now for the explanation of why it is naïve:

[A] group, such as a species or a population within a species, whose individual members are prepared to sacrifice themselves for the welfare of the group, may be less likely to go extinct than a rival group whose individual members place their own selfish interests first. Therefore the world becomes populated mainly by groups consisting of self-sacrificing individuals. This is the theory of 'group selection', long assumed to be true by biologists.

Right! This explains how "for the good of the group" traits might evolve. Now for the explanation of why they might not evolve.

The quick answer of the 'individual selectionist' to the argument just put might go something like this. Even in the group of altruists, there will almost certainly be a dissenting minority who refuse to make any sacrifice. If there is just one selfish rebel, prepared to exploit the altruism of the rest, then he, by definition, is more likely than they are to survive and have children. Each of these children will tend to inherit his selfish traits. After several generations of this natural selection, the 'altruistic group' will be over-run by selfish individuals, and will be indistinguishable from the selfish group. Even if we grant the improbable chance existence initially of pure altruistic groups without any rebels, it is very difficult to see what is to stop selfish individuals migrating in from neighboring selfish groups, and, by inter-marriage, contaminating the purity of the altruistic groups.

Done. Allow me to make three observations about these passages.

1) Dawkins' portrayal of within- and between-group selection is utterly standard, and that's a *good* thing. Throughout the T&R series, I have stressed the simplicity of the group selection controversy. From Darwin to Dawkins, it's all about what I have called the original problem (see T&R II).

2) Dawkins implies that between-group selection (described in the second passage) is no match for within-group selection (described in the third passage), but he provides no proof. Models (such as the modified haystack model), experiments, and field studies are required to make this determination, not rhetorical flourishes.

3) The status of genes as replicators -- what Dawkins calls the fundamental law of gene selfishness -- is utterly beside the point. Genes are the replicators regardless of whether altruism wins or loses in Dawkins' own scenario (also see T&R X). Using the replicator concept to argue against group selection is arguably the greatest case of comparing apples with oranges in the annals of evolutionary thought!

I do not believe the cynical adage "science progresses -- funeral by funeral" but I worry that it might be true for Richard Dawkins on the subject of group selection. In my dreams, I imagine him reading my modified haystack model and saying "Well done,

David! I have been wrong all these years. It turns out that a gene coding for altruism *can* plausibly evolve on the strength of between-group selection, even when it is selectively disadvantageous within groups. I do think it is important to keep in mind, however, that when altruism evolves by group selection, it is still an example of gene selfishness because the gene for altruism is more fit than the gene for selfishness, all things considered."

Scientists would clap their hands red at such an act of nobility, but it hasn't happened yet. Instead, Dawkins has behaved like a cowboy fighting off the Indians in an old western movie. When one gun runs out of ammo, he grabs another and another. Here are three guns that have run out of ammo.

The selfish gene gun. As we have seen, this gun didn't have any bullets to begin with.

The vehicle gun. Recall that if individual organisms don't qualify as replicators, they must qualify as something else to be so manifestly well adapted. That "something" is variously called "interactors", "targets", or "vehicles" (Dawkins' term) of selection. In one of Dawkins' famous metaphors, genes in individuals are like rowers in a rowing crew. Since they are literally "all in the same boat", they must "pull together" to win the race. As soon as Dawkins threw away the selfish gene gun, he started to claim that groups fail as vehicles because individuals in groups are not completely bound together in a common fate in the same way as genes in individuals. But this was never a requirement for group selection to occur! The groups in the haystack model and in Dawkins' own portrayal of group selection quoted above aren't like individuals in this respect, but they suffice for altruism to evolve despite its selective disadvantage within groups.

The extended phenotype gun. When the vehicle gun didn't work, Dawkins decided to bury the vehicle concept altogether by describing genes as having extended phenotypes. Two examples of extended phenotypes are a bird's nest and a beaver's dam. The first is an individual-level adaptation in conventional terms; birds that build better nests raise more offspring than birds in the same group that build worse nests. The second is a group-level adaptation in conventional terms; beavers that build better dams are providing a public good for all of the beavers in the pond at their own expense. The fact that the genes result in alterations of the physical environment in both cases is irrelevant. In short, the concept of extended phenotypes doesn't address the original problem and certainly doesn't provide a novel solution.

With the Indians closing in, Dawkins has now started to throw chairs, bite, and kick. Consider his response to my recent article with Edward O. Wilson in *American Scientist* magazine titled "Evolution 'For the Good of the Group'"

Genes Still Central: David Sloan Wilson's lifelong quest to redefine "group selection" in such a way as to sow maximum confusion--and even to confuse the normally wise and sensible Edward O. Wilson into joining

him--is of no more scientific interest than semantic double talk ever is. What goes beyond semantics, however, is his statement (it is safe to assume that E.O. Wilson is blameless) that "Both Williams and Dawkins eventually acknowledged their error [that the replicator concept provides an argument against group selection]...I cannot speak for George Williams but, as far as I am concerned, the statement is false: not a semantic confusion; not an exaggeration of a half-truth; not a distortion of a quarter truth; but a total, unmitigated, barefaced lie. Like many scientists, I am delighted to acknowledge occasions when I have changed my mind, but this is not one of them. D.S. Wilson should apologize. E.O. Wilson, being the gentleman that he is, probably will.

Gracious! What a hierarchical guy! Dawkins acts as if he is the No. 2 monkey, kowtowing to the No. 1 monkey (Ed) while dishing it out to the No. 3 monkey (me)! As Ed commented to me after reading Dawkins' comment, "What does he think--that you slipped me a Mickey?"

If you still have the patience, let me make a few observations about this gem of a tantrum. First, why on earth would Dawkins title his response *Genes Still Central* ? Isn't he *ever* going to get over the fact that selfish genes have no bearing whatsoever on the group selection controversy?

Second, I trust that I have provided ample evidence that the original problem has provided the basis for defining group selection for everyone, including Dawkins and myself. There has been no redefining.

Third, when it comes to semantic confusion, you can't beat selfish gene theory. Genes are "the fundamental unit of selection" but this has no bearing on the "levels of selection" controversy. A gene might be selfish because it is selectively advantageous within groups, or it might be selfish because it evolves in the total population all things considered. Individuals might be perfected "vehicles" of selection now, but we also need to use the term "vehicle" to explain how such perfection evolved. This is how the simplicity of the original problem has turned into a terminological quagmire.

Dawkins continued his tantrum on his website after Ed and I quoted the passage in *The Extended Phenotype* where he abandons the replicator argument and takes up the vehicle argument:

The Wilson quotation from *The Extended Phenotype* is a ludicrous attempt to justify their lying statement that I "eventually" acknowledged an earlier error. For one thing, *The Extended Phenotype* was published way back in 1982, which makes nonsense of Wilson's "eventually". But more important, the point I was making in 1982 (and would make again now) was a general one about the important distinction between replicators and vehicles...I was explaining that those models of group selection that had

been proposed were vehicle models not replicator models. I was not for a moment suggesting that I accepted those models as valid. They were (and are) invalid vehicle models, as opposed to invalid replicator models.

There you have it from Dawkins himself. The word "eventually" is appropriate for the six-year period between 1976 and 1982, regardless of how much time has elapsed since then. Poor Richard is still trying to fend off the Indians with the butt end of his replicator gun ("genes still central") and vehicle gun ("invalid vehicle models"). If only Bill Hamilton was still alive to fight alongside and defend his brilliant ideas!

Fortunately, Bill Hamilton wrote plenty while he was still alive, showing that Richard Dawkins fights on alone.

XII. Multilevel Selection Theory, Salsa Style

Meet [Athena Aktipis](#)--evolutionist, mother of two, and salsa dance instructor in her spare time. Perhaps it was the dancer in Athena that caused her to teach multilevel selection by having the students get up and *move*.

Each student is given a wooden stick with an **A** (for Altruistic) or **S** (for Selfish) written on one end. Information on the blackboard tells them that altruists give three fitness units to their partners at a cost of one fitness unit to themselves. Selfish individuals receive without giving. Then they are instructed to move around the room and find a partner at random without revealing their identities. At the count of three, they reveal who they are and write their gains and losses on a 3x5 card. After repeating the process of pair formation and social interaction several times, the students total their score and take their seats for a few minutes of instruction.

I have started to use Athena's method in my classes and it is wonderful to see how the students come alive when they are allowed to move. Before they were fighting to stay awake in their chairs, but now a party atmosphere develops as they find their partners. Groans and cheers erupt when they present their sticks to each other. Altruists experience the joy of receiving, in addition to giving, when they are paired with another altruist, resulting in a net gain of +2, but they experience the agony of betrayal when paired with a selfish individual, receiving a loss of -1. Selfish individuals score big when paired with an altruist, for a gain of +3, but it's a drag to encounter another S, resulting in a 0.

Athena's method enables the students to understand the concepts of within- and between-group selection more vividly than from a dry lecture. Altruism is *locally disadvantageous*, which I have called "the original problem" throughout the T&R series. The students experience this for themselves when **S** trounces **A** in every mixed pair. But altruism is successful at a larger scale, as the students also experience when **AA** pairs produce a net gain of 4, compared to only 2 for **AS** pairs and nothing for **SS** pairs. What

evolves in the total population depends upon the net effect of the opposing selection pressures. With random pair formation, within-group selection trumps between-group selection. The average **S** accumulates more points than the average **A** and wins the Darwinian contest. A message to the wise: beware of your partner in anonymous social interactions.

Now the exercise is repeated with a single twist. Partners are allowed to stay together by mutual consent. Only students on the rebound from unhappy unions must seek new partners and they can't break up happy couples. After several rounds of play, most of the altruists are smiling and most of the selfish individuals are looking pretty grim. **AA** pairs elect to stay together while **AS** and **SS** pairs break apart. After several rounds, most of the **A**'s have found each other, forcing the **S**'s to interact by default. Within-group selection still favors selfishness and between-group selection still favors altruism. Only the *balance* between levels of selection has changed in the second example, by concentrating individuals into **AA** and **SS** pairs and gradually eliminating the **AS** pairs. In her scientific research, Athena creates theoretical models similar to this version of the exercise, which she calls "walk-away" models.

In a third version of the exercise, each student is given both an **A** and **S** stick to present as they see fit and several interactions take place within each pairing. Now the mind games begin, as some students try their luck with the selfish option, typically resulting in retaliation from their partner during the next round of play. No matter how complicated the strategy of employing **A** and **S**, however, the basic logic of multilevel selection applies. Selfishness is the unbeatable strategy within each pair; altruists *never* beat their own partner; they can only lose or draw. It is necessary to increase the scale of comparison to find fitness differences weighing in favor of altruism.

I have created a fourth version of the exercise to illustrate the principle of kin selection, which begins by forming the students into groups of six. Two members of each group are designated as Mom and Dad, who are about to have four children. Mom and Dad are given two sticks each, which might be 2 **A**'s, one **A** and one **S**, or two **S**'s. These are their two chromosomes, since it is necessary to include sexual reproduction to illustrate kin selection. The **A** allele is assumed to be dominant, so **AA** and **AS** genotypes behave altruistically and **SS** genotypes behave selfishly.

Now Mom and Dad proceed to have four kids by randomly showing one of their sticks to each of their four children. It's not as much fun as having sex, but it will have to do! In this fashion, each kid obtains their genotype from their parents, just like Mendel's peas. For example, if Mom is **SS** and Dad is **AS**, then all four kids get an **S** from Mom, while half (on average) get an **A** from Dad and the other half get a **S** from Dad. When the kids start interacting with each other, half will behave altruistically (**AS**) and half will be selfish (**SS**). The composition of each group of siblings will depend upon the genotypes of their parents in similar fashion.

What is the result of this exercise? When the siblings interact with each other, the basic

logic of multilevel selection remains unchanged. Mixed groups are still formed (as in the above example) and selfishness still wins within each mixed group. The new twist that is introduced with kin selection is in *the way that the groups are formed*. Sibling groups are formed through the funnel of their parents' genes, which increases the likelihood of altruist-altruist and selfish-selfish pairings and decreases the likelihood of altruist-selfish pairings, even though they still occur. This way of forming groups has the same effect as the second version of the exercise, when individuals could select their own partners. Perhaps this explains why we are so nice to both family and friends. In both cases, altruism evolves because between-group selection trumps within-group selection.

Athena's teaching method gives students a visceral feel for the generality of multilevel selection. Social interactions almost always take place within groups of individuals that are small compared to the total population. The minimum group size is 2, but everything that my students learned in pairs applies to larger groups. No matter how the groups are formed--at random, on the basis of experience, or through the funnel of genetic relatedness--no matter how flexible the choice of behaviors--altruism is *locally disadvantageous* and requires higher-level selection to evolve. It doesn't matter whether you call it group selection, kin selection, reciprocity, game theory, selfish gene theory, or anything else. All evolutionary theories of social behavior include the original problem and solve the problem only by identifying factors that enable between-group selection to overcome within-group selection. As Ed Wilson and I concluded at the end of our review article titled "[Rethinking the Theoretical Foundation of Sociobiology](#)", "Selfishness beats altruism within groups. Altruistic groups beat selfish groups. Everything else is commentary."

William D. Hamilton, the legendary founder of inclusive fitness theory (dubbed kin selection by John Maynard Smith), required several years and lots of math to reach the same conclusion.

XIII. Hamilton Speaks

Pity people who become icons. Once they represent an important idea in the minds of others, they can't change their iconic status, even when they change their own minds.

Such was the fate of [William D. Hamilton](#), the legendary founder of inclusive fitness theory, which was dubbed kin selection by John Maynard Smith (see T&R VIII). Hamilton became world famous for explaining how altruism can evolve according to the rule $br - c > 0$, where b is the benefit that the altruist gives a recipient, c is the cost to the altruist, and r is the chance that the recipient shares the same altruistic gene through a common ancestor. At least that was the *original* interpretation of r ; eventually it morphed into something different, as we shall see.

Why was Hamilton's theory regarded as so important? After all, multilevel selection already provided a framework for studying altruism. Hamilton's theory was regarded as a breakthrough because it seemed to explain altruism *without invoking group selection*. That was the whole point of Maynard Smith's haystack model (see T&R VIII and IX),

which claimed to show that group selection didn't work and that Hamilton's theory provided a viable *alternative*. Thanks to Hamilton, the controversy over Wynne-Edwards (see T&R III) and everything else associated with group selection could be rejected in favor of his elegant rule, which predicted that altruism should be doled out in direct proportion to genealogical relatedness.

Hamilton's rule also enabled altruism to be interpreted as *a form of self-interest*. After all, the altruist maximizes *its own inclusive fitness* by helping its genes in the bodies of others. No more foolish "for the good of the group" thinking! Inclusive fitness theory made evolution seem just like economics, in which everything can be explained as a form of utility maximization at the individual level.

With the benefit of hindsight, we can see that comparing the two theories is not so straightforward. Multilevel selection theory shows how altruism can evolve, despite being selectively disadvantageous within groups. Inclusive fitness theory shows how altruism can evolve, but it isn't obvious from Hamilton's rule what happens within single groups. It's not as if groups are absent; social interactions always take place within groups and the coefficient of relatedness specifies how groups are formed in the case of interactions among relatives, as we saw with Athena's class exercise (see T&R XII). Hamilton's rule correctly predicts when altruism evolves in the total population, given the assumptions of the model, but if we want to know *if it is an alternative to group selection*, we need to figure out what goes on within single groups.

Hamilton himself didn't figure this out until he encountered another rule formulated by another theoretical biologist named [George Price](#). The Price equation is not as famous as Hamilton's rule among the general public, but theoretical biologists regard it as a work of art. I won't print it here, because some readers are so afraid of math that even a formula only slightly more complicated than Hamilton's rule might cause them to lose bladder control, but I will describe it in words. On one side of the equation, the term ΔP shows whether a given gene evolves in the total population. On the other side of the equation, two sets of terms show the contributions of within- and between-group selection. The Price equation is regarded as beautiful precisely because it so cleanly splits evolution into its components. There is a term that looks much like r in Hamilton's rule, but it does not stand for the probability of sharing a gene identical by descent. Instead, it stands for the importance of between-group selection relative to within-group selection.

When Hamilton examined his own theory through the lens of the Price equation, he saw that altruism is selectively disadvantageous within each group of relatives containing both types, making his theory a *confirmation* of group selection rather than an *alternative* to group selection. Only then did Hamilton realize what students can learn in an afternoon through the kin selection version of Athena's exercise (see T&R XII).

It is fascinating to read Hamilton's own account of his revelation, which he wrote in his [collection of autobiographical essays](#). Here is how he describes his first encounter with the Price equation.

A manuscript did eventually come from him but what I found set out was not any sort of new derivation or correction of my 'kin selection' but rather a strange new formalism that was applicable to every kind of natural selection...His voice was squeaky and condescending, rather guarded on the phone...He spoke of his formula as "surprising for me too--quite a miracle"... "Have you seen how my formula works for group selection?" I told him, of course, no, and may have added something like: "So you actually believe in that do you?" Up to this contact with Price, and indeed for some time after, I had regarded group selection as so ill-defined, so woolly in the uses made by its proponents, and so generally powerless against selection at the individual and genic levels, that the idea might as well be omitted from the toolkit of a working evolutionist.

This passage shows with crystal clarity how thoroughly group selection had been rejected by the late 1960's, by Hamilton along with everyone else. Now here is how he describes his reaction to the Price equation, shortly before Price, a tragic figure, committed suicide.

I am pleased to say that, amidst all else that I ought to have done and did not do, some months before he died I was on the phone telling him enthusiastically that through a "group-level" extension of his formula I now had a far better understanding of group selection acting at one level or at many than I had ever had before.

Three aspects of Hamilton's account are worth noting. First, why did both Price and Hamilton find it so easy to recognize group selection in the Price equation? It is extremely abstract and can be used to describe many different kinds of groups, but neither man fretted over details. The reason is that in all cases, the Price equation reveals the selective disadvantage of altruism within groups, which is the essence of the group selection controversy. As Bill Clinton might have put it, "It's the Original Problem, stupid!"

Second, why did Hamilton fail to see group selection in his original formulation? Precisely because it did not showcase what happens at a local scale on its way toward showing what evolves in the total population. You can't see the need for group selection unless you note a *discrepancy* between what is favored locally and what evolves in the total population.

Third, neither Price nor Hamilton were prejudiced against group selection. It was not Hamilton's goal to explain the evolution of altruism without invoking group selection. His goal was to explain the evolution of altruism and he was happy to acknowledge group selection's essential role as soon as it was revealed to him through the Price equation.

Let's pause to savor this moment in the history of evolutionary thought. Group selection had been thoroughly rejected in favor of inclusive fitness theory, which seemed to explain altruism as a form of self interest. Then it emerged that inclusive fitness theory is not an alternative to group selection after all; the role of group selection was merely obscured by the way it was formulated. Hamilton, who had become an icon as the originator of inclusive fitness theory, happily changes his mind. What happens next?

Here's what *should* have happened. The whole field should have revisited the consensus formed only a few years earlier, concluding that group selection can be important after all and that there *is no alternative* explanation for the evolution of altruism, in contrast to what inclusive fitness theory seemed to provide.

Here's what *did* happen. Theoretical biologists began to take notice of the Price equation, while the rest of the field continued to treat group selection as a heresy and inclusive fitness theory as a wondrous alternative. Poor Hamilton had become an icon and it didn't matter that the person had changed his mind.

I recently had the opportunity to demonstrate this sad state of affairs in an e-mail dialogue that I organized among theoretical biologists titled "If the theorists can't agree...", meaning that if those who understand the models in intimate detail can't achieve a new consensus, then there is little hope for everyone else interested in evolutionary theory. Steven Frank, a distinguished theorist and authority on the Price equation, stated toward the end of the dialogue that:

[S]tarting with Hamilton and Price... we have the only framework that really exists. The 1960s don't count, because almost no one even cited Hamilton's work in that decade. Steve was referring to his fellow theorists. I promptly did a citation analysis for all scientific publications, showing that Hamilton's first formulation (represented by his 1964 article) and second formulation (represented by his 1975 article) are cited in a 15:1 ratio with *no trend whatsoever* for the 1975 paper to become more frequently cited over the decades. And this is the *scientific literature*!

When I give academic seminars on this subject, I ask my colleagues in the audience to predict the result of my citation analysis before presenting the answer. Usually they guess it right, noting that most people who cite the 1964 paper haven't read either one. That gets a laugh, but what does it really say about the study of evolution as a scientific discipline? It means that science as practiced is often a far cry from science as idealized. Certitudes are passed unquestioningly from teachers to students, especially when they confirm cultural biases, in a way little different than the transmission of religious dogmas.

Even worse, it turns out that the theorists *can't* agree. Core differences remain among the experts, even after they agree on the details of any particular model. The group selection controversy is like a battle that moves among battlegrounds. The claims that caused group selection to be rejected in the first place are no longer defended, but other claims are defended just as fiercely.

XIV. Group Selection in the Laboratory

In the storybook portrayal of science, theories are tested by experiments, which are conducted in laboratories so that the conditions can be rigorously controlled.

How would group selection be tested in the laboratory? Let's begin with the thousands of

selection experiments that have already been conducted in the laboratory at the individual level. A population of animals, such as fruit flies or chickens, is measured for a particular trait, such as bristle number or egg productivity. Individuals that score high or low (depending upon the desired direction of selection) for the trait are selected to breed the next generation. If the average value of the trait in the offspring generation shifts in the direction of selection, then the trait is heritable and there has been a response to selection. Over many generations, artificial selection can cause organisms to become completely different from their ancestors, as our domesticated plants and animals attest.

Group selection can be studied in the laboratory by a simple extension of the protocol outlined above. A population of *groups* is created, a particular trait is measured for the groups, and the highest (or lowest) scoring groups are used to breed the next generation. If the average value of the trait in the offspring generation shifts in the direction of selection, then group selection is proven to be efficacious, at least under the conditions of the laboratory experiment.

To make the procedure less abstract, consider my favorite group selection experiment, which I have written about in *Evolution for Everyone*. [William Muir](#), an animal breeder at Purdue University, selected for egg productivity in hens in two different ways. Both involved housing hens in cages (groups), which is standard practice in the poultry industry. The first method involved selecting the most productive hen within each cage to breed the next generation of hens. The second method involved selecting the most productive *cages* and using all the hens from those cages to breed the next generation of hens. It might seem that this is a subtle difference, that the same trait (egg productivity) should be selected in both cases, and that the first method should be more efficacious. After all, eggs are produced by individual hens, so why not directly select the best? Why select at the group level, when even the best groups might have some individual duds?

The results told a completely different story. The first method caused egg productivity to perversely *decline*, even though the most productive hens were chosen each and every generation. The second method caused egg productivity to increase 160 percent in six generations, an astonishing response as artificial selection experiments go.

What happened? If you've been paying attention to my Truth and Reconciliation blogs, you'll recognize a classic case of multilevel selection. Natural selection *within* groups is sensitive only to relative fitness, relentlessly favoring hens who lay more eggs than their neighbors. The first method favored the nastiest hens who achieved their productivity by suppressing the productivity of other hens. After six generations, Muir had produced a nation of psychopaths, who plucked and murdered each other in their incessant attacks. No wonder egg productivity plummeted! It would be hard to imagine a more graphic example of what I have called "the original problem" throughout this series of blogs; traits that are "for the good of the group" are not always locally advantageous within the group and require a process of group-level selection to evolve.

That's why the second method worked. Selecting the most productive *groups* favored

peaceful and cooperative hens, despite their selective disadvantage within groups. Moreover, group-level selection was sufficiently strong to successfully counteract selection within groups, which was taking place within cages for the second method, just as much as the first. Muir's experiment proves the efficacy of group selection, at least under the conditions of the experiment.

By the way, the groups of chickens were siblings. When some of my colleagues learn this fact, they shout "Aha! It's kin selection, not group selection!" Wrong. The groups were siblings in *both* methods, so their kinship cannot explain the difference *between* the methods. As I relate in T&R XIII, everything about kin selection theory can be understood in terms of the parameters of multilevel selection theory. Creating groups of siblings caused the psychopaths to cluster in some groups and the peaceniks to cluster in other groups, providing lots of variation to select upon at the group level. Psychopaths still beat peaceniks within each group; the fact that they were siblings is beside the point.

This experiment also raises important questions about what counts as an individual trait. Egg productivity seems like an individual trait because you can count the eggs coming out the hind end of a hen. The experiment reveals that egg productivity is in fact a highly social trait that depends upon the genetic composition of one's group, not just the individual's genetic composition. This example has profound consequences for how we think about human traits that seem individual but in fact are highly social.

This is only one of many experiments demonstrating the efficacy of group selection in the laboratory, for creatures as diverse as insects, plants, and vertebrates. In 1997, I organized a symposium on multilevel selection in my capacity as Vice President of the American Society of Naturalists, one of the premier evolution-oriented societies. The symposium took place at their annual meeting and was published as a special issue in the *American Naturalist*, arguably the premier journal for evolutionary research at the time. Among the speakers was John Maynard Smith, one of the premier evolutionists in the world and a chief critic of group selection, as I recount in T&R VIII and IX. I mention these credentials not to boast, but to emphasize how much the symposium occupied center stage in the world of evolutionary biology.

Another speaker at the symposium was [Charles Goodnight](#), a student of [Michael Wade](#), who conducted the first group selection experiments in the 1970's. Charles reviewed the literature and concluded that *every group selection experiment conducted in the laboratory demonstrated an efficacious role for between-group selection, even when between-group selection was opposed by within-group selection*. You can judge for yourself from the published version of Charles' talk (co-authored with Laurie Stevens) titled "Experimental Studies of Group Selection: What Do They Tell Us About Group Selection in Nature?", which is available on [his website](#).

As Charles recently recounted to me, he was convinced that his talk would be a career-maker for himself and a turning point for acceptance of group selection. Why not, given the import of his conclusions for one of the most important controversies in evolutionary

theory, the prominent forum, and the likes of John Maynard Smith in the audience? He was sorely disappointed. The laboratory evidence for group selection had virtually no impact on the acceptance of group selection by the evolutionary community at large. So much for the storybook portrayal of science.

The only legitimate reason to discount the results of a laboratory experiment is when the conditions are highly artificial, therefore irrelevant to real-world situations. But this is not the case for the group selection experiments, in which groups are formed much as they might form in nature. Moreover, the whole beauty of laboratory experiments is that conditions can be varied in a systematic fashion. If a critic thinks that the conditions of one experiment are artificial, the answer is to conduct another experiment, not to discount laboratory evidence entirely.

In fact, group selection is so efficacious in the laboratory that even the proponents of group selection were surprised. As often happens, the laboratory experiments revealed factors operating in real biological systems that were beyond the imagination of the theorists. In particular, the theorists had limited their models to traits with a simple genetic basis, such as selfish and altruistic genes that code directly for selfish and altruistic behaviors. Given this assumption, phenotypic variation among groups corresponds directly to genetic variation among groups, which in turn depends critically on the number of individuals initiating each group. The larger the initial group size, the less variation among groups for between-group selection to act upon. That is the entire import of kin selection and the early conclusion that group selection requires special conditions, such as small initial group size, to be efficacious.

In the laboratory, groups vary substantially at the phenotypic level, even when they are initiated by large numbers of individuals -- because the relationship between the genetic composition of a group and its phenotype is complex rather than simple. Even when groups initially vary by only a small amount, complex interactions within groups causes them to become more variable over time, a kind of "butterfly effect" that also accounts for why complex physical systems, such as the weather, are so variable.

An experiment that I performed my former student, William Swenson, will make this idea less abstract. We grew a fast growing plant called *Arabidopsis* in small flowerpots. The soil was sterilized except for a slurry of six grams of unsterilized soil from a single well-mixed source. To be precise, to make the slurry, we placed unsterilized soil and sterilized water in a kitchen blender and blended it like crazy before delivering six grams of soil to each pot of sterilized soil. If you know anything about microbiology, you know that *millions and millions* of microbes comprising *hundreds and hundreds* of species are contained in a single gram of soil. Thus, the initial variation among pots in the genetic and species composition of the soil microbes was vanishingly small.

We grew the pots under constant environmental conditions until the plants were large enough to harvest. We weighed the biomass of the plants and performed a standard artificial selection experiment with a single twist. Instead of the selecting the largest or

smallest *plants* to breed for the next generation, we selected the *soil from under the largest and smallest plants* (in separate treatments) to make into a slurry and inoculate the next generation of pots. In other words, we were selecting at the level of *whole microbial ecosystems* rather than at the level of individual plants. Plant biomass was being used as a *phenotypic trait of the ecosystem*.

Even though the initial variation among pots was miniscule based on the large number of microbes colonizing each pot, variation did not stay miniscule because each pot was a complex biological system. Just as a butterfly flapping its wings can change the trajectory of a complex physical system such as the weather, each pot embarked upon a separate trajectory during the course of the first plant generation. This was apparent even to the naked eye; for example, some pots but not others developed a mat of algae over the surface of the soil. These differences *made* a difference for plant growth, so that by selecting the soil from beneath the largest and smallest plants, we were selecting microbial ecosystems that caused the plants to become large or small. Over a number of ecosystem "generations" (each comprising many microbial generations), the high and low selected lines diverged from each other -- proof that variation among ecosystems was heritable. This work was published in one of the nation's premier science journals, the *Proceedings of the National Academy of Sciences*. Once again, I say this not to boast, but to demonstrate that if multilevel selection experiments in the laboratory have failed to have an impact, it is not for lack of legitimacy or exposure. As with Goodnight's review of the literature, however, our experiment had virtually no impact on attitudes about group selection by the evolutionary community at large.

Muir's chicken experiment and our soil ecosystem experiment show that multilevel selection is not just an arcane scientific subject; it can be put to practical use. The eggs in your refrigerator come from group selected hens, regardless of what you might think of group selection. In a second set of experiments, Bill Swenson and I selected microbial ecosystems to degrade a toxic compound. In his current research, Bill Muir and his colleagues are using group selection to create strains of livestock that have not been inadvertently selected to make each other miserable. What else might we select groups and ecosystems to do?

Multilevel selection experiments in the laboratory vividly illustrate why a truth and reconciliation process is needed for the subject of group selection. The experiments are published in the best journals because a core group of evolutionists *does* understand their import. For them, the storybook portrayal of science actually takes place. For the evolutionary community at large, however, the rules governing the acceptance and rejection of group selection are a different story.

XV. Group Selection in the Wild

In T&R XIV I showed that prejudice against group selection is impervious to evidence from laboratory experiments. It is also impervious to evidence from the wild.

I will focus on one of many examples that can be provided. In 1995, Robert Heinsohn

and Craig Packer published [an important paper on territorial defense in lions](#) in the journal *Science*. As good experimental field biologists, they had played recordings of lions from neighboring territories to observe how females of the focal territory responded. They discovered that the same individuals consistently arrived first at the scene while others consistently lagged behind. There seemed to be bravehearts and cowardly lions within the same pride.

Heinsohn and Packer looked for an advantage to counteract the cost of territorial defense for the bravehearts within their own pride and couldn't find it. The bravehearts weren't socially dominant, they didn't have more offspring, and they didn't punish the cowardly lions, who simply seemed to be cheating and getting away with it. The bravehearts were providing a public good at their own expense, an animal version of the tragedy of the commons made famous by Garrett Hardin in the 1960's. Here is how Heinsohn and Packer described the situation to the best of their knowledge:

Female lions share a common resource, the territory; but only a proportion of females pay the full costs of territorial defense. If too few females accept the responsibilities of leadership, the territory will be lost. If enough females cooperate to defend the range, their territory is maintained, but their collective effort is vulnerable to abuse by their companions. Leaders do not gain "additional benefits" from leading, but they do provide an opportunity for laggards to gain a free ride.

Let me pair this passage with the canonical passage by Darwin that I also quoted in T&R II:

It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over other men of the same tribe, yet that an increase in the number of well-endowed men and advancement in the standard of morality will certainly give an immense advantage to one tribe over another. There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection.

I hope you can see the similarity between these two passages. Darwin was identifying what I call the original problem; traits that benefit the whole group are often disadvantageous within the group. The counterbalance for cheating does not reside within the group; it resides in the process of more cooperative groups outcompeting less cooperative groups. Darwin's example was hypothetical. Heinsohn and Packer seem to be providing a real-world example with territorial defense in lions. They even stress the importance of between-group competition as the primary influence on the evolution of lion sociality.

Before continuing, let me issue two caveats. First, I have the highest respect for Heinsohn and Packer. They are topnotch scientists who can only be admired, not only for conducting such arduous research but also for attempting controlled experiments in the wild. Second, the last word has not been written on lion social behavior. Perhaps they or

someone else will find a within-group advantage for bravehearts in the future. I'm interested in how they interpret their *current* data. They don't interpret it as a provisional example of group selection. They don't even *mention* group selection as a possibility. I doubt that it even *occurred* to them to regard group selection as a viable possibility, even though a description comparable to Darwin's flowed from their own pen!

For those who feel impelled to shout "kin selection!" because lion prides are composed of related females, my reply is the same as for the chicken example discussed in T&R XIV. Genetic relatedness explains why bravehearts are clustered in some prides and cowards in others. Cowards still have the advantage within each pride, the observation that Heinsohn and Packer find so puzzling. If they had a better understanding of kin selection seen through the lens of multilevel selection theory (see T&R XIII), they wouldn't be so mystified by their own data.

This example illustrates a problem that pervades the evolutionary literature. Group selection became such a pariah concept that most people don't look for it. They haven't looked for it for so long that they forgot what it looks like and can't even recognize it when it bites them in the butt! Even when they do recognize it, they are tempted to describe it in a way that doesn't use the G word to make it more palatable to their peers. In this fashion, our students continue to learn that the rejection of group selection was a triumphant advance for evolutionary theory while the evidence for group selection lies all around us.

Science is no better than political revisionism if this situation is allowed to persist. One reason that I am writing this series of blogs is because I am an idealist about science. I regard it as the best cultural system we have for holding people accountable for what they say. Scientists have a responsibility to keep track of the history of their ideas and to acknowledge mistakes from the past, no matter how large. Unfortunately, like religion, science as practiced often falls short of science as idealized. The group selection controversy is an embarrassment for science and the sooner its shortcomings are corrected, the better.

XVI. Individualism is Dead: Long Live Major Transitions

Just as Brutus was a close companion to Caesar but proved to be his undoing, evolutionary theory seemed to provide a rock-solid foundation for individualism-- until [Lynn Margulis](#) came along.

Lynn is famous so you might already know her story. In the 1970's she proposed the radical theory that nucleated (eukaryotic) cells evolved not by small mutational steps from bacterial (prokaryotic) cells, but as symbiotic communities of bacteria that became so integrated that the group became a higher-level organism. She was fiercely opposed but carried the day, an accomplishment so great that she was admitted into the National Academy of Sciences in 1983.

The concept of organism as group was generalized in the 1990's by [John Maynard Smith](#) and [Eors Szathmary](#) in two books titled [The Major Transitions of Evolution](#) and [The Origins of Life: From the Birth of Life to the Origins of Language](#). Their theory was multilevel selection theory with a twist. The evolution of group-level adaptations requires a process of group-level selection and is undermined by selection within groups. Now for the twist: The balance between levels of selection is not static but can itself evolve. When between-group selection sufficiently dominates within-group selection, the group becomes a super-organism and the lower-level organisms acquire the status of organs. The evolution of nucleated cells was just one of many major transitions, preceded by the evolution of the first cells and possibly even the origin of life itself as groups of cooperating molecular interactions, and followed by the evolution of multicellular organisms, social insect colonies, and--as we shall see--human social groups.

John Maynard Smith is the same person who opposed group selection in the 1960's, as I recount in T&R VII and IX. Somehow he managed to make group selection the lynch pin of major transitions without ever acknowledging an error in his earlier views. Eors Szathmary, his coauthor, fully appreciates the continuity of ideas. [Joel Peck](#) is another theoretical biologist who is fully comfortable with multilevel selection and was close to John during the last years of his life. I recently asked Joel how John could have been so schizophrenic about his early and later ideas. Joel shrugged and replied with a question of his own: How does anyone believe in ideas that are inconsistent with each other, such as scientists who also accept religious dogma? Perhaps Maynard Smith simply couldn't bring himself to thoroughly reconsider his earlier ideas on the basis of his own later ideas.

It might seem that the evolution of multi-cellular organisms from single-celled organisms would be simple when they begin as a single cell, because then all the cells are genetically identical and there can be no selection within groups. Wrong. Mutations occur with every cell division and there are thousands of cell divisions in the lifetime of a multi-cellular organism such as you and I. Mutant cells that are selectively advantageous within the organism are certain to arise and spread, regardless of their effect on the welfare of the group. Cancer is just multilevel selection in which we are the groups. Over the eons, elaborate physiological mechanisms have evolved by between-individual selection to suppress within-individual selection as much as possible.

The concept of major transitions is one of the most important developments in modern evolutionary thought, but the implications for individualism and multilevel selection theory are seldom discussed. Individualism is the claim that individual organisms are a privileged level of the biological hierarchy, that all of nature and human nature can be explained in terms of individual-self interest, that groups can emphatically not be regarded as organisms writ large, that the idea of individuals evolving "for the good of the group" is deeply erroneous. If within-group selection invariably trumps between-group selection, then all of these claims would be true and evolution would indeed provide a rock-solid foundation for individualism. That's why the issues at stake in the 1960's seemed, and were, momentous.

The issues remain momentous when we decide that between-group selection is important after all and can even dominate within-group selection in the case of major transitions. If we noted the rock-solid foundation that evolutionary theory seemed to provide individualism before, we should equally note when the foundation crumbles. Individualism has nothing left to stand on. Individual organisms are highly integrated and tightly regulated societies. Organisms turn into mere groups when their organization is disrupted by natural selection from within. Mere groups turn into organisms when between-group selection trumps within-group selection. When selection operates at both levels, individuals become strange hybrids of solid citizens and self-seekers, while groups become strange hybrids of coordinated units and dysfunctional outcomes of conflict from within.

Some people will mourn and others will celebrate the death of individualism, but everyone needs to bury it and move on to explore the implications of multilevel selection theory, especially in the realm of human affairs.

XVII. The (Crude) Human Superorganism

[John Maynard Smith](#) and [Eors Szathmary](#) boldly expanded the symbiotic cell theory of [Lynn Margulis](#) to include other major transitions. They were a bit timid in their discussion of human evolution, however, restricting themselves to the genetic basis of language. Now it appears likely that human evolution was a full-fledged major transition. The reason that we are so unique among primates is because our ancestors became the primate equivalent of a single organism or a social insect colony.

Recall that the key ingredient of a major transition is the suppression of fitness differences within groups, causing between-group selection to become the primary evolutionary force. In most primate species, including our closest ancestors, intense within-group competition limits the opportunities for cooperation among members of the group. This is in contrast to extant human hunter-gatherer societies, which are fiercely egalitarian. What accounts for this shift and when did it occur in human evolution?

Humans are incomparably better at throwing projectiles than other primates, an ability that required whole-body anatomical changes and evolved early in the hominid lineage. Although the original purpose of throwing was presumably to deter predators and competing scavengers, it could also be used to suppress bullying and other domineering behaviors within-groups. This hypothesis, developed by [Paul Bingham](#), is a specific version of a more general hypothesis of guarded egalitarianism, originally advanced by [Christopher Boehm](#) on the basis of the egalitarian nature of most extant hunter-gatherer societies. However it was accomplished, guarded egalitarianism provides the key ingredient of an evolutionary transition. It has been common in the past to regard advanced human cognitive abilities, such as a theory of mind, as the first step of human evolution that made widespread cooperation possible. Now it appears that the sequence needs to be reversed. The first event was the suppression of fitness differences within groups, which did not require a change in cognitive ability. Then, between-group selection favored forms of mental cooperation in addition to physical cooperation. After

all, symbolic thought and the social transmission of behaviors are fundamentally cooperative activities that are unlikely to take place among uncooperative individuals. Even human capacities that we take for granted, such as the communicative nature of our eyes, our ability to point, and awareness of others that emerges early in infancy, are forms of cooperation that appear to be uniquely human. [Michael Tomasello](#) and [Jonathan Haidt](#) are two prominent researchers developing this thesis.

In retrospect, human evolution has all the hallmarks of a major transition. It was a rare event, occurring only once among primates. It had momentous consequences; cooperation enabled our ancestors to spread over planet, eliminating other hominids and many other species along the way. We also diversified to occupy all climatic zones and hundreds of ecological niches, although by cultural evolution rather than genetic evolution. The advent of agriculture enabled us to increase the scale of society by many orders of magnitude by a process of cultural multilevel selection. Finally, the transition was not complete. Within-group selection still takes place and is merely suppressed compared to between-group selection. [Peter Richerson](#), who pioneered the modern study of cultural evolution with [Robert Boyd](#), likes to call human groups *crude* superorganisms, cooperative units to be sure, but not in the same league as bodies or beehives. I'm happy with this qualifier, but even thinking of human groups as crude superorganisms has vast implications, especially against the background of individualism that has dominated the intellectual landscape for the last half century. The corpus of Pete and Rob's work leaves little doubt that cultural change is both an evolutionary process and a *multilevel* evolutionary process in which group selection can seldom be ignored. No wonder our students think so naturally in terms of "for the good of the group". We are a highly group-selected species.

XVIII. The End is Near

August 22, 2009. I am at the annual meeting of the European Society for Evolutionary Biology (ESEB) in Turin, Italy. Twelve hundred evolutionists have gathered to strut their stuff and party over a five-day period. I'm here to speak at a symposium on levels of selection that is being held on the first day.

The symposium is one of six held concurrently and all of them are preceded by a plenary talk in a room large enough to accommodate everyone.

The plenary speaker is [Hanna Kokko](#), a theoretical biologist from Finland who has risen to the top of her field. I just turned 60 and Hanna seems awfully young to be giving plenary talks, but anyone who worries about women in science should see her lead the huge audience through her theoretical models on diverse ecological and evolutionary topics.

Hanna's first two examples illustrate the fact that evolution at a local scale can be maladaptive at a larger scale and can even lead to extinction. In the first example, a species of fish in which the females are asexual but still need to mate with males of a sexual species for their eggs to develop outcompetes the sexual species and therefore

drives itself locally extinct. In the second example, an endangered bird species on a small island evolves large territory sizes, reducing its population size and increasing its chances of extinction. If local evolution favors traits that are so detrimental over the long term, how can more sustainable traits evolve? When Hanna mentions group selection as a possibility, she shows this image of a man so panicked that he's about to jump out the window (thanks to Hanna for providing me the image).



No one laughed harder than me at Hanna's humor slide, which speaks volumes about the current status of group selection among professional evolutionists and evolutionists-in-training. Group selection is *still* a taboo subject that seems shocking when seriously invoked. Most people in that vast audience had been taught only one thing about group selection: Don't do it. Can you imagine this image making sense, even as a humor slide, for any *other* subject in evolutionary theory?

Hanna's plenary talk is the perfect advertisement for the levels of selection symposium. The room is filled to capacity. The first speaker is [Samir Okasha](#), an excellent philosopher of biology and author of the highly regarded [Evolution and Levels of Selection](#) (2006). I can follow Samir's presentation but sense that most other people in the audience are mystified. They need a basic tutorial explaining why group selection is no longer taboo. Samir is discussing highly derived issues, such as the merits of different covariance formulas and types of group selection.

I'm up next and try to provide the tutorial that I think the audience needs, starting with the all-important original problem that I have stressed throughout this series. I assure you that it was new material for most people in the audience. That is the degree to which the stigmatization of group selection has led to basic ignorance within the profession. The [remaining speakers](#) give a whirlwind tour of current topics in multilevel selection theory, including species-level and ecosystem-level selection. [Daniel Rankin](#) and [Kevin Foster](#), the symposium organizers, are pleased with the result of their labors and feel that they have provided an important service to their scientific community.

But the anti-group selectionists aren't going quietly into the night. [Andy Gardner](#), a young theorist who won last year's prestigious John Maynard Smith award, is scheduled to speak at a symposium on cooperation the next day. He actually changes the title of his talk to "Why I Am Not A Group Selectionist" in response to the levels of selection symposium. Whatever he means by this title, he has no quarrel with fact that between-group selection is often a significant evolutionary force, as measured for example by the Price equation. His talk and the other talks in the cooperation symposium are filled with slides showing traits that evolve on the strength of their group-level benefits, despite being selectively disadvantageous within groups. Even though Andy acknowledges that

multilevel selection theory and inclusive fitness theory are equivalent and even calls the distinction "empirically empty", he regards inclusive fitness theory as superior in some important sense. He also makes a distinction between group selection and group adaptation, based on a new article that he has co-authored with [Alan Grafen](#).

Most of the action at a conference such as this takes place in the halls, at meals, and drinking sessions that go far into the night. The multilevel selectionists are as angry as a disturbed hornet's nest. We're sick of seeing example after example that anyone would have called group selection in the 1960's presented without using the G-word. Where does Andy get off saying that his formalism leads to greater insights when we also publish in the best and most rigorously peer-reviewed journals? Does Andy and the other anti-group selectionists even *read* the literature framed in terms of multilevel selection? Not very much, judging by what they cite. We're especially irritated by an [article](#) that appeared in the journal *Nature* several months earlier by [Geoffrey Wild](#), Andy Gardner, and [Stuart West](#), claiming to explain the evolution of decreased virulence in parasites without invoking group selection. In truth, the avirulent strain is selectively disadvantageous within local groups and evolves only on the strength of their differential contribution to the total gene pool--in other words, classic group selection. All the model does is state the result in the lingo of inclusive fitness theory. Another demonstration of equivalence isn't new, but not only is the article published in *Nature*, but it's featured in *Nature's* News section with the title "[The Nail in the Coffin for Group Selection?](#)" No wonder the whole world remains confused! We're so mad that [Mike Wade](#) has coordinated a multi-authored letter to submit to *Nature* in protest.

The ESEB conference richly illustrates how the group selection controversy remains both settled and unsettled at the same time. The original problem has been settled: Contrary to the consensus that emerged in the 1960's, between-group selection is often a significant and sometimes even a dominating evolutionary force. That's why Andy and the other anti-group selectionists are willing to say--in this context--"We're all group selectionists."

Then there are a number of derived issues that cause Andy and his colleagues to proclaim that they're not group selectionists. I will provide a brief guide to these derived issues in the final installment of the T&R series. Whatever we decide about them, they should not be confused with the original problem. I'm reminded of a scene in an old western movie where a cowboy is riding furiously on his horse. His horse is shot and the cowboy jumps onto an adjacent horse to continue riding furiously without skipping a beat. Whatever horses the anti-group selectionists are riding now, everyone needs to be aware that the first horse is dead.

You might think that we're all so pissed off at each other that we refuse to talk or get into ugly shouting matches. Not so! George Williams and I are old friends, as I have already mentioned. On one of my visits to his house, he taped a hand-lettered sign on his lawn mower at the driveway entrance that read "superorganisms welcome here," which has graced the door of my laboratory ever since. At the ESEB conference in Turin, the

jousting was intense but cordial and leavened with humor. If there must be controversy, let it be over Italian food and wine in an open air restaurant in August. Ciao!

XIX. Happily Ever After

We have reached the end of the T&R series. In a truth and reconciliation process, truth is required for reconciliation. There must be a consensus on *what happened*, even if all wrongs cannot be righted. I have had my say on what happened during the group selection controversy. Anyone who wishes to challenge my account is welcome to do so. This period in the history of evolutionary thought deserves the same kind of scholarship that is lavished upon Darwin and his contemporaries. The more scholars the merrier. Much of what I have reported in the T&R series is drawn from my book with Elliott Sober, [Unto Others](#), which was published in 1998 and has largely withstood the test of time. I'd like to think that Samir Okasha, author of the highly respected [Evolution and the Levels of Selection](#) (2006), agrees with my account. If not, I hope he will speak up.

Once a consensus is reached on what happened, scientific inquiry can proceed in a more unified fashion than before. I end this series with a summary of what a fully reconciled field of sociobiology will look like. For a more detailed account, please consult my 2007 article co-authored with E.O. Wilson titled "[Rethinking the Theoretical Foundation of Sociobiology](#)".

1) The original problem is the fundamental problem of social life. Darwin put his finger on the key problem with the evolution of social adaptations. Traits that are "for the good of the group" are not necessarily locally advantageous. If they evolve, it is not because individuals bearing the trait survive and reproduce better than individuals bearing alternative traits in their immediate vicinity. This deserves to be recognized as the core problem of sociobiology.

2) There is only one solution to the original problem. If a trait is locally disadvantageous wherever it occurs, there is only one way for it to evolve in the total population--by being advantageous at a larger scale. Groups of individuals displaying social adaptations must survive and reproduce better than other groups, to counterbalance the disadvantage of the same adaptations within groups. All evolutionary theories of social behavior embody this logic. The groups and fitness differentials within and among groups are there for anyone to see, once one knows what to look for.

3) Selection within and among groups are factual matters, not matters of perspective. Once the groups relevant to the evolution of a particular trait are identified (something that all models of social behavior must do), selection within and among groups can be straightforwardly measured--in a model, experiment, or nature. The question of whether a given trait evolves on the strength of within-group selection, between-group selection, or a combination or both has an answer upon which everyone can agree.

4) The categorical rejection of group selection in the 1960's was an error, pure and simple. It is simply not the case that lower-level selection invariably trumps higher level selection. Period. End of discussion. Textbooks and other accounts that imply otherwise need be revised. The erroneous rejection of group selection was especially tragic because it made the only solution to the original problem appear wrong, motivating a search for other solutions that in retrospect turned out to be the only solution in disguise. Why would anyone want to perpetuate this confusion once it is seen clearly?

5) If it walks like a duck and quacks like a duck, maybe it's a duck. Avoiding a stigmatized term makes sense as a short-sighted strategy for avoiding controversy, getting your article published, etc., but it is no way for a scientific discipline to conduct itself. If scientists aren't going to keep careful track of what was said and meant during the history of a given subject, who will? Failing to mention group selection when discussing issues that have always been central to the group selection controversy is poor scholarship and should be grounds for rejection in a peer review journal.

6) Derived issues associated with the group selection controversy should not be confused with the original problem. From Darwin to Dawkins, group selection has been centered on the original problem, as I have shown in considerable detail. During the last few decades, however, a number of other issues have arisen. The first thing we need to know about these derived issues is that they do not bear upon the original problem. Secondly, we need to evaluate them on their own merits. A short list of derived issues includes the following.

7) My formula is better than yours. Given the same set of biological assumptions about the evolution of a given trait, there is more than one way to calculate what evolves in the total population. Some methods highlight local fitness differentials in addition to the global outcome. Other methods report only the global outcome, for example by averaging the fitness of individuals across groups or the fitness of genes across all contexts. Since all of the methods make the same biological assumptions, the differences between them are empirically empty, as Andy Gardner put it (see [T&R XVIII](#)). Nevertheless, one might be preferable to another based on other criteria, such as the compactness of the formula or certain insights that are highlighted by some formulations and obscured by others. For example, Hamilton's original formulation of inclusive fitness theory obscured the fact that altruism is locally disadvantageous even in family groups, which jumps out of the Price equation. However, the Price equation can misclassify a nonsocial trait that evolves by pure individual-level selection (e.g., type A has a fitness of 1 and type B has a fitness of 0.75, no matter how they are grouped) as an example of group selection when the types are clustered into separate groups. The empirically empty preference of one formulation over another should never be confused with the empirically meaningful issues associated with the original problem.

8) Type one vs. type two group selection. Some traits, such as altruism, can be measured in individuals. Other traits, such as group size, can only be measured in groups. Samir Okasha refers to these as type 1 and type 2 traits, respectively. Whatever the merits

of this distinction, it is important to realize that virtually all of the examples of group selection discussed throughout its history have been of the type 1 variety--traits that can be easily measured in individuals but require group selection to evolve because they are locally disadvantageous. A trait need not be a "group-level" trait (type 2) to evolve by group selection. Conversely, a "group-level" trait such as group size can evolve by pure within-group selection, as we saw in [T&R XVIII](#) for the endangered bird species discussed by Hanna Kokko.

9) Everything that evolves as a form of individual selfishness. Whenever altruism evolves by group selection, the average altruist is more fit than the average non-altruist in the total population, which can be conceptualized as a form of individual selfishness. The same gambit allows individual-level adaptations to be conceptualized as a form of gene selfishness. The problem with these expanded definitions of selfishness is that they don't deny what they seem to deny. Gene selfishness is no argument against group selection and neither is the fitness of individuals averaged across groups. Theoretical biologist Alan Grafen is going to great lengths to build a formalism in which natural selection operating at all levels of the biological hierarchy (in multilevel selection terms) can be represented as a form of fitness maximization at the individual level. Strictly speaking, this enterprise is doomed to failure because natural selection operating below the level of the individual, resulting in such things as cancer and meiotic drive, can never be represented as for the good of the individual. Thus, Grafen must assume that these examples are trivial to proceed with his agenda. Even then, however, what is the point of trying to represent natural selection as a maximizing process at a single level of the biological hierarchy, much less the individual level?

10) Group selection vs. group adaptation. Generations of students have been told to avoid "for the good of the group" thinking because it requires group selection. Another way to say "for the good of the group" is "group-level adaptation". Nevertheless, according to a recent article by Andy Gardner and Alan Grafen, a trait does not count as a group-level adaptation just because it evolves by group selection; it must evolve almost exclusively by group selection. It's amazing how fast this argument has been taken up as the newest defense of individualism in evolutionary thought. Critics and proponents of group selection alike would have been mystified by it in the 1960's. For them, the question was whether group selection *ever* happens. The idea of restricting the concept of group-level adaptation to cases where group selection *only* happens would never occur to them. It shouldn't be necessary, but Elliott Sober and I are preparing to spell this out in yet another article as the academic arms race continues.

It's worth asking why so many derived issues have arisen after the original problem was settled. In the spirit of discussing cultural influences for current science rather than waiting 50 or 100 years, (see [T&R VI](#)), I submit that when the rejection of group selection failed, those drawn to individualism felt the need to produce new arguments on its behalf. All of the derived issues buttress the concept of the individual as a privileged level of the biological hierarchy. Individualism is the primary issue at stake and when one argument fails, others are created to take its place. Once we let go of individualism, these

arguments seem pointless and contrived. Adaptations can evolve at all levels of the biological hierarchy, from genes to ecosystems, but only when certain conditions are met. Truth and reconciliation for group selection means regarding this statement in a positive sense and exploring its rich implications.