

## Book Review

### The Challenge of Human Social Behavior

A review essay stimulated by Hammerstein, Peter (Ed.) 2003. *Genetic and Cultural Evolution of Cooperation*. Cambridge, Massachusetts, and London, England: MIT Press.

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This 23-chapter, 485-page, 40-author Dahlem Conference volume focuses on the nature and effects of cooperation across the entire spectrum of life – cooperation among genes, cells, individuals, and groups of individuals. The authors – about half biologists and half social scientists – represent a small group of investigators engaged in an important and difficult task. They are testing the question whether all of the social activities of humans can be accounted for by the process of organic evolution – by the history of natural, sexual, and social selection. To the extent that we wish to understand what we humans do, we must also understand why we do those things.

One dimension of understanding the why has to explain how our social activities contribute to the reproduction of our genetic materials, the only process that has any possibility of explaining why particular forms of life, and their particular traits, or behavioral repertoires, continue to be represented today. The focus on culture is partly because the cultural behavior of humans seems most likely to call into question the hypothesis that, except for (1) accidents involving rapid changes to novel situations and (2) incidental or pleiotropic gene effects, traits of organisms persist and become elaborate only when they serve the genetic reproduction of the individuals displaying them. The focus on cooperation is because the participants in this Dahlem Conference want to find out if all social beneficence – costly or "altruistic" investment in others – can be explained in evolutionary terms. Cooperative human cultural behavior that is learned and involves costly investment may be regarded as the most likely potential falsifier of the hypothesis that everything about life is somehow a consequence or a byproduct of adaptation via differential reproduction during the process of organic evolution in the environments of history.

Because group-living carries with it automatic costs owing to resource competition among individuals in close proximity (Alexander, 1974), the question becomes: Is cooperation always a form of competition? Is generosity and congeniality always but one side of the "coin," the other side being competition between groups that are congenial within themselves? In our species this question is particularly

disturbing because it is possible that we alone may have as our principal “hostile force of nature” (our principal competitor and predator) other groups within our own species. This amity-enmity proclivity can be taken as not only a startling “original sin” metaphor, but as the most important background of the problem of attempting to reduce pain, misery, and suffering, and intentional shortening of human lifetimes around the globe. The size of the problem can be glimpsed by the *National Geographic's* recent (Jan. 2006, p. 30) review of 48 instances of mass murder during the 20th century, totalling 50 million premature deaths (murders of single individuals and small groups are not included). With regard to immediacy, the question for this evolutionary biologist seems to be whether acknowledging and utilizing an approach that primarily takes into account deep knowledge of the cumulative effects of our history of differential reproduction can reduce aggressive and anti-social behaviors by starting with studies of behavior itself, rather than having to struggle across, say, decades until molecular, physiological, and developmental biology – and archaeological, paleontological, and phylogenetic studies – have provided sufficient information about complex sequences of causation to yield the broad behavioral answers we require.

Including studies of cooperative behaviors of non human species, and of molecules and cells, is of course an essential part of the best method of exploring every possibility in the effort to discover how all aspects and systems of cooperation and competition work. The range of recent studies encompassed in the volume is impressive. As Robert Trivers said in his review in *Science*, “. . . if you want a very broad view of the subject, treated in some depth, this [volume] is your baby.”

These authors are for the most part a long way from the people studying cooperativeness in culture 55 years ago, when University of Michigan cultural anthropologist Leslie White wrote in *The Science of Culture* that to expect an anthropologist to see pattern in his own culture is like expecting a fish to discover water. White saw culture “. . . as a thing *sui generis*, as a class of events and processes that behaves only in terms of its own principles and laws and which consequently can be explained only in terms of its own elements and processes. Culture may thus be considered as a self-contained, self-determined process; one that can be explained only in terms of itself.” There is a thread of truth in this statement, and also an apparent error. The apparent error is that culture cannot be explained entirely in terms of itself because its basis is ultimately an outcome of genetic evolution and continues to be guided by differential reproduction, even if in large part via evolved restraints on learning and channeling of learning. The thread of truth in the statement is that culture has elements in how it changes, the speed of its changes, and the forms it takes, that are related to genetic evolution in ways that may possibly be unique, and that we still have not entirely clarified.

The task these contributing authors, and all students of evolution and human behavior, have set for themselves is difficult almost beyond imagination. First, we are required to analyze the very traits we are using to do the analyses. Second, the human species is so distinctive as to severely restrict comparative study that depends on

either homologies or parallelisms and convergences (the latter termed “homoplasies” by modern phylogeneticists). Investigators of humans are all too often restricted, in essence, to an N of one. In the same way that theoretical physicists are restricted in how to explain the only universe available to them at the moment, human behavior theorists are often limited to looking at observable human (evolved) functions and seeing if there are any that don’t fit with the particles or principles of social interactions that we already know about, such as from the “breakthrough” innovative theories of people like George C. Williams, William D. Hamilton, and Robert L. Trivers, in recent work most notably between 1967 and 1982.

Third, as some of those writing in this volume have noted, a good deal of what we humans do socially is not a part of our own conscious understanding. Indeed, much of it has apparently been kept out of the conscious by evolutionary selection, and on that account may be even more difficult to study (and easier to reject) than parallel functions in non-human species. This difficulty exists partly because we are evidently evolved to deny that we have evolved to be genetically self-serving, this in turn at least partly because in social situations such denials contribute to our actually being self-serving through their effects on how at least some of our associates view us.

Fourth, a growing number of biological and social scientists are testing the hypothesis that the nature and complexity of the human brain is largely a consequence of its design as a social tool, explicitly to deal with other members of the human species. The intensity of the necessary selection, and the accompanying complexity of ontogeny or development, can be glimpsed by a few of the more (or less) confident estimates that one can hear bandied about today: some 30 billion neurons of 200 different kinds in the cortex of the human brain; a million billion connections among those 30 billion neurons; up to ten billion neuronal interactions taking place in the human brain during less than a second. The effects of these numbers are surely multiplied almost indefinitely by the way the external environment influences behavioral possibilities the organism generates cumulatively as a result of prior extrinsic (environmental) effects – in humans across maximum average lifetimes of 85-100 years. The most dauntingly complex extrinsic effects – the ones responsible for the evolution of the uniquely complex human brain – are the streams of consequences from competitive and adversarial versions of parallel and equally complex internal events taking place within other human individuals. They require responses by individuals and by cooperative groups of individuals at every level of social organization, from the fractional assessments of the consequences of investment in individuals of partial genetic relatedness to directly and indirectly reciprocal interactions in groups, now including nations of up to more than a billion individuals, and even alliances of such nations. The only likely background for this “runaway” expansion of cooperative groups, and their outlandish brains, may be the existence of other competitive human groups because they alone can never be left more than a step behind (Alexander 1971, 1979).

Of course the prodigious task of self-analysis that these authors have set for

themselves is the same task that armies of philosophers, social scientists, and other humanistic thinkers have pursued across all of recent human history. But the investigators represented in this volume differ from these armies of the past in knowing that, barring truly dramatic new findings, to accomplish this most difficult of all tasks requires that whatever is worked out must somehow be compatible with the evolutionary process – with natural selection and differential reproduction. This is why biological and social scientists not only investigate pattern changes in the hominid line across time via fossils and environmental history, and employ the extreme reductionism of nanotechnology and molecular biology, but as well try to understand the whole modern human organism through a deep knowledge of the evolutionary process.

The project set out in this book calls for understanding along multiple axes of behavioral expression: deliberate and not deliberate, conscious and not conscious, and known to be learned and not known to be learned. We cannot yet say that any behavior is known not to be learned, partly because our definitions of learning are not yet sufficiently precise, and partly because we know so very little about (1) ontogenetic or developmental processes, both in general and with regard to specific behaviors, (2) the cumulative effects of long-term genetic change (evolution), and (3) cumulative learning changes (cultural change) – and how these forms of change act and interact. We know too little about how non conscious and non deliberate acts underlie and influence conscious intent, and vice versa. This is so partly because questions about human social actions have so infrequently been asked in the context of evolutionary functions.

It would seem obvious, then, that whoever seeks to set any bit of human behavior into an evolutionary context that makes complete sense had better be extraordinarily good at detecting every possible avenue of cost and benefit to reproduction from every possible social act of humanity. Analyses that fail in this respect necessarily fail in their conclusions. Even if we are properly sympathetic about the difficulty of the tasks the investigators represented in this volume have chosen, we are not likely to be forgiving when everyday causes and effects are not taken into account, or are interpreted incompletely. If we say that something humans do is not compatible with evolution because we missed something, the error is not trivial.

Only persistence ultimately counts in evolution, and only the stable and duplicative process of reproduction characteristic of the genetic materials results in persistence. Short-lived genomes and the short-lived individuals that result from them are the agents of the genes' persistence, and they are as specialized to this task as the genes are to the task of persistence. Accordingly, no matter how distasteful it may seem, every investigator of human behavior who wishes to understand human social behavior is required, at the very least, to test to the last detail for evidence of genetically self-serving function in every human action.

In such light, it is a virtual certainty that some tests of human social behavior will appear – at first – to yield results contrary to evolution, or unexplainable by it.

Perhaps nothing any kind of scientific investigator does is more likely to be inadequate than the designing and interpretation of some of the experiments necessary to account for human social behavior. We have not necessarily evolved to detect every possible avenue of beneficent returns – only to conduct our social behavior appropriate to such returns with or without complete awareness.

When an observed behavior appears unexplainable in light of current evolutionary models, our first effort should be to make absolutely certain that this appearance is not being misinterpreted, that the behavior is indeed unexplainable by those existing models. As George Williams once noted, if your pickup truck does not start, you don't generally feel it necessary to start doubting the fundamental laws of physics. In such a spirit I have developed this rather narrowly focused review as if it were an effort to falsify every implication in this volume that existing concepts – such as kin help and investments in direct and indirect social reciprocity – cannot explain all of the cooperative human social behavior discussed in the volume.

### **The Meaning of the Book's Theme**

I am initially uneasy about the approach suggested by the title of the volume, “Genetic and Cultural Evolution of Cooperation,” which may imply that non cultural behaviors are “genetic” and cultural behaviors are “non genetic”; that the two are separate rather than part of the same process; that there is no connection between them; that environments and phenotype, and processes like learning, may not be involved in genetic evolution. Even if we have not previously understood the nature of the connections between genes and environment, it is too easy, from such an impression, to forget that all behaviors – indeed, by definition, all aspects of the phenotype – are neither entirely “genetic” nor entirely “environmental.” Directions and patterns of cultural change are not independent of the (overall) genetic makeup of humans, and sometimes may either include or result in some genetic change. Although some discussions of learning in this volume are sophisticated and seem to be on target (e.g., Henrich et al, pp. 448-451), others raise questions of the sort implied by the nature of the book title (e.g., Hammerstein, p 5; Richerson et al p. 366, 381).

Flinn and Alexander (1982) detailed four reasons for believing that “. . . the culture-biology [or culture-genetic] dichotomy derives from continued misunderstanding and misstatement of certain aspects of biological theory.” I will add to them here, and state them somewhat differently:

1. Fear that to admit an influence of genes on behavior will lead to genetic determinism.
2. Belief that learned behavior – and by extension, culture -- has no connection to genes.
3. Fear that accepting a potency for individual level selection suggests justification for selfish behavior.

4. Belief that cooperative and conciliatory behavior contradicts the notion of potent individual-level selection; that if selection can be construed to be most potent at group (“cultural”) levels it automatically becomes a gentle, peaceful process that promotes compassion and good will, and thereby sidesteps the nastiness of competition at the individual level.
5. Failure to understand that such situations as long-term correlations between amounts and kinds of social interactions and relatedness can lead to tendencies and biases in social learning, such as tolerating and assisting close associates, and accepting their advice, because proximity and close association alone can make them likely to be genetic relatives.
6. Failure to take into account that if our apparently unique human ability to treat whole collections of relatives appropriately to their degrees of genetic overlap with us is generated via social learning, then some particular kinds of mistakes are likely, and must be taken into account in assessing whether social experiments are contrary to expectations from evolutionary theory.

One has to wonder if the “genetic and cultural” dichotomy in the title of this volume is intended to refer to genetic change via natural selection *versus* cultural change via learning: that is, natural selection on organisms that lack culture (or selection on traits other than culture) versus the kind of change via cumulative social learning that Dawkins (1976) intended when he spoke of memes as changing independently of their consequences to the organisms using them – i.e., operating as parasites on humans – and that others may intend when they speak of “dual inheritance” models. But genetic change – at least in today’s world – in general proceeds via the (reproductive) improvement of phenotypes (organisms, traits) that result from the interaction of gene effects (via genotypes) with variable environments. Culture is part of the human phenotype, part of the environment within which genes must survive by reproducing, so we must at least begin with the hypothesis that cultural traits differ from other traits primarily in the sense that much of cultural change proceeds via behaviors cumulatively learned from generation to generation. The problem of understanding culture, then, seems to be a matter of focusing on how evolution has biased and guided learning so as to cause directions and rates of changes in learned behaviors, and how cumulative changes in learning contribute to the reproductive success of the individuals comprising the populations that create, exercise, and maintain the patterns of culture (see also sections below on culture and memes).

When humans became able to build scenarios and plan what they were going to do, they completed the feedback between need and novelty that organic evolution had otherwise never been able to accomplish. This feedback is surely critical for understanding the rates and directions of cultural change. Evolutionarily novel environments are like phenotypic mutations because (1) they change the phenotype in the way that genetic mutations change the genotype, thereby influencing the direction of both cultural change and genetic change (most selection, having no access to the

genome, works on the phenotype and affects the genome only indirectly); and (2) especially in non human organisms, evolutionarily novel environments are typically negative in their effects on organisms because their causes (changes in the environment, including the social environment, and also any learning that is well outside the box with respect to favoring the genes that initially created the flexible phenotype) are, like the causes of mutations (primarily atmospheric radiation), independent of the causes of selection – Darwin's Hostile Forces of Nature. But, owing to our ability to build elaborate mental scenarios, humans became capable of creating novel environments that instead have predictably positive effects – for example, dreaming up how to construct a plow or a computer or a theory of relativity (Alexander 1979, 1990a).

The feedback between environmental novelty and phenotypic change (leave aside genetic change for a moment) is, of course, why culture marches on so rapidly and so directionally, and why it tends to accelerate; and it is surely why the brain evolved to become what it is now (taking into account that *socially* significant scenarios were probably the most important ones). In other words, the effect on the evolution of certain traits, such as the brain's capabilities, represents a focusing of genetic evolution as a result of changes in the evolutionary environment induced by the human ability to plan inside the brain in "fruitful" ways; and it is responsible for an itinerary of phenotypic change via cumulative learned-learning piggy-backed on scenario-building and in some regards (or temporarily) "exceeding" or "outrunning" genetic change. In the sense just described, phenotypic changes as a result of environmental changes, including social learning, "lead" both genetic evolution and cultural change (West-Eberhard 2003), and surely do so in humans on a scale that is huge – and more dramatically explanatory of the actual processes involved – than in any other organisms. Compared to the part of cultural change dependent on this feedback, most of the overall genetic change in humans today, affecting social traits – in all the diverse, mobile, and interbreeding human populations in the almost endlessly variable environments across the globe – may be best regarded as a kind of evolutionary fibrillation.

Any change in the phenotype because of a change in the environment will in turn change the direction of selection, therefore the direction of genetic evolution. Humans are the all-too-obvious case because not only does even learning "mutate" the phenotype, changing that aspect of the environment of the genome and the direction of selection, but the transmission of learned behavior by learning creates a parallel to genetic evolution (culture) while also guiding genetic evolution – in this case to produce our most vaunted organ, the social-tool brain.

### **Nepotism and Reciprocity**

The participants in this conference make it clear that they at least begin by recognizing nepotism and reciprocity as the two major kinds of social interactions that facilitate, account for, or comprise culture, therefore including all of human

social cooperation. Nepotism extends from (1) simple direct nepotism to a single class of relatives, requiring only the ability to distinguish relatives and non relatives, or offspring, from all other individuals to (2) extensive differential nepotism, in which multiple classes of relatives are recognized as such and treated appropriately to their relatedness (Hamilton 1964). Extensive differential nepotism may be unique to humans (Alexander 1990b, 1991).

Social reciprocity varies along two central axes: (1) amount of risk (and potential return) involved and (2) directness of returns for beneficence (see also, below). Minimal-risk reciprocity (e.g., the simplest forms of tit-for-tat and parceling) occurs among many non human animals, typically involving immediate and parceled exchanges (Connor, 1992). High risk reciprocity is extensively involved in modern human social behavior, and perhaps only there. Reciprocity can be either direct or indirect (Trivers 1971; Alexander 1987; see below).

Among other things the authors of this volume follow Nowak and Sigmund (1998) in seeking to discover whether differential nepotism and direct and indirect reciprocity are sufficient to explain culture. At least some of them seem to disagree with the conclusions of Nowak and Sigmund that they are sufficient.

### *Nepotism*

The uniquely extensive differential nepotism of humans (kinship systems) accounts for less than two pages in this volume, presumably in part because Hamilton's (1964) papers were believed to provide an adequate basis for understanding its expressions as adaptive. But, as Eric Smith notes in his essay, "What about Kinship?" (p. 422), understanding the details of kinship systems is not so simple. He puzzles because different family groups often cooperate with each other in ways that seem not to reflect closeness of kinship. Among other things, however, kinship cooperation also involves both intermarriage and incest avoidance, which in turn may (but does not necessarily) involve positive intergroup (interfamilial, interclan) interactions. He comments that ". . . kinship is often defined in ways that do not line up well with the calculus of inclusive fitness." This happens partly because (1) kinship *terms* are frequently used for unrelated partners in reciprocity, as in modern urban society; (2) observers from other societies (e.g., anthropologists) are, for various reasons, not always as accurate in assessing kinship as the participants themselves (cf., Alexander 1979); (3) kinship terms are often manipulated, for example to make particular marriages possible (e.g., Chagnon 1981), (4) in-laws, though not technically relatives, are expected to be treated in ways similar to their spouses because the two share interests in the offspring and other descendants they produce together, and (5) because kin recognition that evolves in the context of differential nepotism comes about by social learning, dramatic changes in family structure and other social interactions can result in non-kin being treated as kin and vice versa.

Smith notes that reciprocity becomes confusingly involved with kinship



behavior, especially among distant relatives; that kinship is one of many possible conventions used to define in-groups that compete with out-groups; and that "In effect, unilineal kin groups [which to him seem contrary to kin selection] are a means of forming coalitions to compete with other coalitions." They are also reflections of male dominance (hence, sometimes, patrilinearity and patrilocality) and the importance of cooperativeness within one sex (as when related and unrelated men in patrilocal societies cooperate in hostile encounters with other groups, or related women in matrilocal societies cooperate to work gardens that are inherited matrilineally). Smith's evaluation of kinship systems sometimes parallel the comments of Marshal Sahlins (1965), which I have criticized in detail (Alexander (1977; 1979: pp. 197-202). Rather than casting doubt on the central importance of understanding kinship systems, Smith's observations seem to highlight the importance of (1) knowing the fine details in the makeup of kinship systems, (2) understanding what extrinsic forces mold the cooperativeness of kin and reciprocity groups and thus how the two systems co-mingle, and (3) recognizing that, as with modern societies, cooperative kin groups are changing continually with regard to forces molding unity, rather than remaining in static relations that are simple to understand (see below).

### *Reciprocity*

Social reciprocity is by far the most extensively discussed topic in this volume, and deservedly so. Although it is an ancient concept in the social sciences, reciprocity was first discussed in evolutionary terms by Robert L. Trivers (1971), in one of the most elegant papers in the history of evolutionary biology. The nomenclature of the different forms and expressions of reciprocity, however, may have become confused since Trivers's paper. Perhaps it's worthwhile to return to the original concepts and their labels, especially because social reciprocity is socially learned, therefore modifiable, and because it forms the basis for virtually all of the behaviors on which we must depend to change human behavior so as to reduce the lamentable amount of human pain, misery, and suffering and the enormous number of premature deaths caused either deliberately or through neglect.

Except for variations in riskiness, there are only two basic forms of reciprocity, direct and indirect. A beneficent individual can be reciprocated either directly by the individual helped or indirectly by some other individual or some group. Direct beneficence to others and beneficence as a result of punishing violators of a moral or legal code are both investments in reciprocity. Every other adjective of reciprocity defines a special case of either direct or indirect reciprocity, or of the two in combination.

Trivers referred first to direct reciprocity as "altruistic partnerships" within society. He used the term "generalized reciprocity" to refer to multiparty systems in which altruistic acts are dispensed among more than two individuals, leading to formulation of rules of conduct: "In short, selection may favor the elaboration of

(society-wide) norms of reciprocal conduct.” (p. 52). Trivers also noted that one mechanism for establishing reciprocal relationships “might be the performing of altruistic acts toward strangers, or even enemies, in order to induce friendship.” These comments I see as relevant to arguments about reciprocity made by authors in this volume.

Generalized reciprocity, as Trivers used it, thus refers to multiparty systems that incorporate both direct and indirect reciprocity. I used the adjective “indirect” to avoid confusion with generalized reciprocity, as used by Sahlins (1965) in a way that included investments in relatives with investments in non relatives that do not involve expectations of direct reciprocity (Alexander 1975, 1977, 1979). Indirect reciprocity I defined as “represented by rewards from society at large, or from other than the actual recipient of beneficence” (Alexander 1979, p. 49; 1987, p. 85).

Direct reciprocity, then, is when someone is reciprocated by the person he or she has helped. Indirect reciprocity is all the rest – all the circumstances in which the return for social investment comes from someone(s) other than the assisted party. So far as I can tell, so-called “strong” reciprocity – as discussed in this volume – is, first, not reciprocity at all unless one identifies and describes the returns on social investment, which the authors who use this term typically leave vague and sometimes seem to be denying. Even with the returns included, it seems to be an indicator of the intensity of reciprocity – the willingness of participants in a society-wide system of reciprocity to invest – rather than a “kind” of reciprocity. An evolutionary biologist assumes that there are returns, or the tendency to invest will eventually collapse. Punishment of those who don't invest socially, or who break the rules, can thus be an example of indirect reciprocity whenever it is directly or indirectly in the interests of the punitive person (investor) that those rules not be broken. It is extremely difficult to be certain that no return – actual or legitimately expected – is involved in a human action (or transaction) such as “strong reciprocity” because of (1) the possibility of indirect reciprocity, (2) long-time delays in returns, and (3) what I will call the “insurance factor.” Burnham and Dominic (2005) conclude that strong reciprocity cannot be explained by group selection, kin selection, or reciprocal altruism (see also, below).

Indirect reciprocity occurs not only when one individual helps another and is himself or herself helped later by some other individual(s) because of that initial help. It also occurs whenever anyone does something designed (consciously or unconsciously – i.e., by evolution, directly or indirectly) to save the entire group (some “entire” group, small or large). This kind of investment is adaptive, for example, when the fate of the individual approaches that of the “entire” group: the canoe rushing toward the deadly waterfall; imminent or actual attack by another human group, especially if they are deemed to be bent on genocide; etc. There doesn't have to be any witnessing of the investment, or returns from any specific individual(s). It can all be entirely anonymous because the helping individual is also helping him- or her-self, as is required in reciprocity that persists. Nor does the situation have to be understood consciously. Hence, contrary to virtually all current

usage, effects on the reputation of individual investors are not an essential ingredient in all kinds of indirect reciprocity.

In my 1987 discussion of indirect reciprocity (the most recent and best source for a review of my views on that topic), I said the following: "Returns from indirect reciprocity may take at least three major forms: (1) the beneficent individual may later be engaged in profitable reciprocal interactions by individuals who have observed his behavior in directly reciprocal interactions and judged him to be a potentially rewarding interactant (the 'reputation' or 'status' of the investor is enhanced, to his or her ultimate benefit), (2) the beneficent individual may be rewarded with direct compensation from all or part of the group (such as with money or a medal or social elevation as a hero), and (3) the beneficent individual may be rewarded by simply having the success of the group within which he or she behaved beneficently contribute to the success of his or her own descendants and collateral relatives."

Leaving aside maladaptive accidents or errors, I can think of at least three other possible adaptive (indirect reciprocity) explanations for what some authors in this volume call "one-shot" social investments: (4) the return may be to the beneficent individual's relatives or friends, and the nature of social information spread as a result may be such as to make this kind of return consistent with investment being self-serving; (5) The investment may also be done as part of the individual practicing how to engage in reciprocity adaptively, as with individuals who practice while alone for success in, say, being humorous, or in lecturing, or in developing a useful conscience, or any other social behavior (i.e., as a way of learning how to invest socially in a more rewarding – more profitable – way). This is not reciprocity per se, nor is it evidence of net-cost beneficence; rather, it is investment that in the end functions to improve the individual's later engagement in social reciprocity. In my experience we do this kind of thing all the time, and I regard it as an essential part of knowing how to behave socially in one's own interests. Finally, (6), the investment may be part of an individual's effort explicitly to elevate the general level of reciprocity in society. Thus, generous donations to people affected by a disaster, or efforts to enlist in the armed forces at the onset of war, can have snowballing effects on donations or rates of enlistment that raise the level of social investment generally – and may benefit the individual by various indirect reciprocity returns. Whenever the general level of social investment is raised, all persons had better pay attention and act wisely, or they will be viewed as laggards or self-serving and stingy. It is not necessary, however, that the reputation of any individual contributing to the rise in social investment be involved. Such donations can be entirely anonymous and the donor can still gain, as whenever his or her interests are close to those of the entire group.

General changes in levels of beneficence, or risk-taking with acts of beneficence within a society, if they are adaptive, are adjustments of systems of indirect reciprocity. Anyone who carries out acts that raise the level of beneficence within a society is investing in indirect reciprocity. There may often be huge risks – and frequent losses – involved in individual attempts to change society toward a

greater level of beneficence. But, obviously, there can also be huge benefits, either in the form of rewards directly to the social beneficence pioneer, or to the anonymous pioneer in the particular form of a generally more beneficent society which may (a) increase the likelihood of a healthy persistence of the society harboring the pioneer's circle of kin and/or (b) yield an outright bias of benefits to the kin of the social pioneer. When you cannot move from one group to another, or cannot do so inexpensively, it is virtually a given that your interests will now and then tend to approach those of your group. An obvious example is the sexual genome between the moment of zygote formation and the ultimate death of the resulting individual. Not surprisingly, given the way the meiotic process works to equalize the reproductive likelihoods of all genes, the genes in such a genome tend to cooperate almost completely; the strength of our attention to the trivially few exceptions (e.g., meiotic drive) supports the point. In wholly asexual organisms most conflicts of interests are permanently erased, so that the genome in essence becomes the functional gene (Alexander 1993).

Genic cooperation – within the genome – during the lifetime of the organism was presaged by Theodosius Dobzhansky (1961) in this profound observation, or hypothesis: “Heredity is particulate, but development is unitary. Everything in the organism is the result of the interactions of all genes, subject to the environment to which they are exposed. What genes determine are not characters, but rather the ways in which the developing organism responds to the environment it encounters.” I interpret Dobzhansky’s statement to mean that, contrary to virtually all opinion in biology up to that time, all genes are both pleiotropic and epistatic. Yet none of us would argue that the probably uncountable and presumably unrestricted and uninhibited “social investments” of the genes in the genome are somehow contrary to evolution because there are no easily visible or measurable returns. The returns are realized by individual genes via the success of the genome because of the unity of function of the organism.

In evolutionary analysis, it is wrong to think of reciprocity as altruism, or as done (solely) for the benefit of another. It cannot be (evolved) reciprocity unless on average it serves both parties. Thinking that if someone else is being helped, the act is done "for" that someone else, rather than (in the end) for one's self leads to confusion when someone invests in the survival of a "whole group" that serves the investor by simply surviving, because the act is then seen as egoistic – i.e., the group is being saved because this saves the individual, so reciprocity (beneficence) must not be involved. All evolved beneficence has to be egoistic on average unless it is nepotistic (phenotypic returns are not necessary for beneficence to a relative to be adaptive). Because we have apparently evolved to convince ourselves of something socially useful to us about our motivations does not change the way the evolution of reciprocity proceeds. Thus, to insist that we “care about” a person we are about to help must mean that for some reason we have decided that he or she is a good bet to return our kindnesses with interest (or else the return will be from potential reciprocators or reputation-builders among the observers of our beneficence). The

hypothesis to falsify is that we “care about” persons we help because we stand to gain from helping them, whether or not we think so or admit it – to ourselves or anyone else. The reason for the argument that saving our whole group cannot benefit us (differentially) is likely that we are (erroneously) thinking that “the group” is our only source of competition. But there are always other groups out there – and other competitive individuals – and we cannot continue in competition with them if we have perished with the group we refused to help.

In 1993, I discussed the question of unity of development and function in the organism as follows:

Some traits of organisms are identifiable, or give the appearance of being partially independent, because of the modularity of the selective environment. All such traits, however, cannot be explained in this way. Consider a gasoline engine. [Like the organism it] . . . is designed for a singular function, to create maximum torque at a certain speed [perhaps better, certain combinations of torque and speed] on a particular shaft, the “drive” shaft. Nevertheless, it will have different “traits” just as does the organism: cylinders, pistons, valves, spark producers, distributors, timers, cooling devices, intake and exhaust systems, crankshaft, fuel tank, etc. Some of this modularity occurs because of previously perceived efficiency by the designers. Worn-out parts are more easily replaced if they are made separately and fastened together. Some components of an engine are more easily constructed by creating separate parts and fastening them together. Even excepting these examples, ‘traits’ will still exist, just as organisms have separate circulatory, filtering, locomotory, and alimentary devices. Part of the evident particulatness of the organism as well as the engine therefore is due to efficiency of specialization of parts. But a significant part of organismic phenotypic modularity is surely caused by the particulatness of the external environment.

In effect, design features that give the appearance of modularity or independent activity, whether involving the ways that different somatic elements or different genetic elements function, cannot be assumed to cast doubt on Dobzhansky’s claim of “unity” unless the function of the organism as a whole can be described as other than singular; when function is singular, we expect that all parts or traits with seemingly different (or independent) functions will have those functions compromised to serve the singular function – regardless whether there is evidence of communication among them in this regard. The main point here is that whenever human social groups temporarily experience similar unity of function (e.g., ultimate patriotism), we may be confused by what appear to be “selfless” acts of beneficence by individuals, seemingly unexplainable in evolutionary terms, which serve the individual by serving the group.

Indirect reciprocity, then, includes assistance to others as a result of experiencing particular levels of generosity (cooperativeness) within a social group. Shirkers become those who do not achieve the general level of cooperativeness, whatever it may be, and rewards for social investment come from the benefits of functioning within a cooperative society. It is also indirect reciprocity when selection becomes virtually the same process at group and individual levels, and cooperativeness evolves accordingly; the rewards to each benefit-giver come from the success of the group defining the success of the individual. It may be that several kinds of indirect reciprocity need to be distinguished, but, by definition, it would seem that all reciprocity that is not direct is indirect.

Direct reciprocity may be best understood by thinking of two categories: (1) reciprocity that only evolves when risks of defection or deception are small, and probably evolves by minimizing risks (Minimal Risk Reciprocity, or MRR) and (2) reciprocity in which high gains are favored and therefore high risks are accepted (High Risk Reciprocity, or HRR). Trivers (1971) has given the best overall discussion of the complex social strategizing that thrives in environments saturated with opportunities for HRR.

MRR may be the only reciprocity practiced widely among nonhuman organisms (perhaps excepting certain primate groups). Unlike HRR, MRR resembles mutualism and does not select for extraordinarily complex social strategizing. In both humans and non-humans, parceled benefits can be exchanged instantaneously, such that the risk of receiving no return benefit is almost nil, and no great complexity in brain function is required (the possible exception of vampire bats is discussed rather thoroughly by Hammerstein, pp. 88-89). As Hammerstein points out (p. 88), MRR is exemplified by mutual neck-nibbling (historically, a parasite-removing action) in hoofed mammals. In informal field tests of my own, when a horse is set into nibbling by being nibbled, and the initiator terminates, the other tends to give either one additional nibble or none, depending on the stage of its own action when the other stopped. That is the precise expectation for MRR. In 100 repetitions in my test, the average of additional nibbles was 0.7, very close to the expected 0.5. Perhaps ironically, in humans MRR may be most prevalent in modern urban societies in formal transactions that take place between relative strangers – often meeting but one time – as when a shopkeeper simultaneously hands the purchase to the customer with one hand and accepts payment with the other. There is a huge lesson in this example. Trust and commitment do not typically accompany unfamiliarity.

These various arguments are not matters of mere terminology, but prerequisites of thorough understanding of what is actually going on in society, and what is meant by the categories of social acts that have been developing as a result of the evolutionary analysis of human sociality. The more difficult the concept, and its consequences in society, the more likely there will be misinterpretations. Indirect reciprocity is arguably the most difficult and complex – in a way the most “elite” of all human social phenomena. It is important to further progress, and especially to eventual simplification and broader understanding, that misinterpretations be

straightened out along the way.

### **Puzzling Cases in This Volume**

#### *Friendship as Not Contrary to Evolutionary Models*

With regard to direct reciprocity, and behaviors that seem not to match current evolutionary models, Joan Silk's chapter (p. 37) is titled provocatively, "Cooperation without Counting: The Puzzle of Friendship." She notes that "A considerable body of empirical work indicates that people value balanced reciprocity in their relationships with friends, but avoid keeping careful count of benefits given and received, and are offended when friends reciprocate immediately and directly." "Thus," she says, "the dynamics of friendship does not fit the logic of models of reciprocity and presents a puzzle for evolutionary analysis." Later she concludes: "None of our models of reciprocity can accommodate the psychology of human friendship."

Silk is not alone in drawing this conclusion, and indeed her conclusion is cited elsewhere in this volume, either neutrally or favorably, suggesting that puzzlement is widespread. But one everyday form of social reciprocity (or investment in social reciprocity) is called insurance, a concept I did not find in this volume, but that has been mentioned in this context (Alexander 1975, 1979). Formally, insurance is a contractual promise that the party in need will be helped no matter the cost to the insurer from having to give the aid at particular times or in particular circumstances that incidentally make it unusually expensive for the insurer. This kind of promise is perhaps the central component, and ultimate test, of "real" friendship. A supposed friend that insists on repaying social debts immediately, at the "friend's" own convenience, is in fact denying friendship – denying the promise of assistance whenever needed regardless of the cost to the reciprocator as a result of (unpredictable) timing and situation. That is the reason for getting upset when a friend carefully repays promptly. "Real" friendship means that either friend is willing to insure the other in the way just described – including willingness to do more than repay previous favors (in formal insurance, more than has been paid into the contract), and that the insurance continues as long as the friendship endures (see also, Nesse 2001, on commitment).

Millions of people pay regularly across their entire lives to maintain multiple formal contracts with insurance companies to provide special kinds of assistance in special kinds of disasters or calamities. Mostly they wish never to have to collect on those policies. Insurance companies are thus paid to be there, like friends, prepared and willing to supply assistance when it is needed. Insurance thus seems a suitable model for the kind of friendship Silk is discussing, and for the problem she sees in explaining friendship according to existing models of reciprocity (Alexander 1979, p. 51).

On p. 446, Henrich et al refer to Joan Silk's chapter on friendship as discussing "seemingly costless acts of contrition and apologies" as "atonements" for

social “violations.” If acts of contrition and apologies are costless, we should imagine that they are always given without reluctance. Yet we know that they are often withheld fiercely and obstinately – even fearfully, and in the face of death. It is worth looking again to assess the costs and benefits of any act of attrition or apology, and wrong to assume that changes in prestige and “losing face” involve no reproductive costs.

Friendship as insurance must be distinguished from the commitment that accompanies spousal relations and nepotism, because these interactions involve genetic returns in the absence of social reciprocity at the phenotypic level. The “friendship” or “insurance” kind of reciprocity, however, can occur between individuals that are not “special” friends within their group. It is probably often virtually universal within small stable communities because its sometimes large and public cost to the investor can make it essential that individuals receiving the kind of help it yields respond in kind whenever the opportunity arises. The power of indirect reciprocity within, for example, farming or other communities where the same families have lived together for generations, can cause behaviors that appear to outside observers to be unreciprocated or even “unreciprocatable” altruism. But no act of beneficence need go unrewarded in a situation in which all acts of beneficence are known to all group members, and in which all group members are aware that times will almost certainly come when they too need assistance. Much of the time there is no actual weighing of social investments because everyone knows that everyone else will do whatever is needed when it is needed. If someone’s house or barn is destroyed by fire or wind, everyone may participate enthusiastically in its replacement, regardless of any personal histories other than the general pattern of cooperativeness in the community. Perhaps, when the melding of direct and indirect reciprocity is somehow “complete,” or approaches an “ideal,” meaning partly that everyone in the community knows it (or behaves as though it is universally known), asymmetries in beneficent acts lack significance because of confidence about long-term insurance-like effects. This is one of the circumstances in which a “one-shot” test or view of social investment may be thought to be inconsistent with evolution.

At the “ultimate” or “ideal” level of morality, individuals may not only be indifferent to costs of beneficence but may strive to maximize the benefits (to others) of their own cooperative or beneficent acts. This level will work, for example, when all of the interests of the individuals in a community are identical (either temporarily or permanently); again, this will happen whenever no one can change groups (or changing groups is extremely unlikely and expensive) and the individual’s success therefore depends on the success of the group. Everyone will gain from looking for all possibilities to help others and then helping as much as possible, limiting help only when too much help or misdirected help will impair future helping sufficiently to damage the overall cooperative efforts of the collective. An example, already cited, is the genes in a genome, between meiotic events in sexual organisms, and all the time in entirely asexual organisms (Alexander 1993). But this case is surely an outcome of mutualism rather than social reciprocity,



It might be argued that maximum effort in paddling, as in the example of the canoe heading for a deadly waterfall, also cannot be viewed as social reciprocity because everyone in the group is being helped equally and there is no risk of defection. There is no reason to argue, however, that every individual in such a cooperating group is contributing equally to the interests of the group, or that, if the group survives, everyone is helped equally by the paddling of every other person. To understand this proposition one must also consider that the canoe may not always be swept over the waterfall, even if one or a few passengers malingers.

The canoe example has every likelihood of having arisen as a part of social reciprocity, that everything leading up to the seemingly "complete" or "perfect" morality that would have all individuals in the boat paddling as hard as they could, would be investment in social reciprocity.

If the boat always fails and everyone dies unless everyone paddles as hard as he or she possibly can, there would be at least two possible outcomes: (1) the boat goes down anyway and everyone dies. This outcome is of no interest to us, although the fact that everyone paddled as hard as possible might be (incidentally, we don't care what people think about why they are paddling – only the evolutionary why of their paddling, which may be different from the paddlers' perspectives); (2) the boat doesn't sink: (a) sometimes when everyone is paddling as hard as possible and (b) sometimes when one or more people are not paddling as hard as they can. However, anyone who witnessed any of these incidents and knew that any particular person on the boat was either paddling as hard as he could or else malingering, could spread that information around, and it would affect the relatives of the person being talked about in a way appropriate to the way he or she functioned on the boat. So there is risk, and there is a possibility of defecting – by malingering. Moreover, we cannot ignore the fact that hard paddling by one or more individuals may stimulate harder paddling by others – that levels of social investment by some individuals can increase them in others.

I wonder if we can ever call something mutualism, or by some name other than social reciprocity, when the entire background of the incident and the behavior in it is derived from a system of social reciprocity. Mutualism – the only real alternative to social reciprocity in things of this sort – does not give rise to big brains or calculated social investment. Social reciprocity, however, creates a situation in which the individual evolved to be good at calculated social investment may always turn situations like these into efforts at social reciprocity.

I went through these arguments to make the point that there are situations in which social investment will occur without any easy identification or measuring of reciprocation.

One reason humans differ from genes, already mentioned, is that humans oscillate continually between intra- and intergroup competition. Consider our extreme ability and fervor to assist offspring, extended family, and the entire kin circle as we recognize it, within the larger group (Alexander 1990a). Then consider the seemingly virtual opposite: patriotism so extreme as to induce complete willingness to sacrifice

our own lives, or the lives of our most precious relatives, in inter-group confrontations. Some evolutionary biologists regard such willingness as a result of duping, but I don't think the basis for it can legitimately be so categorized; after all, almost any adaptive behavior can be manipulated so as to become maladaptive to someone. In 1987, I cited the case of Japanese soldiers near the end of World War II, reported to have volunteered 100%, and then competed with each other, for the privilege of operating suicidal submarine-like one-man plywood vessels to destroy U.S. ships expected to participate in the invasion of Japan. It is probably no accident that this was happening in a society in which, historically at least, a single relative believed to have acted in a dishonorable way could cause family members to commit suicide in shame, or have all their relatives penalized socially if they did not. Similar suicide missions are known in societies in which for various reasons young men, in particular, are disenfranchised with regard to climbing the usual ladders of affluence within the society.

Because selection does not adjust sex ratios to reflect marriage or mating systems, polygyny – and the power to successful males that correlates with polygyny, arranged marriages, and exchanges of daughters – may be one such reason. It ought not to be surprising that some large proportion of willing “suicide bombers” are young men coming from polygynous societies – or societies recently polygynous and still retaining some of the consequent structure – or that young men are lured into suicide attacks by the promise of accessibility to a large number of virgins after death: 10,000 polygynous men in a society that allows harems of four wives disenfranchise 10-30,000 young males. Surely, the establishment of climbable ladders of affluence within every society, including reasonable access to marriage partners at appropriate times in life, is a significant component in the establishment and maintenance of tendencies toward democratic and peaceful governments.

I have argued previously that rapid and repeated alternation between the two conflicting extremes of inter-individual competitive striving within groups and patriotic cohesion in inter-group competition and aggression (ID-IG Alternation?) may be required to account for the evolution of complexity in the human psyche, and our enormous investments in parental care – hence, the value of coordinated sets of human traits, such as concealment of ovulation, confidence of paternity, extended biparental care, infant altriciality, menopause, and the long human juvenile life during which rapid and extensive learning prepares the juvenile for later adulthood in the complexity of human sociality (Alexander 1989, 1990a, 2005).

*Anonymous Social Investment as Not Necessarily Contrary to Evolution*

The reports in this volume lead me to suggest that, in an important sense, there are no two-party games in human sociality. An example is that every person involved in an exchange with another can carry the details of that exchange as an event remembered within his or her own mind, to be recounted or used in any subsequent context deemed useful or desirable. If I participate in a supposedly

completely anonymous interaction, whether set up for purposes of experimentation or merely an incidental aspect of everyday life, I can retain (and elaborate or alter) the details of the experience, and my performance in it, and relate and use them – presumably to my own advantage – in any subsequent circumstance, involving any other person or collection of persons. Indeed, I can set up or participate in such an encounter explicitly for the purpose of learning how to use the encounter to my own advantage later in other social situations. We are all likely to do this, on occasion, and to know at the time of the initial interaction or experiment that we are doing so. Moreover, we can be so adept at this kind of activity – so capable of retaining and relating our own personal account effectively, and accurately within the usual structure of social interactions – as to cause almost the same reactions as would have occurred if the subsequent audience(s) had actually been part of the original experience. This example shows how difficult it is to be certain about all the subtle workings and consequences of indirect social reciprocity. Yet all of the consequences of social reciprocity cannot be taken into account without this realization. This is an aspect of potential gain from social reciprocity which shows why interpretations of even anonymous “one shot” experiments – especially those leading to conclusions that individuals cannot profit, in evolutionary terms, from particular kinds of experiences, or that experiences do not fit particular kinds of human social activities such as indirect social reciprocity – may have a greater likelihood of being wrong than we at first imagine.

An example is worthwhile. Many years ago, my former boss and good friend, the distinguished University of Michigan Biology Professor Theodore H. Hubbell, was a wonderful skeptic and critic regarding the evolutionary approach to human social behavior. For example, he read my book *The Biology of Moral Systems* and told me that he had enjoyed it and learned a good deal. Then he precipitated a lively discussion of proximate mechanisms by adding gently, “But I could not find the word compassion anywhere in it.” One day, while stirring his coffee in preparation for a session with me, he spoke as follows: “Dick, this morning on my way to work I saw a caterpillar moving across the sidewalk. I knew it had fallen off its host plant, so I picked it up and replaced it on the proper plant species. Was that not an act of pure altruism?” I replied, “It may have been, until you told me about it.” I do not know if Professor Hubbell – who laughed a long time at my response – planned this trick on me, or if it only occurred to him as a good example after he had moved the caterpillar. But the point, I think, is clear. This was not even a *two-person* game, and it was definitely a “one-shot” encounter. Yet it was useful to both him and me in understanding human sociality. Even if he had not mentioned the incident to me it need not have included anything that conflicts with evolutionary theory, if only because of consequences from the effect on his view of himself.

The ability of humans to build scenarios as preparation for all kinds of games, and to use our unique language capacities to communicate to others about the games and the scenarios at different times and places, and in different social groups – about whether we play games, the way we play games, and what we do as a result of

playing them – all of these things – all six of the above kinds of returns from indirect reciprocity – must be taken into account when considering whether the games are consistent with evolution.

*Reciprocity as Derived from Extensive Differential Nepotism*

Silk also finds the relationship that Alexander and others have suggested between differential nepotism and social reciprocity “unconvincing because it assumes that people are less flexible in their behavior than other primates.” I am puzzled by this impression. The reference she cites to my own work includes the following (1979, p. 50, see also pp. 52-58, *Historical relationships between Nepotism and Reciprocity*): “In human history, expansion of nepotism to non descendant relatives and increasing group size must have set the stage for an increasing prominence of reciprocal transactions. In large and highly organized states or nations, as compared to simpler forms of social organization, indirect reciprocity must generally be more prominent – indeed, probably a criterion. Simple bands must have been predominantly systems of nepotism to descendant and non-descendant relatives with relatively little complexity in reciprocal transactions. Opportunities to engage advantageously in reciprocal transactions must have begun to appear as systems of nepotism among non-descendant relatives became extensive and complex, which also increases the potential for cheating by recipients of nepotism. Selective pressures leading to larger groups thus promoted increased engagement in reciprocal transactions, and increasingly elaborate social cheating and ability to detect and thwart it. (From Alexander, 1977).”

The caution to “Never do business with relatives” carries within it an explanation: The plus side of doing reciprocity with a relative is that it involves less risk than helping a non relative for the particular reason that if the relative does not reciprocate some potential gain remains for the donor because of the sharing of genes. The risk, or downside, of doing “business” with a relative is that the relative may welsh explicitly because the donor is a relative, and will not be expected to take revenge or exert effort to damage the relative seriously, including by giving it a bad reputation (Alexander 1979).

There is no suggestion in the passage quoted above – or of any other that I know about – of the kind of behavioral inflexibility Silk seems to be invoking. Instead, it describes a kind of flexibility that allows us to absorb the increased risk of doing reciprocity with increasingly distant relatives and thereby pre-adapts us to step right into doing the same with non-relatives in ways profitable to both parties. Extensive differential nepotism – known only in humans and apparently universal among humans – assumes almost exactly the same form as reciprocity, especially under certain conditions. Thus, nepotism involves risky investment (the relative may die, or for some reason not use the assistance to reproduce its genes or not use it as well as another relative to whom it might have been given). And it involves a return leading to an increased success in reproduction – more direct in nepotism but just as

surely in reciprocity. The optimal practice of extensive differential nepotism seems to require some mental abilities and tendencies similar to those required in the practice of reciprocity. Reciprocity with relatives, including in-laws, seems an inevitable concomitant or overlay of extensive differential nepotism. Nepotism and reciprocity with relatives surely contributed to the evolution of the mental faculties discussed in detail by Trivers (1971), which set us up to engage in profitable reciprocity with non-relatives. It is not that nepotism tricks us into behaving like reciprocators, but that much of nepotism takes the form of social reciprocity because there is always a risk of no return, or net loss. Many of the tendencies and abilities to calculate risks and act accordingly would thus become prominent, especially when nepotism came to involve multiple individual relatives and relatives of differing degrees (Alexander 1990b). An overlay of social reciprocity is almost certain to arise gradually in a society in which differential nepotism extends more or less throughout the group, especially when the group is also expanding.

All of this seems to make human history as a society with extensive differential nepotism virtually the perfect model for the appearance of social reciprocity, and perhaps even a prerequisite for it, giving at least a partial answer to Peter Hammerstein's title question, "Why is Reciprocity So Rare in Social Animals?" To my knowledge, no non human species has been demonstrated to distinguish or show differential nepotism to more than two classes of relatives. And these are scarcely differential nepotism when the distinction is between (1) relatives and non-relatives or (2) offspring and all others within a social group made up entirely of relatives. Studies supposedly demonstrating kin recognition, even differential recognition of kin, in contexts such as territoriality or sexual selection may not involve differential nepotism (i.e., no beneficence is involved) and sometimes appear to be incidental gradations of imperfect social learning; others involve methodological flaws, including failure to conduct investigations "double-blind" (Alexander 1990b, 1991). It is probably no accident that high-risk social reciprocity and extensive differential nepotism may be restricted to humans.

Because kin recognition in humans evidently comes about through social learning (Alexander 1990b, 1991), rapid changes in social learning situations (and opportunities for adaptive manipulation) – such as characterize all modern urban societies – can cause people to treat non relatives as kin, therefore nepotistically to varying degrees and in varying ways. Unless this possibility is taken into account in every study of presumed reciprocity, it can be extremely difficult to unravel and measure the adaptive consequences of behaviors between non relatives. Evolved biases in learning, as the connection between genetic change via natural selection and cultural change, deny that so-called duality of inheritance evolves to yield independence between learning and culture, and genetic evolution. Learning evolves not because it can lead to anything at all, but because it leads to genetically most appropriate behaviors in environments that are only immediately predictable more effectively than do other available ontogenetic mechanisms (Alexander 1990b).

*Culture as Proximate Mechanism, Memes as Parasites, and Group Selection*

Richerson et al say two things in their chapter (p. 366) that are intriguing in the effort to understand culture: “Many evolutionary social scientists assume that culture is a strictly proximate mechanism, akin to individual learning (e.g., Alexander 1979), or is so strongly constrained by evolved psychology as to be virtually proximate (Wilson 1998). As Alexander (1979, p. 80) puts it, ‘Cultural novelties do not replicate or spread themselves, even indirectly. They are replicated as a consequence of the behavior of vehicles of gene replication.’ We think both theory and evidence suggest that this perspective is dead wrong.”

Richerson et al then continue by discussing the question of group selection among competitive human groups. They note that “Hamilton (1975), Wilson (1975, pp. 561-562), Alexander (1987), and Eibl-Eibesfeldt (1982) have given serious consideration to group selection as a force *in the special case* of human ultrasociality”(italics in original). They make the valuable point that “For some of the most violent groups among simple societies, wife capture is one of the main motives for raids on neighbors, a process that could hardly be better designed to erase genetic variation between groups, and stifle genetic group selection.” They mean that for group selection to be potent – to be responsible for changes in the genetic makeup of humans, as opposed to potentially different directions of selection at lower levels of organization – the groups involved must be sufficiently genetically different.

My first lengthy discussion of the possibility of group selection in human evolution appeared in 1974 (pp. 376-377). I said the following: “For two reasons human social groups represent an almost ideal model for potent selection at the group level. First, the human species is (and possibly always has been) composed of competing and essentially hostile groups that frequently have not only behaved toward one another in the manner of different species, but also have been able quickly to develop enormous differences in reproductive and competitive ability because of cultural innovation and its cumulative effects. Second, human groups are uniquely able to plan and act as units, to look ahead and purposely carry out actions designed to sustain the group and improve its competitive position. These features may actually represent an exhaustive list of the precise attributes of a species that would maximize its likelihood of significant group selection, or evolution by differential extinction of groups. Thus group selection involves the paradox that competing populations must be sufficiently isolated to become different in ways that may lead to their differential extinction yet close enough together that they can replace one another. This condition is obviously fulfilled with sympatric competing species, which are intrinsically isolated. So, to some extent, are hostile neighboring populations of humans.”

Intrinsic isolation means that different species can diverge, and the differences between them that may lead to one replacing the other cannot be dissipated by interbreeding. Any time one species replaces another is an instance of group selection. Hamilton (1971) initially noted that the concept of group selection seems

more viable at the species level than at the population level.

Although I explained why I thought that humans are an “almost ideal model” for group selection, I did not make any claims about the force of group selection in this “almost ideal” case. We all know that some groups of humans have virtually annihilated other groups, and, regardless of our backgrounds, we can be reasonably sure that some of our ancestors have been involved in such events. Differential extinction of groups by other groups in the same species is group selection, but this says little about the overall effectiveness of group selection in determining the present traits of humans, and I deliberately left the question open because I didn’t know the answer.

Continuing from Alexander (1974): “It is an important result of the above considerations that in seeking to define the adaptiveness of culture, to analyze directions of cultural change, and to identify sources of cultural rules, we cannot ignore or downplay effects significant at the group level. . . . On the other hand existence of group functions does not erase functions at individual and family levels, and therefore does not preclude significant within-group reproductive competition.” I then continued by discussing the appearance in individual humans of both “personally or directly selfish (or reproductive) actions and group-sustaining or indirectly selfish actions; for it is combinations of these often conflicting tendencies that will lead their bearers to maximal reproduction in the long run.”

In 1987, I ended another discussion of this same topic as follows: “Darwin sometimes gives the impression that he sees the ‘approbation and disapprobation’ of ‘fellow-men’ as a manipulative device which turns what would otherwise be altruistic acts into self-interested ones. I would see this as completely compatible with a modern biological view of moral systems. But Darwin does not ever clarify this point, and he frequently says something that suggests the opposite (e.g., p. 493): ‘Finally the social instincts, which no doubt were acquired by man as by the lower animals for the good of the community, will from the first have given to him some wish to aid his fellows, some feeling of sympathy, and have compelled him to regard their approbation and disapprobation.’ Accordingly, I think we must give authorship of the idea that ‘heroism’ is reproductive to Fisher (1958, 1930): ‘The mere fact that the prosperity of the group is at stake makes the sacrifice of individual lives occasionally advantageous, though this, I believe, is a minor consideration compared with the enormous advantage conferred by the prestige of the hero upon all his kinsmen’ (p. 265). Fisher at once shows that the group and individual level selection arguments are not entirely incompatible (both may be operative), while supporting the latter as of greater importance. His theory is, in general, the same as that I am presenting here. Considerable elaboration is needed, however, before a simple statement that heroic tendencies evolved because they help kin can be translated [incorporated might be a better word here] into a general theory of moral systems.”

With regard to the relative importance of individual level selection and group level selection (of genes) it appears that we have not settled much, and we may not have progressed beyond Darwin and Fisher. Both levels of selection are surely

operative in human evolution, and there may be wide fluctuations in their relative effectiveness. Whenever two groups of humans that meet are so different that interbreeding is absent or minimal, something resembling group selection may take place. Every pogrom or deliberate effort to extinguish another human population can become an instance of group selection, even if it can be carried out only because of cultural differences such as those involving weaponry.

When I said in 1974 that humans represent an almost ideal model for group selection I intended to give the reasons for the possibility so as to increase the likelihood that appropriate discussions and tests might be more likely, including use of the necessary and sufficient reasons for group selection in humans to judge its likely potency in other species. But what of cultural selection? Is it a complete parallel? Should we even think of comparing cultural change to genetic change – especially when it is obvious that the agents of genetic reproduction, and therefore change, use what Dawkins thought of as parallels to genes – the cultural units he labeled as memes – to improve their genetic competition with other humans, both within and between groups?

Richerson et al – and multiple other authors – apparently subscribe to the characterization of cultural units (memes) as replicating themselves in a way paralleling the replication of genes, but independently of the genes, therefore (potentially?) acting as parasites on the humans that multiply and spread them. Thus, the opposite of the perspective described earlier by Richerson et al as “dead wrong” would seem to be: “Cultural novelties replicate themselves, both directly and indirectly. They are not replicated as a consequence of the behavior of vehicles of replication.” This perspective is probably consistent with Richerson and Boyd’s dual inheritance model of human evolution, in which culture is seen as a separate system of inheritance that parallels the inheritance of genetic materials. This perspective would also account for Richerson et al continuing as follows: “However, *cultural* variation is more plausibly susceptible to group selection than is genetic variation. For example, if people use a somewhat conformist bias in acquiring important social behaviors, variation between groups needed for group selection to operate is protected from the variance-reducing force of migration between groups (Boyd and Richerson 2002; Henrich and Boyd 2001; Boyd and Richerson 1985).” As indicated by the number of mass murders cited earlier, humans have in fact been unusually good at treating members of other groups as if they belonged to other species. As suggested in the earlier quote from Alexander (1974), rapid cultural changes can help some groups to become more powerful than their neighbors (e.g., inventing or acquiring better weaponry) and also cause groups to become more hostile toward one another (e.g., as a result of instituting different sacred rules or beliefs).

Writing alone and with others I have repeatedly referred to social learning as the principal proximate mechanism of culture – partly because the kin recognition that enables the extensive differential nepotism unique to humans is apparently a matter of social learning (Alexander 1990b, 1991). So, in response to the accusation that some of us have claimed that culture is a proximate mechanism I would suggest



that, unless there is some factor other than proximate mechanisms and ultimate functions, it has to be true. The reason, as I see it, can be summarized as follows:

Culture can be divided into the capacity for culture and the expressions (items, units, and patterns) of culture.

The capacity for culture includes the machinery for the acquisition of culture and the machinery for individual and group use, communication, and sharing of its items or units.

The items of culture, or its units, are all the learned, communicated, shared, or otherwise used items and patterns resulting from the capacity for culture.

The capacity for culture could not evolve unless the items and patterns it yielded on average served the reproductive success of individuals and groups using them – served it better than it was being served in the same genetic lines prior to the generation of a capacity for culture. Despite voluminous writing to the contrary, this statement seems to me to apply firmly to what Dawkins labeled as memes. Barring novel environments and mistakes, memes that do not contribute to the reproduction of their bearers are, like deleterious mutated genes, temporary, because they are not independent replicators. Those who discontinue use of reproductively deleterious memes will gain at the expense of others who do not.

Proximate mechanisms exist in long and complex cause-effect chains involving genes and environment, and all the functions of the organism: development (ontogeny), learning, physiology, morphology, and behavior. Evolved proximate mechanisms are adaptations, but they are by definition not ultimate functions.

Ultimate function is a term that implies the actual securing of reproductive success by the genetic replicators – or the reproductive success that is secured by them. The end result of the functioning of all the mechanisms in a chain that collectively leads to reproductive success thus may be termed the evolved function of the entire underlying chain. The evolved function of an act or a trait is not a mechanism per se but the outcome or result of a chain of acts or mechanisms.

Therefore, it seems to me that both the capacity for culture and its expressions are necessarily proximate mechanisms.

There is a bit of confusion here because culture, as I said in 1974 (see above), must also be viewed as a part of the environment into which individual humans are born and must live their lives. To the extent that culture assists individual humans across their lifetimes it apparently must be seen as a proximate mechanism of reproductive success. From an individual's point of view, one might also think of some aspects of culture as hostile forces of nature, to be added to Darwin's list of the hostile forces that result in differential reproduction. Forces of nature are also proximate mechanisms in the sense that they are responsible for directions of

evolutionary change and the nature of the traits of living creatures. As hostile forces, however, they are not proximate mechanisms in the sense of developmental and physiological mechanisms evolved to contribute to the reproductive success of their bearers. It may be more difficult to change what appears to be a hostile force in the makeup of culture, because the cultural practice in question may be to someone else's benefit. This is what I meant in the following 1979 statement:

If human evolution, like that of other organisms, has significantly involved selection effective at genic levels, realized through the reproductive strivings of individuals, neither humans as individuals nor the human species as a whole have had a single course to chart in the development of culture but rather a very large number of slightly different and potentially conflicting courses. In this case it would indeed be difficult to locate 'a function for,' or even 'the functions of,' culture. Instead, culture would chiefly be, as Sahlins' view may be slightly modified to mean, the central aspect of the environment into which every person is born and where one must succeed or fail; developed gradually by the collections of humans that have preceded us in history; and with an inertia refractory to the wishes of individuals, and even of small and large groups. Culture would represent the cumulative effects of what Hamilton (1964) called inclusive-fitness-maximizing behavior (i.e., reproductive maximization via all socially available descendant and non-descendant relatives) by all humans who have lived. I regard this as a reasonable theory to explain the existence and nature of culture, and the rates and directions of its change." I have not found reason to alter this view of culture, but I would like to have emphasized in it the importance of those desperate periods of intergroup conflict when extreme danger provokes extreme patriotism and group unity.

Proximate mechanisms are not single-layered but multiply and hierarchically organized. There are proximate mechanisms of proximate mechanisms of proximate mechanisms. All of them, at every level, are nevertheless compromised in their special functions, compromised in the service of the ultimate function, which is success in the competition for success in reproduction of the genetic materials. Only a little reflection shows that it will not do to study proximate mechanisms solely in terms of the next layer upward in the hierarchy, for compromise in the service of the ultimate function is not restricted to only certain contributing mechanisms. If one wishes to understand any trait or behavior in evolutionary terms it is necessary to develop and test hypotheses about ultimate reproductive functions – it is necessary to generate and try to falsify what Stephen Jay Gould liked to call "Just-so stories." In the words of Richard Feynman, "First, we guess. . ." (Sykes 1994).

Because there can be many ontogenetic and physiological routes to realization

of a proximate function, remaining in the realm of proximate mechanisms in an effort to understand, say, religion or humor or other such widespread or universal human activities, may never yield a significant clue. Ignoring these facts has cost dearly those concerned with proximate mechanisms who have had no way of understanding – and sometimes believed they had no interest in understanding – what function those supposed mechanisms were evolved to serve. Medical scientists may have had a little more success than social scientists in “blindly” treating mechanisms as if they were “ultimate,” because their interests are typically in returning the mechanism to its original function (as they understand it) within the body. Organs such as livers, kidneys, and hearts are all somewhat modular proximate mechanisms that, despite their seeming separateness, are surely in some ways compromised in even their functions, to the end of the entire organism functioning well in reproduction. Nevertheless, once the within-organism functions of such organs have been fairly well worked out, for many purposes they can be treated as separate functional units, to be maintained or restored as nearly as possible to their original efficiency. Social scientists, however, have had a considerably different proposition in trying to understand the function (operation) of the human brain as a set of proximate mechanisms because of the complexity in how the brain’s functions are achieved and greater ignorance about its modularity.

It is obvious that the evolution of the ability to learn creates opportunities to make special kinds of mistakes – at least for a while. Equally obviously, these mistakes cannot regularly have negative effects on reproduction that are larger than their positive effects, else learning would disappear, or the existing form of it would disappear. Even with today’s dizzyingly rapid cultural changes, we humans seem uncannily adept at manipulating our environments of cultural units until we are once more serving our own reproductive ends. It is difficult to argue that we do this solely by accident. There is every reason to believe that we do it because social learning is molded and biased and guided by natural and social selection so as to serve the genetic interests of individuals, whether they are behaving alone or in variously complex social groups. If we don’t like this “genetic interests of individuals” business, the thing to do is not merely to deny it or close our eyes to it but rather to either prove it wrong or find ways of making it progressively less influential in thwarting happiness and all forms of the “good life” as we see it.

### **More on Culture and Memes**

One person prominent in writing and speaking about memes puts his apparently widely accepted view this way: “Don’t even think about what memes are good for!” He follows with, “After all, what is the common cold good for?” The first statement exhorts us to accept that, in the process of becoming replicators in their own right, memes have (sometimes?) become entirely separated from connections to the (rest of the) human phenotype – and genotype – in a way that makes them either irrelevant to human reproductive success or else antagonistic to it, as is implied when

anyone suggests that memes can become parasites on the human phenotype. This argument says that, even if memes started out as communicative units, and part of human sociality, with respect to their own replication they have somehow escaped this connection and become independent of the human phenotype and its underlying genotype. The second statement re-emphasizes that memes have acquired a relationship to humans which even allows behavior similar to that of a parasite like the common cold virus, which does not serve us, rather infects us and debilitates us and presumably reduces rather than increases our reproductive success. The speaker was implying that memes, although historically a product of human genes via the evolution of (1) social learning, (2) complex communication that began to utilize memes, and eventually (3) a virtual flood of continuously cumulative social learning (culture), now use human genes for their own replication rather than the other way around.

Suppose we were to answer the second statement of the person quoted above by saying, “The common cold is good for this: It contributes to the replication of the virus molecule from which its effects spring. In effect, the common cold is the phenotype of the virus molecule. It is the virus’s way of creating its own environment of reproduction, utilizing the human phenotype (just as we use other animals and plants as food with which to create our phenotypes). It is the vehicle of the reproduction of the virus, just as the human phenotype is the vehicle of the reproduction of human genes.” Our speaker might reply: “Correct! In each case a replicator has generated a complicated means, or phenotype, for continuing its replication. The replicator has thereby become an independent entity, responsible for its own reproduction and persistence. In organisms, genes, or the molecules comprising them, are the replicators. In viruses, viral molecules are the replicators. In culture, memes are the replicators. Culture has become the phenotype – the environment of the memes, and the mechanism of their replication. The cold virus and memes have in common that they are using the human phenotype to its disadvantage to replicate themselves. Memes have reversed their original relationship with human genes and now use the products of the genes to replicate themselves, sometimes at the expense of the genes.”

I will begin countering this view somewhat indirectly with the observation that even within my own adult lifetime many analysts of humans believed that behavior cannot evolve. Somewhat later it was still believed that, even if some behavior can evolve, learning, at least, cannot, and still later that, whatever is true of behavior or learning, cultural behavior – or cumulatively learned learning – has essentially no connection to gene action. Each of these activities of humans at one time or another seemed somehow released from the then even less well understood hold of the genes on the phenotype. Still earlier in the history of biology there was probably widespread belief that any kind of “plasticity” at all in the phenotype was somehow uncoupled from the genes, hence could not in any way be changed by evolution. This happened partly because trait variations known to correlate with genetic variations were regarded as subject to evolution, while trait variations that did

not correlate with genetic variations seemed to have no substantial connection to genes or genetic change. This view has not entirely disappeared, and that is part of why I raised questions about the title and the theme of this volume. The reason these views changed is that we progressively learned how ontogeny can generate effects via environmental influences so as to make behavior and learning adaptive (cf. West-Eberhard 2003). Surely it is difficult to imagine how differential reproduction could take phenotypes in the opposite direction for long – making their outcomes less and less adaptive, or removing them from the tool kits of adaptation.

One way of interpreting these early attitudes is that a belief persisted that behavior, learning, and culture (later, learning and culture, and still later, culture) are so much more changeable – so dependent on environmental variations – that they cannot be linked in any fashion to genes; that environmental variation is so fickle and so extensive that there can be no significant feedback leading to genetic change from variations in environmentally malleable aspects of the phenotype. Another perspective is that differential reproduction was viewed so lightly that it was accepted that behavioral traits could readily become detached from their roles in furthering genetic reproduction, and that learning and culture were examples.

These attitudes seem alive and well today in some circles, at least with respect to cultural behavior and memes. If we cannot make concrete the exact connections between gene action and some aspect of behavior, then some may think it is reasonable to doubt that any connection exists. But this argument is contrary to the most basic view of evolution. First, we are constantly gaining new insights into the possibilities of ontogenetic and experiential connections between gene action and behavior. Second, the chances that the ordinary life activities of organisms will be conducive to the reproduction of their genes by accident – meaning without evolved (appropriate) connections in ontogeny and learning – are extremely remote. And, in any case, whenever any such accident happens, the chances that it will not become incorporated into the makeup of the life form in which it occurs, as a result of differential reproduction, are equally remote. Accordingly, we should feel compelled to continue the search for the connections that make our life activities genetically reproductive, and be extremely skeptical about claims of complete severing of connections between differential reproduction of genes and any aspects of the phenotype at all. None of my arguments here reflects a moral position, and none constitutes unsupportable genetic determinism. We humans simply have to come to grips with the unpleasant paradox that we have evolved to deceive not only others but ourselves as well, about the nature and background of some aspects of our everyday behavior, and how they came to be.

I suggest – I hope not too boldly – that students of human behavior and evolution need to become experts in at least four areas: (1) the evolutionary significance of environmental novelties (which are truly massive and difficult to analyze and understand in the modern world of culture), and adaptive mistakes, especially with respect to rapidly changing cultures; (2) systems of communication (including memes as useful transmitted and shared information) – e.g., what is

necessary and sufficient for the items of communication, and systems of communication, to survive and flourish (I recommend Otte 1974 as the seminal paper); (3) the diverse ways in which differential reproduction can influence – and be influenced by – plastic behaviors, social learning, and cultural items and patterns (I recommend West-Eberhard's 2003 pioneering volume); (4) the levels at which differential reproduction is most potent (whether primarily individuals or groups, and when and how often cycles between these two situations are favored), and (5) the true nature of learning, especially how environments of learning can be consistent in ways that allow and enable learning to evolve so as to promote reproduction.

It is easy to look at culture and be confused about the nature of the focus on differential reproduction – whether at group or individual levels, and when one or the other level is being emphasized. If we view certain ideas or practices (memes) as hostile to our own interests or wishes, we must reflect that natural selection does not save only those memes that appear to us as individuals (or subgroups) to be the most positive ones, or those best serving our particular interests at any particular time. Thus, it seems obvious that some cultural groups have accepted premises (memes) that can be shown to be inconsistent with facts that seem incontrovertible today. This does not mean, however, that those premises did not serve those groups well in earlier cultural environments – and may even continue to do so today. To argue that the rise of memes has influenced the whole of human reproduction negatively (owing to memes becoming independent replicators and neutral or negative in their effects on human reproduction) begs the question not only of why culture has become so elaborate, but of why the human population has soared, and whether as a result of our success the planet is in serious jeopardy as an environment capable of sustaining life. Even if a long-lasting and highly successful meme may appear to be detrimental, or is wrong because it contradicts currently understood facts, because of social and moral implications it may nevertheless have furthered success in the reproduction of the individuals and groups who accepted and promoted it, and may still be doing so.

## **Conclusion**

I apologize for this review being spotty and incomplete, discussing only a few things in a few chapters in a specific way. I also apologize for not being able to cite all the most recent literature bearing on some of the questions I have discussed. And I apologize for this review having taken so long to complete after I accepted David Barash's invitation to write it. I am grateful to Mark Flinn, David Lahti, and Andrew Richards for providing criticism and encouragement.

I have limited my comments to what seemed to me to be the most important topics, and the ones I thought I might know enough about for my discussion to be useful. Among these topics, the most generally important one is that people who investigate the inner workings of human social behavior in evolutionary terms keep striving to comprehend the immensity and complexity of their problem, and the applications of it. In the March 2005 AARP Bulletin, Richard Lederer, discussing

what he called “gobbledy-gook,” wrote as follows: “In 2003, the Brits’ Plain English campaign awarded Secretary of Defense Donald Rumsfeld their Foot in Mouth ‘prize’” The prize was awarded for Rumsfeld’s analysis of the questions surrounding Iraq’s possibility of having a cache of weapons of mass destruction. Paraphrasing, Rumsfeld said that there are things we know we know, things we know we don’t know, things we don’t know we know, and things we don’t know we don’t know. Leaving aside the context of Rumsfeld’s statement, and my own strong sympathy for the Brits’ general position, this bit of Rumsfeld “gobbledy-gook” (which is actually part of a fine old saying that I learned from my father two-thirds of a century ago) is something that all students of human social behavior ought to consider seriously. In my opinion, any investigator who is not aware of all four of these categories of knowledge about human social behavior is unlikely to “get it straight.” Conscious knowledge is but a fragment of our useful knowledge. A good many things have been kept out of our consciousness by evolutionary selection, both by removing all indicators of their existence and by removing our interest in them and therefore our attention to them, even when clear indicators remain in “plain view” (and as a result are sometimes made conscious in modern society). To be successful as students of the evolution of human sociality requires that we be entirely aware of this problem and exert considerable effort to deal with it appropriately. I think we humans are much more complex – or convoluted – than even most students of evolutionary biology are aware. I said at the outset that there is no more difficult problem than analyzing human social behavior. Nor is any task more potentially useful.

I thank Mark Flinn, David Lahti, and David Barash for their assistance.

## **References**

- Alexander, R. D. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics* 5:325-383.
- Alexander, R. D. (1975). The search for a general theory of behavior. *Behavioral Science* 20:77-100.
- Alexander, R. D. (1977). Review of : *The Use and Abuse of Biology* by Marshall Sahlins. *American Anthropologist* 79:917-920.
- Alexander, R. D. (1979). *Darwinism and Human Affairs*. Seattle: University of Washington Press.
- Alexander, R. D. (1987). *The Biology of Moral Systems*. NY: Aldine de Gruyter.
- Alexander, R. D. (1989). The evolution of the human psyche. In: *The Human Revolution*. C. Stringer and P. Mellars (Eds.). Edinburgh: University of Edinburgh Press, pp. 455-513.
- Alexander, R. D. (1990a). How Did Humans Evolve? Reflections on the Uniquely Unique Species. *University of Michigan Museum of Zoology Special Publication* 1:iii + 38 pp.
- Alexander, R. D. (1990b). Epigenetic rules and Darwinian algorithms: The adaptive

- study of learning and development. *Ethology and Sociobiology* 11:241-303.
- Alexander, R. D. (1991). Social learning and kin recognition. An addendum. *Ethology and Sociobiology* 12:387-399.
- Alexander, R. D. (1993). Biological considerations in the analysis of morality. In: M. H. and D. V. Nitecki (ed). *Evolutionary Ethics*. Albany, NY: State University of New York Press, pp. 163-196.
- Alexander, R. D. (2005). Evolutionary selection and the nature of humanity. In: V. Hosle and C. Illies (Eds.). *Darwinism and Philosophy*. Notre Dame, Indiana: University of Notre Dame Press, pp. 301-348.
- Burnham, Terence C. and Johnson, Dominic D. P., (2005). The biological and evolutionary logic of human cooperation. *Analyse & Kritik* 27: 113-135.
- Chagnon, N. (1988). Male *Yanomamo* manipulations of kinship classifications of female kin for reproductive advantage. In: L. Betzig, M. Borgerhoff Mulder, and P. Turke (Eds.). *Human Reproductive Behavior*. Cambridge, England: Cambridge University Press, pp. 23-48.
- Connor, R. C. (1992). Egg-trading in simultaneous hermaphrodites: An alternative to tit-for-tat. *Journal of Evolutionary Biology* 5:523-528.
- Dawkins, R. (1976). *The Selfish Gene*. NY: Oxford University Press.
- Dobzhansky, Th. (1961). In: J. S. Kennedy (Ed.). *Insect Polymorphism*. London: Royal Entomological Society, p. 111.
- Fisher, R. A. (1930) (1958). *The Genetical Theory of Natural Selection*. 2<sup>nd</sup> edition. NY: Dover Press.
- Flinn, M. and R. D. Alexander. (1982). Culture theory: the developing synthesis from biology. *Human Ecology* 10(3):383-400.
- Hamilton, W. D. (1964). The genetical evolution of social behavior I, II. *Journal of Theoretical Biology* 7:1-52.
- Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology* 31:295-311.
- Nesse, R. M. (2001). *Evolution and the Capacity for Commitment*. NY: Russell Sage.
- Nowak, M. A. and K. Sigmund (1998). Evolution of indirect reciprocity by image scoring. *Nature* 393: 573-577.
- Otte, D. (1974). Effects and functions in the evolution of signaling systems. *Annual Review of Ecology and Systematics* 5:385-417.
- Sykes, C. (Ed.). (1994). *No Ordinary Genius: The Illustrated Richard Feynman*. NY: W. W. Norton.
- Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35-57.
- West-Eberhard, M. J. (2003). *Developmental Plasticity and Evolution*. NY and London: Oxford University Press.
- White, L. A. (1949). *The Science of Culture: A Study of Man and Civilization*. Reprinted 1969. NY: Farrar, Strauss, and Giroux.