4 Levels of Selection: An Alternative to Individualism in Biology and the Human Sciences

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Biology and many branches of the human sciences are dominated by an individualistic tradition that treat groups and communities as collections of organisms without themselves having the properties implicit in the word ''organism.'' In biology, the individualistic tradition achieves generality only by defining self-interest as ''anything that evolves by natural selection.'' A more meaningful definition of self-interest shows that natural selection operates on a hierarchy of units from genetic elements to multispecies communities, and that a unit becomes organismic to the degree that natural selection operates at the level of that unit. I review levels-of-selection theory in biology and sketch a parallel argument for the human sciences.

Introduction

The related concepts of adaptation, function, intention and purpose are central to both biology and the human sciences. Natural selection endows species with the functional design required to survive and reproduce in their environments. Humans organize their behavior to achieve various proximate goals in their everyday lives.

Biology and the human sciences also share a controversy over the units that can be said to have the properties of adaptation, function, intention, and purpose. Almost everyone would grant these properties to individuals, but some biologists also speak of social groups and multi-species communities as if they were single purposeful organisms. Similarly, some psychologists, anthropologists, and sociologists speak of culture and society as superorganisms in which individuals are mere cells.

In recent decades the hierarchical view of functional organization has fallen on hard times. Larger entities are regarded as mere collections of organisms, without themselves having the properties of organisms. In biology the reductionistic trend has proceeded so far that even individuals are sometimes treated as upper units of the hierarchy, mere collections of ''selfish'' genes (Dawkins 1976, 1982). The human sciences are more heterogeneous, but many of its branches appear to be dominated by the individualistic view.

Despite its widespread acceptance, the case for individualism as a general prediction that emerges from evolutionary theory, or as a general principle to explain human behavior, actually is very frail. In this chapter I will describe why functional organization in nature is necessarily hierarchical and then will attempt to sketch a parallel argument for the human sciences.

The Evolution of Altruism

In biology, the debate over units of adaptation has centered on the evolution of seemingly altruistic behaviors that benefit others at the expense of the self. Consider a population of N individuals. Two types exist, A and S, in proportions p and $(1 - p)$, respectively. Each A-type expresses a behavior toward a single recipient, chosen at random from the population. As a result, the recipient has an additional number b of offspring while the altruist has c fewer offspring. The average number of offspring, W, can then be calculated for each type.

$$W_A = X - c + b(Np - 1)/(N - 1), \qquad W_S = X + bNp/(N - 1) \qquad (1)$$

X is the number of offspring in the absence of altruistic behaviors, and is the same for both types. In addition to the cost of being an altruist, each A-type can serve as a recipient to the $(Np - 1)$ other altruists who are distributing their benefits among $(N - 1)$ individuals in the group. Selfish S-types have no cost of altruism and can serve as recipients to all Np altruists in the group. S-types have more offspring than A-types whenever $W_S > W_A$, which reduces to the inequality.

$$b/(N - 1) > -c. \qquad (2)$$

This inequality always holds, because b, c, and N are positive numbers and N is greater than 1. Thus, selfish types always have more offspring than altruistic types. To the degree that the behaviors are heritable, selfish types will be found at a greater frequency in the next generation.

A numerical example is shown in table 4.1, in which $N = 100$, $p = 0.5$, $X = 10$, $b = 5$, and $c = 1$. Thus, the altruist bestows an additional 5 offspring on the recipient at a cost of 1 offspring to itself. The average altruist has 11.47 offspring, while the average selfish type has 12.53 offspring. Assume that the types reproduce asexually, such that the offspring exactly resemble the parents. The proportion of altruists among the progeny is then $p' = 0.478$, a decline from the parental value of $p = 0.5$. Since populations cannot grow to infinity, we also assume that mortality occurs equally among the A- and S-types, returning the population to a density of $N = 100$. At this point we expect approximately 52 selfish and 48 altruistic types. If this procedure is iterated many times, representing natural selection acting over many generations, the A-types continue to decline in frequency and ultimately become extinct.

Table 4.1
Evolution in a single population

$N = 100$, $p = 0.5$, $X = 10$, $b = 5$, $c = 1$
$W_A = X - c + b(Np - 1)/(N - 1) = 10 - 1 + 49(5)/99 = 11.47$
$W_S = X + bNp/(N - 1) = 10 + 50(5)/99 = 12.53$
$N' = N(pW_A + (1 - p)W_S) = 100(0.5(11.47) + 0.5(12.53)) = 1200$
$p' = NpW_A/N' = 100(0.5)(11.47)/1200 = 0.478$

Note: The altruistic type declines from a frequency of $p = 0.5$ before selection to a frequency of $p' = 0.478$ after selection.

This is the paradox that makes altruism such a fascinating subject for evolutionary biologists. As humans we would like to think that altruism can evolve, as biologists we see animal behaviors that appear altruistic in nature, yet almost by definition it appears that natural selection will act against them. This is the sense in which evolution appears to be an inherently selfish theory.

The paradox, however, can be resolved by a simple alteration of the model. Table 4.2 differs from table 4.1 in only two respects: (1) we now have two groups instead of one; and (2) the groups have different proportions of altruistic and selfish types. Looking at each group separately, we reach the same conclusion as for table 4.1; selfish types have more offspring than altruistic types. Adding the individuals from both groups together, however, we get the opposite answer: altruistic types have more offspring than selfish types.[1]

What has happened to produce this interesting (and for many people counterintuitive) result? First, there must be more than one group; there must be a *population of groups*. Second, the groups cannot all have the same proportion of altruistic types, for then the results would not differ from a single group. The groups must *vary* in the proportion of altruistic types. Third, there must be a direct relationship between the proportion of altruists and the total number of offspring produced by the group; groups of altruists must be *more fit* than groups without altruists. These are the necessary conditions for the evolution of altruism in the elaborated model. To be sufficient, the differential fitness of groups—the force favoring the altruists—must be great enough to counter the differential fitness of individuals within groups—the force favoring the selfish types.

Readers familiar with evolutionary theory immediately will recognize a similarity between the above conditions and Darwin's original theory of natural selection, which requires a *population of individuals*, that *vary* in their genetic composition, with some variants *more fit* than others. Thus, natural selection can operate simultaneously at more than one level. Individual selection promotes the fitness of individuals relative to others in the same group. Group selection promotes the fitness of groups, relative to

Table 4.2
Evolution in two groups that differ in the proportion of the altruistic type

Group 1	Group 2
$N_1 = 100$, $p_1 = 0.2$	$N_2 = 100$, $p_2 = 0.8$
$W_A = 10 - 1 + 19(5)/99 = 9.96$	$W_A = 10 - 1 + 79(5)/99 = 12.99$
$W_S = 10 + 20(5)/99 = 11.01$	$W_S = 10 + 80(5)/99 = 14.04$
$N_1' = 1080$	$n_2' = 1320$
$p_1' = 0.184$	$p_2' = 0.787$
Global population	
$N = 200$, $P = 0.5$	
$N' = N_1' + N_2' = 2400$	
$P' = (N_1'p_1' + N_2'p_2')/(N_1' + N_2') = 0.516$	

Note: Values for X, b, c and the functions for W_A and W_S are provided in Table 1. The altruistic type declines in frequency within each group (compare p_1' with p_1 and p_2' with p_2) but increases in frequency when both groups are considered together (compare P' with P). This is because group 2, with the most altruists, is more productive than group 1 (compare N_2' with N_1').

other groups in the global population. These levels of selection are not always in conflict. A single behavior can benefit both the individual performing it and others in the group. Altruistic behaviors by definition are costly to self and beneficial to others, however, and so are favored by group selection and disfavored by individual selection.

This simple numerical example shows that the process of natural selection does not inevitably evolve selfish behaviors. A notion of *group-interest* must be added to the notion of *self-interest*, to the extent that group selection is important in nature.

Valid Individualism and Cheap Individualism

Let us now consider the individualistic claim that "virtually all adaptations evolve by individual selection." If by individual selection we mean within-group selection, we are saying that A-types virtually never evolve in nature, that we should observe only S-types. This is a meaningful statement because it identifies a set of traits that conceivably could evolve, but does not, because between-group selection is invariably weak compared to within-group selection. Let us call this *valid individualism*.

There is, however, another way to calculate fitness in the two-group model that leads to another definition of individual selection. Instead of separately considering evolution within groups and the differential fitness of groups, we can directly average the fitness of A- and S-types across all groups. Thus, the 2 A-types in groups one have 9.96 offspring and the 8 A-types in group two have 12.99 offspring, for an average fitness of $0.2(9.96) + 0.8(12.99) = 12.38$. The 8 S-types in group one have 11.01 offspring

and the 2 *S*-types in group two have 14.04 offspring, for an average fitness of $0.8(11.01) + 0.2(14.04) = 11.62$. The average *A*-type individual is more fit then the average *S*-type individual, which is merely another way of saying that it evolves.

Let us now return to the individualistic claim that ''virtually all adaptations evolve by individual selection.'' If by individual selection we mean the fitness of individuals averaged across all groups, we have said nothing at all. Since this definition includes both within- and between-group selection, it makes ''individual selection'' synonymous with ''whatever evolves,'' including either *S*-types or A-types. It does not identify any set of traits that conceivably could evolve but does not. Let us therefore call it *cheap individualism*.

Cheap individualism is so meaningless that no one would explicitly endorse it. Even the most ardent individualists, such as G. C. Williams (1966, 1985), R. Dawkins (1976, 1982), and J. Maynard Smith (1987), believe that there is something outside individual selection called group selection that in principle can evolve altruistic traits. Nevertheless, the history of individual selection from 1960 to the present has been a slow slide from valid individualism to cheap individualism. Before documenting this claim it is necessary to review three reasons why the slide could occur unnoticed.

First, group-structured population models such as the one described above can be applied to an enormous range of biological phenomena. The single groups can be isolated demes that persist for many generations, groups of parasites interacting within single hosts, clusters of caterpillars interacting on a single leaf, or coalitions of baboons that behaviorally segregate within a larger troop. The groups can be communities whose members are separate species, social units whose members are conspecifics, or even single organisms whose ''members'' are genes of cell lineages (Crow 1979; Cosmides and Tooby 1981; Buss 1987). Historically, however, the first group selection models focused on a particular conception of isolated demes that persist for many generations. Thus, it has been possible for biologists studying other kinds of groups to assume that they are not invoking group selection, when in fact their models are miniature versions of traditional group selection models.

Second, many biologists today regard group selection as a heretical concept that was discarded twenty years ago and consider their own work to be entirely within the grand tradition of ''individual selection.'' Gould (1982:xv) remembers ''the hooting dismissal of Wynne-Edwards and group selection in any form during the late 1960's and most of the 1970's,'' and even today graduate students tell me how difficult it is for them to think about group selection in a positive light after being taught in their courses that it ''just doesn't happen.'' The vast majority of authors who claim that such-and-such evolves by individual selection do not even include an explicit model of group selection to serve as a possible alternative. Individual selection truly has become the modern synonym for ''everything that evolves in my model,'' and group

selection is mentioned only as a bogey man in the introduction or the conclusion of the paper.

Third, averaging the fitness of individual types across groups is a useful, intuitively reasonable procedure that correctly predicts the outcome of natural selection. Biologists commonly average the fitness of types across a range of physical environments, and it seems reasonable to average across social environments in the same way. I emphasize that there is nothing wrong with this procedure—it merely cannot be used to define individual selection because it leaves nothing outside of it.

Now I must document my claim that individualism in biology achieves generality only by averaging the fitness of individuals across groups.

Three Examples of Cheap Individualism in Biology

The Evolution of Avirulence in Parasites and Diseases

Disease organisms provide an excellent real-world example of a group-structured population similar to the model outlined above. Each infected host comprises an isolated group of disease organisms, which compete with other groups to infect new hosts. Natural selection within single hosts is expected to favor strains with high growth rates. Excessively high growth rates tend to kill the host, however, driving the entire group of disease organisms extinct (assuming that transmission requires the host to be alive). Avirulent strains therefore can be envisioned as "altruists" that increase the survival of entire groups, but which nevertheless decline in frequency within every group containing more virulent strains. Lewontin (1970) was the first to recognize that avirulence evolves by between-group selection, and the process has been well documented in a *myxoma* virus that was introduced into Australia to control the European rabbit (Fenner and Ratcliffe 1965). Nevertheless, consider the following account in the first edition of Futuyma's (1979:455) textbook *Evolutionary Biology*:

In many interactions the exploiter cannot evolve to be avirulent; it profits a fox nothing to spare the hare. But if the fitness of an individual parasite or its offspring is lowered by the death of its host, avirulence is advantageous. The *myxoma* virus, introduced into Australia to control European rabbits, at first caused immense mortality. But within a few years mortality levels were lower, both because the rabbits had evolved resistance and because the virus had evolved to be less lethal.... Because the virus is transmitted by mosquitoes that feed only on living rabbits, *virulent virus genotypes are less likely to spread than benign genotypes* [italics mine]. Avirulence evolves not to assure a stable future supply of hosts, but to benefit individual parasites.

Thus, by the simple procedure of comparing the fitness of virulent and avirulent types across all hosts (see italicized portion of text), rather than within single hosts, the evolution of avirulence can be made to appear an individualistic process. Futuyma, incidently, is sympathetic to the concept of group selection and properly attrib-

utes avirulence to between-group selection in the second edition of his textbook (1986:496–497). This example of cheap individualism therefore is inadvertent, and shows how easily selection at multiple levels can be represented as occurring entirely at the lowest level.

Inclusive Fitness Theory

Within the individualistic tradition in biology, natural selection is widely thought to maximize a property called inclusive fitness, which is the sum of an individual's effects on the fitness of others multiplied by the probability that the others will share the genes causing the behavior. As Hamilton (1963:354–355) originally put it:

Despite the principle of "survival of the fittest" the ultimate criterion which determines whether G [an altruistic allele] will spread is not whether the behavior is to the benefit of the behavior but whether it is to the benefit of the gene G; and this will be the case if the average net result of the behavior is to add to the gene-pool a handful of genes containing G in higher concentration than does the gene-pool itself. With altruism this will happen only if the affected individual is a relative of the altruist, therefore having an increased chance of carrying the gene, and if the advantage conferred is large enough compared to the personal disadvantage to offset the regression, or "dilution," of the altruist's genotype in the relative in question.

In this formulation, individuals evolve to maximize the fitness of "their genes" relative to other genes in the population, regardless of whether "their genes" are located in children, siblings, cousins, parents, and so on. Aid-giving toward relatives therefore ceases to appear altruistic, and becomes part of an individual's "selfish" strategy to maximize its inclusive fitness. Even sterility and death can be inclusive fitness maximizing if the positive effects on relatives are sufficiently great.

Let us pursue this idea by considering an Aa female who mates with an aa male and produces a clutch of ten offspring, five of whom are Aa and the other five aa. The dominant allele A codes for an altruistic behavior that is expressed only toward siblings. The sibling group therefore is equally divided between altruists and nonaltruists, and the fitness of the two genotypes from equation (1) is

$$W_{Aa} = X - c + b(4/9), \qquad W_{aa} = X + b(5/9).$$

The selfish aa genotype is inevitably most fit, which merely reiterates the general conclusion obtained [previously] for evolution in all single groups. The fact that the group in this case consists of full siblings is irrelevant to the conclusion. To see how altruism expressed toward siblings evolves, we must consider a large number of family groups, initiated by all combinations of parental genotypes $-$AA $\times$ AA, AA $\times$ Aa, Aa $\times$ Aa, AA $\times$ aa, Aa $\times$ aa, aa $\times$ aa. Within-group selection favors the selfish a-allele in all groups containing both altruistic and selfish genotypes. The fitness of entire sibling groups, however, is directly proportional to the frequency of altruistic A-alleles in the group.

Thus, Hamilton's conclusions cannot be reached without combining within-group selection and between-group selection into a single measure of "inclusive fitness."

The idea that aid-giving toward relatives is a form of "true" altruism that requires between-group selection has been reached by many authors (reviewed in Wilson 1983). Nevertheless, evolutionists within the individualistic tradition continue to use inclusive fitness theory as their guiding light to explain the evolution of "apparently" altruistic behaviors, "without invoking group selection." This is cheap individualism.

Diploid Population Genetics and Evolutionary Game Theory

My final example involves a comparison between two seemingly different bodies of theory in evolutionary biology. Diploid population genetics models begin with a population of gametic types (A, a) which combine into pairs to form diploid genotypes (AA, Aa, aa). Selection usually is assumed to occur in the diploid stage, after which the genotypes dissociate back into gametes and the process is reiterated. The most common way for selection to occur in these models is for some genotypes to survive and reproduce better than others, the standard process of between-individual selection. In addition, however, it is possible for some alleles to survive and reproduce better than others *within single individuals*. For example, the rules of meiosis usually cause the two chromosome sets to be equally represented in the gametes. Some alleles manage to break the rules of meiosis, however, biasing their own transmission into the sperm and eggs of heterozygotes. The differential fitness of alleles within heterozygotes is termed meiotic drive, and can cause the evolution of genes that have neutral or even deleterious effects on the fitness of individuals (Crow 1979; Cosmides and Tooby 1981). In short, diploid population genetics models are explicitly hierarchical by recognizing the existence of both between- and within-individual selection.

Evolutionary game theory (also called ESS theory for "evolutionarily stable strategy") begins with a population of individual types (A, a) that combine into groups of size N for purposes of interaction. Selection occurs during the grouped stage, after which the groups dissociate back into individuals and the process is reiterated. Usually $N = 2$, which yields three types of groups (AA, Aa, aa). ESS theory was borrowed directly from economic game theory (Maynard Smith and Price 1973; Maynard Smith 1982) but the two are not identical. In particular, economic game theory assumes that the players are rational actors trying to maximize their (absolute) payoff, while ESS theory assumes that natural selection will favor the strategy that delivers the highest payoff relative to other competing strategies in the population.

It should be obvious that the population structure of genes combining into individuals in a diploid model is identical to the population structure of individuals combining into groups of $N = 2$ in an ESS model. Similarly, natural selection in an ESS model can happen in two ways: groups can outperform other groups or individuals can outperform other individuals within groups. In the familiar hawk-dove model, for exam-

ple, dove-dove groups (in which resources are equitably shared) are more fit than hawk-hawk groups (in which resources are contested), while hawks are more fit than doves within hawk-dove groups. To be consistent with population genetics models we should say that hawks are favored by within-group selection and doves by between-group selection. ESS theorists, however, average the fitness of individual types across groups and call everything that evolves the product of "individual selection." The term "between-group selection" is never used, and Maynard Smith actually borrowed game theory from economics as an alternative to group selection (Maynard Smith and Price 1973; Maynard Smith 1982). As Dawkins (1980:360) puts it: "There is a common misconception that cooperation within a group at a given level of organization must come about through selection between groups. . . . ESS theory provides a more parsimonious alternative." This one passage provides all the elements of cheap individualism: the fitness of individuals is averaged across groups, everything that evolves is called the product of individual selection, and something else is called group selection, outside the model and completely unspecified, except to say that it need not be invoked.

These three examples show that, despite its widespread acceptance, individualism in biology is on very thin ice. Self-interest defined as "whatever evolves" is meaningless, and yet when self-interest is defined more meaningfully as "within-group selection" it cannot claim to explain everything that evolves in nature. We must therefore accept a hierarchical view of evolution in which the properties of functional organization implicit in the word "organism" need not be restricted to individuals. The differential fitness of genetic elements within individuals ushers us into a bizarre world in which the genetic elements are the purposeful organisms and individuals are mere collections of quarreling genes, the way we usually think of groups. The differential fitness of individuals within groups ushers us into a familiar world in which groups are mere collections of purposeful individuals. The differential fitness of groups ushers us into another bizarre world (for individualists) in which the groups are the organisms whose properties are caused by individuals acting in a coordinated fashion, the way we usually think of genes and the organs they code for. See Wilson and Sober (1989) for a more detailed review of levels-of-selection theory in biology.

A Parallel Argument for the Human Sciences

If human behavior is measured against the dual standard of effects on self and effects on others, it appears to show the full range of potential. Individuals have sacrificed their lives for the benefit of others, and they have sacrificed the lives of others for their own trivial gain. Viewed at the society level, some human groups are so well coordinated that they invite comparison to single organisms, while others show all the disorganization of a bar-room brawl.

Humans also are frequently embedded in a complex network of interactions in which single expressions of a behavior affect the actor and a relatively small number of associates. Put another way, human populations are subdivided into clusters of associates similar to the local populations of the evolutionary models outlined above. It seems possible that a theory of human behavior in social networks could be developed that parallels levels-of-selection theory in biology, leading to a similar hierarchical view of functional organization in human affairs.

As with any theory of human behavior, the first step is to specify the rules that cause people to choose among alternative behaviors, which serve as the analog of natural selection in an evolutionary model. Following Axelrod and others (Axelrod and Hamilton 1981; Brown et al. 1982; Pollock 1988), assume that humans adopt behaviors that maximize a given utility, relative to competing behaviors in the population. The utility might be pleasure (to a psychologist), annual income (to an economist), or genetic fitness (to a sociobiologist). The details of the utility are relatively unimportant because the hallmark of a hierarchical model is not the nature of the utility but the way it is partitioned into within- and between-group components. Consider, for example, a behavior that decreases the utility of self and increases the utility of others. If others include the entire population, then the utility of those expressing the behavior will be lower than those that do not, and the behavior will be rejected precisely as it is selected against in the one-group evolutionary model. Now assume that the human population is subdivided into a mosaic of associates in which the expression of behavior is non-random; some groups of associates behave primarily one way, other groups the other way. The utility of the behaviors now depends on the frame of comparison. The behavior fares poorly in all groups in which the alternative behavior is expressed, but may still deliver the highest utility when averaged across all groups, exactly as in the multi-group evolutionary model. Adoption of the behavior therefore depends on two factors, the effect on self and others and the interaction structure within which the behavior is embedded.

Theories of behavior in the human sciences frequently consider both factors but combine them into an overarching definition of self-interest as ''utility-maximizing behavior''—i.e., all behaviors adopted by rational humans! This is cheap individualism, that achieves generality only by definitional fiat. Levels-of-selection theory keeps the factors separate, defining behaviors as self-interested when they increase relative utility within single groups, and group-interested when they increase the average utility of groups, relative to other groups. This provides a framework in which rational (utility maximizing) humans need not be self-interested by definition.

As for the situation in biology, many human behaviors that are catagorized as selfish by cheap individualism emerge as ''groupish'' in a levels-of-selection model.[2] The concept of morality, for example, involves rules of conduct that promote the common

good. This implies a category of immoral behaviors—frequently termed "selfish" in everyday language—that benefit individuals at the expense of the common good. Since moral behaviors are vulnerable to exploitation, they succeed only if they can be segregated from the expression of immoral behaviors. This is nicely illustrated by the following passage from a seventeenth-century Hutterite document (English translation in Ehrenpreis 1978:67):

The bond of love is kept pure and intact by the correction of the Holy Spirit. People who are burdened with vices that spread and corrupt can have no part in it. This harmonious fellowship excludes any who are not part of the unanimous spirit. . . . If a man hardens himself in rebellion, the extreme step of separation is unavoidable. Otherwise the whole community would be dragged into his sin and become party to it. . . . The Apostle Paul therefore says "Drive out the wicked person from among you."

The maintenance of behaviorally pure groups allowed the Hutterites to practice such extreme altruism that their communities are best regarded as the human equivalent of a bee colony (a metaphor that they themselves used to describe themselves). More generally, human societies everywhere possess mechanisms for segregating behaviors, allowing less extreme forms of morally acceptable behavior to be successful. The distinction between moral and immoral behavior, and the mechanisms whereby both can be advantageous, correspond nicely to "groupish" and "selfish" behaviors in a levels-of-selection model. In contrast, cheap individualism is placed in the awkward situation of defining both moral and immoral behavior as brands of self-interest.

Many authors have expressed the idea that higher entities such as biological communities and human societies can be organisms in their own right. Unfortunately, the idea usually is stated as a poetic metaphor or as an axiom that is not subject to disproof. Levels-of-selection theory shows that single-species groups and multispecies communities can become functionally organized by the exact same process of between-unit selection that causes the groups of genes known as individuals to become functionally organized. For the first time, the hierarchical view in biology now enjoys a solid mechanistic foundation. Perhaps this foundation also will be useful within the human sciences to show how people sometimes coalesce into society-level organisms.

Notes

1. Adding the contents of both groups is justified biologically only if the occupants of the groups physically mix during a dispersal stage or compete for the colonization of new groups. See Wilson (1977, 1980, 1983) for a more detailed discussion of the nature of groups in levels-of-selection models.

2. Both cheap individualism and levels-of-selection models define their terms on the basis of utilities, which do not translate easily into psychological definitions of altruism and selfishness based on internal motivation. In outlining his economic theory of human behavior, Becker (1976:7) states that it does not matter how people actually feel or think about what they do as long as the end result of their behavior is utility maximizing. In the same way, behaviors categorized as group interested in a levels-of-selection model do not imply that the actor is internally motivated to help others. This does not mean that psychological definitions of altruism are irrelevant, but only that their relationship with definitions based on utility are complex. I hope to explore the complexities in a future paper.

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