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CONVERSATION : LIFE

THE FALSE ALLURE OF GROUP SELECTION

An EDGE Original Essay

Steven Pinker [6.18.12]



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Genic Selection and Adaptationism: Are We Moving Forward or Back?

It is a welcome relief that Steve Pinker has applied his usual acuity to the ever-vexatious debate on group selection. The first and deepest problem with this debate is that the term *group selection* does not have any single fixed meaning, but has been used over the last half century to convey a huge and tangled thicket of different and conflicting meanings. The great majority of these are seriously defective as a way of describing reality. Various entries in this forum provide good examples of how this terminological black hole still is a vector for spreading confusion: it invites us down garden paths into conceptual tarpits; it leads us to talk past each other; it gives the appearance of life to long dormant and justly discredited ideas, by conflating them with fundamentally different but potentially viable hypotheses; and it even leads us to confuse ourselves about what exactly we are referring to. This multiplicity and indeterminacy of meanings is reason enough to imprison the term in adamant chains and pitch it into the Marianas Trench, limiting its future mischief to unwary coelacanths and unusually credulous archaeobacteria. Banning the term (sadly, a utopian fantasy) might force us all to adopt terminology that clearly distinguishes distinct theories, and distinct (hypothetical or actual) phenomena. This would allow these issues to be cleanly sorted out and settled within our lifetimes, rather than postponing this to the next millennium. Other meaning-chameleons that sow similar confusion are *moral*, *altruistic*, and especially *selfish*. For example, using the definition of selfishness and altruism that biologists use, a loving and self-sacrificing mother is acting selfishly, while a drug addicted mother who starves her children to give all her money to her dealer is an altruist (i.e., she is lowering her own fitness in a way that increases a nonrelative's).

Those new to the group selection debate may not know how truly problematic thinking was about these issues before George Williams and a new generation of evolutionary scientists ushered in the genic selection revolution [1]. For those (still) not exposed to this revolution or working before it, group selection was mostly just a terminological

placeholder for a ubiquitous, promiscuous, fuzzy evolutionary teleology that permeated both scientific and popular thinking. This luxuriant, pervasive, unanchored teleology choked off productive evolutionary reasoning: In the biological world, any good effect on anything else was supposedly explained by Darwinism's benign collectivism: Plants produce oxygen for animals to breathe; predators target the sick and the old to keep the unfit from reproducing, maintaining the balance of nature. The Nobel Laureate Konrad Lorenz, in his much lauded book *On Aggression* taught social scientists, animal behaviorists, and the educated public that dominance hierarchies and ritualized aggression evolved for the good of the population or species—for example, it was good for everyone if the unfit ceded resources to the fit and dominant; inferiors collaboratively joined in their eugenic self-removal because their adaptations were altruistically designed to submit nonviolently to their betters. This collaborative weeding out of the inferior was just one of an endless series of phenomena supposedly explained by a Darwinism that was held to operate by retaining whatever traits contributed to the "survival" of the group, population, species, or balance of nature (for a modern example, think Gaia hypothesis). The zoologist V.C. Wynne-Edwards famously argued that group selection widely selected for adaptations that sacrificed the individual's reproduction so that the local group would not exceed the carrying capacity of the environment. Psychology and anthropology were similar train-wrecks—a typical case being the prominent anthropologist Marvin Harris' early version of cultural group selection, in which he argued that warfare and male-supremacy were a culturally group selected form of population control.

By the laborious application of logic, conceptual clarity, mathematical modeling, and empirical tests, this jungle of misconceptions was largely cleared away, and evolutionary biology was rebooted on the far more rigorous and productive foundation of adaptationism coupled to genic selectionism. This generational act of intellectual reclamation was the most important advance in evolutionary biology since Darwin. As Darwin pointed out, "[t]o kill an error is as good a service as, and sometimes even better than, the establishing of a new truth or fact." This rebooting not only cleared away a huge tangle of errors but in so doing, unleashed a flood of theoretical and empirical advances that are refashioning our understanding of the nonhuman and human worlds. The core of the genic selection revolution is the insistence that selectionist arguments posit a clear pathway of material causal steps that produces feedback from the effects of genes to their subsequent proliferation. That is, theories must specify an explicit chain of causation that leads from a given set of genes, to their recurrent (somatic or extended) phenotypic effects (the adaptation), to the adaptation's interactions with the world; these must have the net consequence of multiplying the frequency of replicas of those genes in subsequent generations.

Agreements and disagreements: Now that the revolution is over, what are we arguing about?

A variety of researchers have now introduced a small and diverse set of new models of hypothetical evolutionary (e.g., genetic) or dynamical (e.g., cultural) processes which they unnecessarily (in my view) insist on labeling as group selection. (Usually, these turn out to be consistent with and traceable to the genic selectionism revolution, although many of these models depend on numerous restrictive assumptions which may or may not allow them to be applied to the real world.) Readers might detect a note of testiness here and there in the responses to these proposals. The reason why is that those who have worked long and hard to clear out the jungle, and to lay a rigorous foundation for modern evolutionary biology see this progress jeopardized by the rhetorical conflation of faulty or implausible (and dormant) ideas with these new models. The problematic but infectious strains of group selection thinking and fitness teleology are, unfortunately, highly

attractive to our evolved intuitions, so small missteps are all it takes to release them from their proper home in biological containment facilities and into the general intellectual population.

Nevertheless, I strongly agree with the new group selectionists on one point: One should never be dogmatic, but should examine all hypotheses carefully without prejudice or partisanship. Indeed, the biological world is so rich and multifarious that it would be foolhardy to say that any particular logical possibility has never been realized anywhere in the seven (or so) kingdoms of life. For example, Paul Ewald's elegant work on parasite virulence and its attenuation invites a group selection analysis; i.e., when encounters with susceptible new hosts are rare, those hosts populated with more deadly strains die before infecting new hosts, ratcheting down average virulence across the parasite meta-population. (However, given asexual reproduction in many parasites, one could just as easily consider the strain inside a host a single biological individual, and not a group.)

Like the British and the Americans, evolutionary behaviorists are separated by a common language. So, it may be useful to see if apparent disagreements (where people are talking past each other) can be resolved into points of agreement, so that we can better understand where any remaining disagreements lie. I am guessing most or all participants:

- (1) accept and value the genic selectionism revolution;
- (2) think that for mammals and similar organisms, the great majority of the traits of organisms are the product of selection to promote inclusive fitness (for simplicity I'll call this individual selection), without needing to invoke processes operating at higher levels;
- (3) agree that multilevel selection theory is not actually a theory, but one of several mutually consistent ways of representing theories; Dave Queller calls these alternatives different languages, and Joe Henrich felicitously likens them to different coordinate systems; multilevel selection models that invoke group selection are equivalent to one particular family of kin selection models;
- (4) agree that traits can be beneficial to the individual, but costly to the group; beneficial to the individual by virtue of being beneficial to the group; costly to the individual, but beneficial to the group, etc.
- (5) agree that humans could hypothetically be designed so that they are far more beneficial to the groups they inhabit than they actually are, but evolution has not made them so;
- (6) agree that traits can evolve in which a functional phenotype is expressed across individuals or by a group; there are innumerable examples, including hive architecture, waggle dancing, group hunting, or hunter-gatherer sharing as risk pooling;
- (7) agree that traits cannot evolve that cause an average net decrease in individual fitness (other than by kin selection).

Agreement on point 7 reflects the extinction of pre-revolutionary patterns of thought, in which individuals supposedly sacrificed themselves for all kinds of implausible ends, from maintaining maximum sustainable species biomass to implementing group eugenics programs to lowering the extinction probability of the species.

Let's pause now to consider some issues where people seem to be talking at cross-purposes. Those who prefer to phrase things in terms of group selection often seem to believe that those who don't deny the existence of functional group phenotypes. They

seem also to equate the existence of functional group phenotypes as evidence for group as opposed to individual selection. In contrast, those who prefer to represent things in terms of individual selection are perfectly happy to recognize the existence of functional phenotypes composed of traits distributed across multiple individuals. However, they see no reason to interpret this as necessarily individually costly, and therefore necessarily falling into the category of things that require group selection explanations. Also, there is interpretive choice in whether one considers the functional phenotype as "really" existing at the individual level (which it must to initiate the feedback pathway), or as "really" existing at the group level (which it must to complete the feedback pathway—eventually, multiplying gene frequencies). Collaborative hunters must have adaptations in individual brains that cause them to hunt in groups, and must also hunt in groups (a group-level functional phenotype) to reap the advantage. Individual selectionists consider this a case of individual selection, because individuals have hunting adaptations, and these increase individual fitness. Group selectionists consider it a case of group selection because fitness increases come to the groups that manifest the functional group phenotype, and not to those that don't. As long as the phenotypic adaptation is correctly described at both the individual and the group level (necessary work that is frequently not done), then the approaches are different in name only.

It is important to recognize that group functional selection pathways do not violate intuitive ideas of self-interested behavior. The individual acts in a way that (on average) makes her better off, with increasing group welfare just being a means through which individual welfare (approximately, inclusive fitness) is increased. Imagine, for example, a lottery, in which there are disproportionate increases in the expected value of lottery tickets the more expensive they are. A dollar ticket has, say, an expected return on one dollar, while a four dollar ticket returns sixteen dollars. If individuals each have one dollar, then those who pool their money to buy four dollar tickets will do better. Nothing about this involves acting against self-interest or receiving a lower payoff. Indeed, since multilevel group selection simply partitions what once was considered individual fitness into two types (or more) of what should also be considered individual fitness, it would be simpler, less confusing, and less retrograde to simply describe it that way.

Still, there are two sets of cases worth distinguishing where group-functionality is driving a selective advantage. In one case, within-group selection selects against the group-functional adaptation in the individual; in the other case, selection pressures on the adaptation are aligned between the individual level and the group level (or at least within-level selection doesn't act against it). The evolution of group functional traits will be far easier and hence more common, other things being equal, when selection is parallel or at least not opposed between the two levels. Yet, curiously, the new group selectionists tend to focus on more problematic cases where within-group selection (hypothetically) puts individuals at a relative disadvantage, recalling the old group selectionists' emphasis on sacrificing for the group. It may tell us something about the strength of group selection in humans that clearcut cases of genetic traits selected against within the group, but favored at the group level have not yet been established.

Multilevel selection theory, heterarchic pathway feedback theory, and competition for phenotypic expression

A major problem I have with multilevel selection theory is its imposition of a hierarchy of nested class inclusion on a biological world that seems to have a very different structure. I favor an alternative that might as well be called heterarchic pathway feedback theory. In general, selection will favor any alleles that establish a positive feedback causal pathway between their effects and their subsequent frequencies. In general, we are better off

modeling, detecting and inventorying these different pathways, rather than attempting to integrate them into a single unitary theory of fitness. These pathways need not be, and often will not be aligned, mutually consistent, or representable as operating at different levels in a hierarchy, but instead will often be cross-cutting and heterarchical. For example, Leda Cosmides and I published a paper introducing a general theory of intragenomic conflict [2], describing how individuals were actually better conceptualized as colonies akin to social insect hives, because the fitnesses of different subsets of the genome were maximized in mutually inconsistent ways: Mitochondria, flagella, the Y chromosome, the paternal genome, the maternal genome—all had different fitness interests, and therefore selected for adaptations that were sometimes designed to disrupt each other (see, e.g., David Haig's work on conflict within the fetus between the maternal and paternal genome). To take one out of dozens of examples, we found evidence supporting the prediction that across a broad range of species, intragenomic conflict disrupted designs in flowering plants in which both male and female functions were combined in the same individual. One set of adaptations or the other were kept from phenotypic expression. Similarly, different social strategies may select for different and potentially conflicting adaptations both within individuals and in group functional phenotypes. Adaptations for reciprocation may conflict with, e.g., adaptations for kin-directed altruism or adaptations for coalitions; or adaptations for kin-directed altruism may conflict with aposematic coloration. Group-functional adaptations may particularly suffer from such disruption, because the total number of possible alternative partitionings into different groups is high, and different partitionings may select for different and mutually inconsistent phenotypic functions, with perhaps the strongest selection pressures winning out. (Indeed, advocates of multilevel selection in different analyses routinely posit different group structures that do not map on to each other; e.g., modeling kin selection as group selection; modeling reciprocation as group selection. In fact, the same individual may be modeled as being in hundreds of dyadic reciprocation groups over the course of a lifetime.) The existence of heterarchic feedback pathways may lead to competition among different adaptations for expression in the phenotype—one of many issues not theoretically well-explored, or well-captured by multilevel selection theory.

Effects on scientific practice

Some aspects of the new group selection research program strike me, at least, as perhaps contributing to the erosion of good scientific practice. Results that straightforwardly falsify theories are presented as if they supported them. [3] The claimed "failures" of individual selection explanations for various empirical findings are extremely weak and polemical (e.g., Henrich's claim that evolutionary psychological approaches predict cross-cultural uniformity in measured behavior is simply baffling, since adaptations like the language acquisition device or reciprocation systems take local inputs as parameters, and generate variable output. [4] Moreover, the eagerness to leap to conclusions has warped good experimental design. For example, experimental designs testing for the existence of "altruistic punishment" are full of what psychologists would see as clear experimental artefacts. There is a strong response bias built into the experiment (subjects can only punish or do nothing), and such a design, even subject error counts as altruistic punishment. Indeed, the extravagant explanatory claims made for many of these models (about altruism, punishment, morality, fairness, etc. in humans) have been accompanied by a growing neglect of testing for or even bothering to characterize the associated neurocomputational adaptations which constitute their phenotypic reality.

Obviously researchers should be free to choose to work with any coherent representational system they like, and I continue to hope that the creative people working in this area may discover important new insights about humans using multilevel selection theory or cultural

group selection theory.

Cosmides, L. and Tooby J. (1981) Cytoplasmic inheritance and intragenomic conflict. *Journal of Theoretical Biology*. 89: 83-129.

Delton, A. W., Krasnow, M. M., Cosmides, L., & Tooby, J. (2010). Evolution of Fairness: Rereading the data. *Science*, 329(5990), 389.

Tooby, J. & Cosmides, L. (2010). Groups in mind: Coalitional psychology and the roots of war and morality. In Høgh-Olesen, Henrik (Ed.), *Human morality and sociality: Evolutionary and comparative perspectives*.(pp.191-234) Palgrave Macmillan.

[1] Best articulated in George Williams 1966 classic, *Adaptation and Natural Selection*, and in Richard Dawkins' 1982 *The Extended Phenotype*

[2] Cosmides & Tooby, 1981

[3] See discussion in Delton, Krasnow, Cosmides & Tooby, 2010

[4 See, Delton et al, 2010



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There is much to disagree with in Steven Pinker's essay. We focus on two important misconceptions that lie at the heart of his argument.

The first misconception is his claim that it is always a mistake to think of function or design at the level of groups. This flies in the face of more than 150 years of thinking in biology. The many examples of intragenomic conflict leave no doubt that there is selection acting on genes within organisms, and this sometimes reduces the fitness of individuals carrying those genes. However, this does not mean that we should abandon the notion of function at the level of individuals. We teach our students in physical anthropology that we can understand the design of the human pelvis by asking how the shape of the pelvis affects the energetics of bipedal locomotion. From the gene's point of view, this is group function. Variation at hundreds (or maybe thousands) of genetic loci affect variation in the anatomy of the pelvis, but their action is coordinated by selection to create function at the level of the individual. Ever since Darwin, physiologists, morphologists, and behaviorists have made much progress using individual functionalist thinking to provide causal explanations for the diversity of life-forms.

The same goes for the function of some kinds of social groups. Just as there is intragenomic conflict within individuals, there is also conflict among individuals within social insect colonies. For example, worker bees sometimes lay unfertilized eggs that develop into male reproductives, while other workers police the hive killing such eggs. Despite such conflicts of interest, many attributes of the colony only make sense in terms of group function—the exquisite design of the cooling systems in termite mounds, the

