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Evolution, Culture, and Human Behavior: Some General Considerations

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Darwin's thoroughness ensured that, after 1859, general theory would remain a central and conscious theme in biology—something that is not always true in all sciences. Even Darwin was unable to cause it to be true universally in biology, as is evidenced by use of the term "evolutionary biology," which implies not only that some people care but that some others do not. On the other hand, even if biologists do care about evolution—and even if they pretty much agree—this does not necessarily mean that they are right. Thus, what some regard as the most important book in evolutionary biology since Fisher (1930) was titled "Adaptation and Natural Selection" but had as its subtitle the phrase "A critique of some current evolutionary thought" (Williams, 1966). If this is not enough, then one has only to recall the screams of outrage and anguish that came mostly from the population of biologists aged over 30 in the wake of Williams' book and that still echo faintly around us now and then.

If general theory has usually been the strength of biology, it has usually been the nemesis of the social sciences. Psychology and sociology have ordinarily been content with their own private view of learning theory as all-encompassing, even though there has been precious little in learning theory to explain either why learning exists or why it takes many of its particular forms, and these shortcomings seem likely to become increasingly important.

Consider anthropology: It is the science closest to evolutionary biology in approach, subject matter, and methods. Indeed, anthropology is the only social science ever much concerned about evolution either as long-term change or as long-term contingency underlying present features. Yet anthropology has always floundered on general theory. Anthropologists have consistently sought general theory, but I think I only echo the vexation of a long succession of its practitioners in saying that they have never found it within their own science.

George Peter Murdock was surely one of the great anthropologists of all time. He wrote plainly, not poetically, and he changed his mind—sometimes rather profoundly. But he was responsible for the development of an enormous cross-indexed file on the behavior of the human species (The Human Relations Area File) that has to be the envy of every biologist who ever fell in love with a group of organisms and set out to monograph all the variations in the life histories and behavior of the different species belonging to that group—something that most of us associated with museums have, in fact, as one of our lifetime goals. Of course, Murdock was tabulating, not what happens in different species but what happens in different cultures within a single species. Nevertheless, his work, more than anything else, established a comparative method (called "cross-cultural analysis" and usually regarded as begun by Tylor, 1889) quite analogous to that used in systematic and evolutionary biology.

The anthropologists, who have filled thousands of pages with every kind of correlation and comparative study they could imagine from Murdock's file and arrived at no particularly earth-shaking conclusions, have decided that there must be something wrong with it. Of course, there is: The data are incomplete and imperfect. Like every repository of so-called information, the file is filled with factual errors, observer bias, misinterpretations, and inappropriate codifications. It may even be worse than most such repositories.

But there has also been something wrong with the efforts to use Murdock's grand file. They never were derived from a useful or even remotely satisfactory general theory. Until very recently, the right questions had simply never been asked.

Murdock, the compiler, must have been thinking in terms of general theory. During most of his career he regarded adaptation in culture as somehow utilitarian to the society as a whole (Murdock, 1949–1967). Society was often the subject of one after another of his explanatory sentences. Society, he said, would have to do this or that for its own good, and society could not afford to ignore this or that. But he was never very specific about this theory nor was he entirely consistent. In retrospect, how could he have been?

But Murdock could change his mind. And in one of his last papers (Murdock, 1972), from an address to the Royal Anthropological Institute of Great Britain and Ireland, he did change his mind, so profoundly that anthropologists have almost totally ignored the paper, which was titled "Anthropology's Mythology," except to cite it occasionally to show how far Murdock went astray (e.g., Sahlins, 1976).

In the 1972 paper Murdock declared that anthropology is suspect *as a science* because no two of its foremost theoreticians can agree on even the most basic issues. He said that he had to conclude that his own approach, across all the years, had been fundamentally wrong; that it now seemed clear to him that society and culture are mere epiphenomena—no more than the products of the collective activities of individuals; and that it is to the behavior of individuals that we must look if we are ever to understand. He said that it is good that anthropology has developed a considerable body of fine ethnographic data, because its efforts at theory will have little part to play in the future science of man.

In all fairness one has to add two caveats. First, Murdock must have known that his own contribution would be recognized as principally not in theory but in making those fine ethnographic data more available. Second, conclusions similar to Murdock's have been approached independently from within anthropology by several investigators; I think particularly of the Europeans, Frederik Barth (1967) and Jeremy Boissevain (1975). But these conclusions are by no means widely accepted. I believe one has to conclude that general theory has simultaneously seemed important and been unattainable within anthropology.

The social sciences lie somewhere between philosophy and evolutionary biology, if the latter is seen as the only natural science with any truly general theories about life. In the broadest sense, philosophers have always theorized about human nature. So, in fact, have ordinary humans. Roger Masters (manuscript) of the department of government at Dartmouth, has traced two major views of human nature through recorded history from the ancient Greeks. They are simple ideas, and they also seem to oppose or contradict one another. One is that we are hedonistic individualists out to serve our own ends and able to cooperate only because we set up social contracts and agree how far we can go in interfering with one another. The other is that we are group altruists, with missions larger than our own selfish ends, here to serve the greater good. I would ask: What ordinary human has not toyed in his mind with the precise riddle posed by these two grand, seemingly contradictory views of himself and his fellows—whether we are selfish individualists or group altruists?

The two ideas are philosophical, and they are also simple theories about human nature—the kinds of theories, it seems, that we are always seeking to explain ourselves. Most social scientists would probably say that they are far too simple, and they would also note wryly that we seem always to be seeking, and too hastily accepting, oversimplified theories about human nature. Yet these two simple, widespread notions are also profound.

Darwin's successful argument, in 1859, that we—as with all organisms—are products

of an evolution guided by natural selection, surprisingly did not solve the riddle posed by the ancient Greeks and, as well, by ordinary thoughtful humans. The reason, as we know now, was that Darwin could never answer a crucial question: Survival of the fittest what? Certainly he could not have meant survival of the individual because, of all the units identifiable in the hierarchy of organization of life, the individual is the shortest lived. Moreover, the vast majority of lifetimes are exceedingly short: hardly anyone competes with redwoods and bristlecone pines. Clearly, during the billions of years available to them, individuals have not evolved to survive.

It is possible that Darwin never realized that conflicts of interest could exist at different levels (e.g., between individuals and groups) as well as at the same level (e.g., among individuals), thus posing the question of which among all the levels of organization of life has actually evolved to survive; but I believe that several of his discussions (e.g., of interspecific hybridization, sex ratios, and sterile castes in social insects) indicate an awareness of this problem and at least a vague realization of his inability to solve it (Darwin, 1859, 1871).

Other than individuals, only two candidates for the evolution of survival ability were available to Darwin's senses: phenotypic traits and species (or populations). Both seem to last a long time—at least sometimes. At different times, Darwin talked about each—traits and species—as if they were the units of selection. Genes, of course, were unknown to him. At best he had only a fragment of the picture in regard to where heritable traits come from.

So Darwin did not resolve the ancient question whether humans are selfish individualists or group altruists. In my opinion, however, the two recent arguments from evolutionary biology responsible for this symposium, and recurring throughout it, have solved that problem, and simultaneously they have shown us how to develop the simple, general theory of human nature that we have always sought. The arguments were presaged by Fisher (1930) and Haldane (1932), and developed, respectively, by George C. Williams (1957–1966) and William D. Hamilton (1963–1964) (see also, in particular, Dawkins, 1976–1977; Leigh, 1977; Alexander and Borgia, 1978). They are, first, that only subgenomic genetic units last long enough to have been evolving to survive, and, second, that these units have evolved to survive by helping their copies reproduce wherever those copies may live. That the genes have evolved to survive by *reproducing*, it seems to me, is itself a comment of the deepest significance about the general nature of the environments of life throughout history—namely, that environments predictably change but in unpredictable ways. Biologists are still trying to discover exactly what this means (e.g., Williams, 1975; Maynard Smith, 1978; Leigh, 1978); probably we will not be able to understand sexuality in adaptive terms until the problem is solved.

We are, then, hedonistic or selfish individualists to the extent that such behavior maximizes the survival by reproduction of those copies of our genes residing in our own bodies; and we are group altruists to the extent that this behavior maximizes the survival by reproduction of the copies of our genes residing in the bodies of others. At least this is what we have evolved to be—and to all accounts it is all that we have evolved to be.

It is paramount to realize, however, that—as opposed to what we have evolved to be—what we actually are or become is whatever we can make of ourselves, given our history, and our propensities and talents, which are great, for creating novelty in our environments at rates and of kinds that the process of genetic evolution has no possibility of controlling or keeping up with. Nowadays, we are closer than ever before to being able to become what we wish to be, if for no other reason than because we know about ourselves the things that I have just mentioned. On the other hand I would caution against a too-loose interpretation of this concept by repeating the wry comment of a comic strip character who said, "Why is it that a human can grow up to be whatever he or she wishes to be, but a caterpillar can only grow up to be a butterfly?"

For the first time in history, then, we are on the brink of formulating a simple and convincing general theory of human nature. With generality and simplicity in its structure,

any theory of human nature must inevitably become exceedingly complex in its application. I stress this fact, particularly for those who hold to the strange idea that there cannot, in principle, be a simple theory of human nature—that any effort in that direction is by definition intolerably reductionistic (One has to wonder how they feel about the elegantly simple 122-year old theory that is demonstrably adequate to explain life in general and has no serious challenge—or, indeed, about $E = MC^2$).

So long as we thought of grand conflicts of interest existing only at the level of the social group, they were simple to consider. Now we have driven those conflicts of interest all the way to the level of the genes. As difficult as it is to conceive, each individual human is a product of the cooperation of thousands, or hundreds of thousands, of separate genetic units, each of them with potentially separate and conflicting interests.

Picture a gene that could guide its bearer to assist other gene-bearers solely on the basis of its own presence in those other gene-bearer's genomes—that is, independently of the presence or absence of other genes in its own genome. Multiply that conflict about a hundred thousand times and you know that this is not the kind of nepotism that has led to the genetic cooperation necessary to create a phenotype unitary enough to be called an individual, to think, philosophize, and examine questions like those in this symposium.

The cooperation of the genome—the unity of the phenotype and of the individual—seems to require that, in general, each gene's action serves all of the genes in its genome equally. In helping one's own phenotype (one's self) there is usually no problem. In nepotism it is not quite so simple. Nevertheless, as we know now, there is an obvious and simple way to be nepotistic yet serve all of one's genes equally in terms of their survival by reproduction. It is to treat supposed relatives in a way that takes account only of the probability of each gene of the nepotist's genome residing in the relative's genome; these probabilities are approximately equal for genes inherited by immediate descent (Hamilton, 1964). Given the genetic roulette of meiosis, the simplest way to accomplish this kind of nepotism, when one must deal with different classes of relatives, is to learn socially who your relatives are—to learn to accept or reject that one or another individual is this versus that class of relative, a relative versus no relative at all (Alexander, 1977-1979).

That social learning is, in fact, the general mechanism of the evolution of nepotism, is, I believe, strongly supported by the ease of inducing adoptions of unrelated offspring and other relatives once the appropriate social situation has been created. I doubt that any organism is immune to this manipulation, regardless of whether it is regularly nepotistic toward one, several, or many classes of relatives. The stringency of the necessary situation should be greater in social species in which accidental adoptions are most likely in nature, and greater at those times when accidental adoptions are most likely (Daly and Wilson, 1979, and Alexander, 1979, review evidence supporting this hypothesis). Similarly, recognition of close relatives in genetic outbreeding appears to occur as a result of social experiences, at least in mice and humans (Hill, 1972; Spiro, 1958; Shepfer, 1971; Wolf, 1966, 1968). A further test of the involvement of social learning in nepotism could examine the likelihood and degree of forgetting appropriate responses to relatives after periods of non-interaction.

Earlier I said that we are on the brink of developing a simple general theory of human nature. When I first drafted this manuscript I thought it proper to say that we had already accomplished this goal but now I believe that what remains to be learned is sufficiently important and difficult as to deny my earlier optimism. It is true that we are now able to specify the genetic interests of humans, singly and in groups, much more precisely than ever before—indeed, so much more precisely as perhaps to justify the claim that we are able to do it “for the first time.” But human behavior—social interactions and the structures of culture that derive from them as history unfolds—is not a simple consequence of gene action or genetic makeup. The conflicts and confluences of interest expressed by human actions are not precisely those reflected by differing amounts of genetic overlap. Behavior is invariably the outcome of genes plus environments, a fact that is as trite to repeat as it is complex to comprehend. Genes cannot act directly in their own interests. They gave up

such possibilities long ago when they evolved to realize their interests through phenotypes, which develop their inclinations and abilities differently in different environments. Even if the genetics of conflict and confluences of interests have been worked out, at least in skeletal form, their actual phenotypic expressions and the reasons for them are not yet similarly understood. We do not yet know how the multiplicity of possible, probable, and actual environments available to humans affects the relationship between their quantifiable genetic interests as individuals, families, and other groups and their actual behavior in relation to those interests. We do not know how to specify the effects of cumulative changes in the cultural environment upon our individual and collective behavior. We have little notion of the way in which the accelerating introduction of novelty into our environment is going to alter our behavioral potentials. I believe that we must draw the connections between genetic interests and phenotypic expressions to a much greater degree before we can argue that a simple general theory of human nature is a fact. In some large part this means that we need to know a great deal more about the nature of learning and how it has functioned, in the past, to maximize the inclusive fitnesses of those showing it. The main reason why we currently have no such understanding is, in my opinion, because learning has never been studied in this context.

A simple illustration of the immensity of the problem of correlating genetic interests and phenotypic expressions is to realize, first, that not all of each person's interests are always conscious, and some may never be conscious. Prior to the advent of an acceptable version of organic evolution, there was no possibility of a conscious knowledge of genetic interests, and prior to the recent refinements of evolutionary theory there was no conscious knowledge of the actual nature and extent of genetic conflicts of interest. Yet, unless we are profoundly in error in the most basic realms of biological science, these interests and conflicts of interest existed and in fact guided human existence throughout all of history. We had no way of knowing that our lifetimes evolved in the interests of effecting the long-term survival of our genes by reproducing them, but we nevertheless learn to love and assist our own offspring, and often help other relatives even in the face of powerful resistance and high risk to our own status or well-being. In other words, we *act* as though we know about inclusive fitness. We do not yet know the precise significance of genetic outbreeding, but like nearly all sexual plants and animals we practice it: We do it by learning to avoid in sexual matters those with whom we associate most intimately while prepubertal—and they are typically our closest genetic relatives. But we do not, in nepotism and genetic outbreeding, conduct ourselves precisely according to our genetic interests; to know why we have no alternative but to study the environment and its effects on human development.

Now I think that psychology can at last, with justification, view learning as broad enough, and as having an adequate focus, to represent psychology's own, general, all-encompassing theory. Psychology accomplishes this transition by the simple step of realizing that the forms and expressions of learning have long-term historical as well as short-term contingencies underlying them, that those long-term contingencies involve genetic inclusive-fitness-maximizing, or genetic reproduction via all relatives, and that the central questions of social psychology are to determine how this has come about and what it means for the future.

To be more specific, I assume that some combinations of rates, kinds, timings, and accumulated numbers of social learning experiences determine the nature and intensity of human social interactions. That is nothing new. But it will be new to assume that the determining rates and kinds of social interactions among individuals have varied consistently and regularly with degrees of relatedness in genes identical by immediate descent; yet I think this assumption is necessary. It will be new to realize that the correlations of social experience with genetic relatedness can be an incidental consequence of geographic and social proximity and that such correlations can be imposed indirectly by those whose interests are served by creating them. It will be new to realize that the fragility of the correlation between social and genetic distance in a mobile, fluid society like our own can lead to mul-

tiple and complex surrogate social-genetic distance correlations, in the end understandable only from knowledge of long-term historical contingencies. It will be new to recognize that disruption of an individual's chances of establishing a pattern in his or her social interactions that reflects the long-term history of social-genetic contingency correlations may lead to that individual's social alienation, to devastating confusion, to feelings of being orphaned, and perhaps even to suicide or outlandish searches for adoptive surrogates, including the substitute kin networks of intensely religious, political, and other support groups. It will be new to establish connections between loss of the social experience of stable kin groups, or their surrogates, and broad-scale rises of concern with the effects of law and public activities on the so-called disadvantaged in every realm, whose vulnerability can be interpreted by even most individuals as paralleling their own. It will be new to hypothesize that variations in cultural patterns stem from variations in how ecological and other extrinsic events modify the social circumstances in which groups of genetic relatives have found themselves during the history of each separate society. It is new to attempt to explain such things as mother's brother, the asymmetrical treatment of cousins, the cloistering of women, the sizes of villages at fissioning, the abuse and neglect of children, clan exogamy, the distribution of male-biased inheritance, and the acceptance or rejection of harem polygyny as consequences of different patternings of social interactions among relatives that lead to outcomes predictable from inclusive-fitness-maximizing in different ecological circumstances and under different histories of cultural patterns and power distributions (cf. Alexander, 1977-1979; Chagnon, 1981; Chagnon and Irons, 1981; Daly and Wilson, 1981; Dickemann, 1981; Flinn, 1981; Irons, 1981). Yet I believe that these are exactly the kinds of subtheories that must be made operational within the social sciences if we are to proceed in the analysis and understanding of ourselves with the least delay and confusion.

I think it will also be recognized eventually within social and cultural anthropology that the central question there is how the different patterns of culture could have derived from the history of individuals behaving so as to maximize their respective inclusive fitnesses according to the environments of history, and what this means for the future. That, too, will be new.

I would like to talk now about one pattern of culture that seems to have been studied relatively infrequently and haltingly by cultural anthropologists. For the most part this pattern of culture is apparently not well represented across the span of human history, and my guess is that it is entirely missing from much of the human chronology. It has evidently remained unusually inaccessible to anthropologists, for a reason apparently well understood by the cultural anthropologist, Leslie White. White used to tell his classes that for a student of human behavior to discover pattern within his own culture would be like a fish discovering water (N. A. Chagnon, personal communications). The culture of which I speak, and of which our own society is a part, has produced essentially all cultural anthropologists, but it seems to create them in such fashion that they are forced to visit alien cultures in order to fulfill the requirements of their profession.

This culture has several striking features, which I will mention not necessarily in the order of their importance. Along with about half of the 862 cultures of the world listed by Murdock, it not only fails to require marriages between first cousins or at least encourage them, it actually disfavors and often disallows such marriages. Like only about 7 per cent of the cultures of the world its members also do not distinguish the several different kinds of cousins—cross-cousins and parallel-cousins, matrilineal and patrilineal cousins. Despite considerable complexity in the structure of this culture, all of the different kinds of cousins are lumped together, and when they are brought up in conversation everyone is confused.

Nevertheless, cousins more distant than first cousins are often traced and identified carefully, especially when they are quite wealthy, heroic, or renowned for their intellectual or political achievement. In general, children learn who their first cousins are and even some of their first cousins once removed or their second cousins. These relationships are taught to them—in my experience, usually by some female members of the family on that side, or, in

the case of truly renowned relatives, even by someone on the other side of the family. In many families some person undertakes to trace the genetic relationships of the family out to extraordinary distances, using his or her own family as the center of the network and tracing in all directions until the evidence disappears or until some relative known to the rest of society or connected to an event known to the rest of society has been identified. The people of this society carry out the same procedures for the animals from which they earn their livings, and they publish and advertise pedigrees for both their animals and themselves.

The third prominent aspect of the culture I am describing, and the first unique one, is that it imposes on its individual members a legal limit of one spouse at a time; like most cultures, it also places barriers of various sorts in the way of changing spouses. Such "socially imposed" monogamy (Alexander et al., 1979) is unique not only among human cultures but as well to humans among all animals. In general, the one-spouse rule applies only in the strict, technical sense of the law to the various rough equivalents of headmen in the society, who, as we all know, are often respected, and even admired by some, for gathering, for some purposes, actual harems. Even high-ranking females sometimes acquire virtual harems of males, although, as in the other societies of the world, this behavior is less frequent and likely to be frowned upon more severely than its equivalent among males.

It is not trivial to realize that, under monogamy and with isolated nuclear families, putative cousins are not only treated most symmetrically, but by all counts are also likely to be genetically most symmetrical (Alexander, 1977, 1979). Outbreeding societies with socially imposed monogamy and symmetrical treatment of cousins may have generated independently in several different parts of the planet. In such societies—where the data are available—the amount of sexual dimorphism and the sex ratio at birth are both about the same as those known in societies which permit harem polygyny, distinguish the different kinds of first cousins, and often encourage or require—that is, arrange—cousin marriages (Alexander et al., 1979). At least in regard to one of these two traits both harem-polygynous and socially monogamous cultures differ from the small bands of humans surviving today in the marginal habitats of the Arctic and on the fringes of deserts and neither imposing monogamy on their members nor very often getting around to polygyny. Males in societies with ecologically-imposed monogamy, as with males of apparently all monogamous non-human species, seem to have all they can do in assisting one wife to rear even widely spaced offspring. In these same societies, two men—usually brothers—occasionally combine to help one woman rear their offspring; and in these societies sexual dimorphism also may be slightly lower (Alexander et al., 1979).

It would seem, then, that the peculiar culture exemplified by the society in which we live is a recent derivative from harem-polygynous societies. This hypothesis develops from morphological, physiological, and behavioral comparisons (Alexander, et al. 1979). The alternative is that socially monogamous societies have undergone a more or less similar kind of male-female divergence in selection wherever they have arisen. It is probably relevant that within recorded history many small or not-so-unified polygynous societies have converted to a socially-imposed monogamy, while virtually none has been able to sustain a change in the other direction. Moreover, socially monogamous groups tend to be the largest of all human social units, ecologically monogamous the smallest, and we have obviously increased group sizes during history. The small ecologically monogamous societies also differ from the large socially-monogamous ones in numerous other features that I will not discuss here, such as premarital and postpartum sexual behavior, family structure, community size and organization, degree of nomadism, and kinds of agriculture, inheritance, cattle, gods, games, and others (Murdock, 1949, 1967; Goody, 1976; Alexander, 1979).

Socially-monogamous culture spreads by conquest, imposes its rules forcibly on others, and perhaps most remarkably has been able to achieve unprecedented combinations of size and degree of unity without evidence of strong tendencies to fission. Even after fissioning episodes, the daughter units are capable of extraordinary cooperative efforts, when these are important, on a scale without the remotest precedent in all of human history;

and following such cooperative efforts they may, for all practical purposes, remain a single socio-political unit.

At the beginning of this essay I argued that the genes could not be expected to cooperate so completely as to produce the unparalleled illustration of unity that is the individual unless they had worked out a way of getting the phenotype to behave in their individual interests more or less equally; and I suggested that social learning about nepotism could be that mechanism. Once set in motion, the stifling of selfish or outlaw nepotistic gene effects by the rest of the genome is as easy to envision as the stifling of dominance expression in deleterious mutants. One needs only to invoke a combination of Fisher's (1930) theory of dominance modification, P. M. Sheppard's (1969) generalization of Fisher's theory to include the concept of developmental canalization in the face of genetic as well as other environmental insults, and Egbert Leigh's (1971, 1977) concept of the parliament of the genes (See also Alexander and Borgia, 1978). The end result is the maintenance of a unity of interest among the genes, at least for all the time that they are involved in actually producing the phenotype and making it successful. Of course it is possible that there are many as yet poorly understood, knock-down-drag-out intragenomic tussles that take place every time somebody has to go into a polar body and be terminated there, but most "skin-in" biologists have not yet adopted the approach that would have caused them to notice such things.

Now I ask whether events like the initiation and maintenance of socially-imposed monogamy are not, in the end, understandable as extraordinarily complex parallels at the social level to simpler intragenomic mechanisms of cooperativeness. Chagnon (1974, 1979), Neel (1978), and others have described harem polygyny as the most powerful continuing force of differential reproduction in small human societies. Maybe this is an exaggeration, even if it does match what we are learning about nonhumans. But, certainly, polygyny is one of the more powerful forces of differential reproduction, and successful polygyny may be the most potent shift that one individual can effect in its own favor. Socially-imposed monogamy eliminates the possibility of such shifts or creates great risks with their achievement, and this kind of monogamy is part of the systems of laws that unite all of the largest most unified modern nations (Alexander, 1978, 1979).

Of course, from the viewpoints of most individuals, monogamy has virtues other than levelling off differential reproduction and, perhaps, creating unity from the realization among individuals that this has occurred and that this particular battle need not be fought continually at every level. For example, it allows one to transmit inheritance through daughters without the jeopardy that such resources may be diverted by a selfish son-in-law to the children of one of his other wives—and Gerald Borgia and I (ms) have found that, just as this idea predicts, inheritance is in fact most male-biased in nonsororally polygynous societies. Monogamy, from whatever source, also creates bonds between spouses, rooted in their common interest in a brood of offspring, and the history of such common interest; as far as adults are concerned, this bond may otherwise be without parallel in all of human history.

The French structural anthropologist, Claude Levi-Strauss (1969), and others have argued that the arranged cousin marriages of most of the world's middle-sized, polygynous societies are vehicles of alliance formation and maintenance. By definition such marriages would tend to set these alliances between groups of relatives—or clans—of rather small sizes. By an extension of the argument the discouragement of cousin marriages in the huge unified societies of the modern technological world may sometimes have generated as part of a multi-faceted discouragement of intense unity at subgroup levels, at the expense of the patriotism of whole-group unity. Emotionally united clans are greeted with hostility in our society unless they are tiny and harmless. Nepotism is almost a bad word. Family means immediate family, or else it too may become a bad word. Subgroups involving recognizable morphological differences, especially when they also involve declarations of first allegiance to one's subgroup rather than patriotism to the whole, have led to the genocidal horrors of history. Organized religion is not permitted to permeate the government unless it

includes the clear majority or the unchallenged power structures; and, as I see it, the unity of large societies is most fearsome when there is a coincidence of government and intense religion or some surrogate of religion as we ordinarily think of it.

I have been speaking as if culture is just biological adaptation. Long ago George Gaylord Simpson said exactly that about culture (Simpson, 1964), and he said that the sooner we recognize it the better off we will be. The problem then was that Simpson and his contemporaries were too far from understanding what biological adaptation is (Williams, 1966). Many investigators have suggested that the advent of culture in human history marked the end of biological adaptation—at least in regard to behavior—or, more recently, that the only way we can understand is through complex analyses of the degrees of separateness of the processes of inheritance of culture and inheritance of other aspects of phenotypes, or by abandoning the whole idea that culture changes in adaptive directions.

What is the heart of this puzzling issue? It seems to me that it is not heritability in the usual sense: After all, cultural changes can be more heritable than genes or they can lack any heritability at all, and because they are heritable through learning, they can go back and forth between these two extremes within one generation. There are two real questions in comparing cultural and organic evolution: The first is not how heritable is culture but when is it heritable and when not: Who decides, and why? The second question is: How do the causes of cultural changes relate to the causes of their persistence and the needs of the practitioners? We know that in organic evolution the causes of genetic mutations are independent of the causes of natural selection, and this is what depresses the rates of mutations and also accounts for the inertia of evolutionary change. Cultural evolution differs, because the causes of cultural novelties are not always independent of the needs of individuals and groups. Cultural novelties are born in the mind's eyes of individual entrepreneurs and planning groups: They have functions, as it were, before they are actually expressed. This, and the mode of inheritance of culture (learning), which allows swift reversals, are the reasons why culture tends increasingly to outrace genetic change. Whatever inertia culture possesses will be owing to the endlessly complex compromises, stalemates, and power plays that derive from conflicts of interests at all different levels (Alexander, 1979).

To discover how cultural change departs from genetic interests we must know who institutes cultural changes, and why, who accepts and resists them, and why, and what are the effects of the novelty that descends upon us at rates ever-increasing and wholly unanticipatable by the forces that produce the human capacity for culture and thus indirectly the novelty itself.

It is, of course, difficult to understand how culture can be the outcome of the collective efforts by individuals at genetic reproduction, and the surrogates of such efforts in novel environments. The most difficult of all questions in this regard, I think, is how slow directional changes in culture—those occurring across many generations—could reflect such efforts. Again, I believe that the answer will come from considering how the individuals and subgroups within any society turn the existing pattern of culture to their own ends, given the unbelievably complex networks of competition and conflicts of interest that typify every human social group. I think, especially, that we will need to know a very great deal about how individuals weigh the consequences of different possible actions by themselves in terms of how others might view them; and by different possible actions I mean to include mere expressions of agreement and disagreement, and satisfaction and dissatisfaction, with particular rules or attitudes discernible within the society. Changes like the institution of women's rights or the suppression of injustice toward minorities come about because increasing proportions of the population decide it is in their interest, and the effect snowballs—sometimes only with special pressure—as more and more individuals sense the shift of attitude and recognize the value of going along. And always, I would say, there lies behind the terribly difficult analysis of all such cultural phenomena the simple theory of human history that is developing largely from evolutionary biology—unless someone proves it wrong or comes up with a more reasonable alternative, which I regard as

exceedingly unlikely.

Our culture emphasizes the immediate family and the individual's set of relatives, as separate from that of every other individual. When subgroup coalitions are discouraged and each individual's personal collection of relatives is continually identified and set before that individual, freer rein is given, at least incidentally, to the individual's abilities and tendencies to serve his own interests so long as, paradoxically, he does not pursue them by establishing too-powerful kin groups or harems. Cultural anthropologists such as Schneider (1968) and Murdock (1949), the sociologist Talcott Parsons (1954), and others have all remarked on the absence of subgroup unity and the emphasis on the individual in the large societies possessing what I have here and elsewhere called socially imposed monogamy.

There follows, perhaps, the capitalistic encouragement of individual initiative in societies with socially imposed monogamy. Moreover, in these most unified societies we all stand to gain from creativity by individuals—hence, one suspects, copyright and patent laws. And we have used our ingenuity in these societies to form new kinds of coalitions—for example, some called corporations and others called cooperatives—both of these, despite their different connotations to some, securing for their members and their immediate families more resources than others would otherwise allow or see as fair shares. Deprived by group rules of the ability to spread resources amongst their clans for the precise purposes of history, and imbued with the drive and creativity of a relatively unleashed individualism, many have become what might be called obscenely wealthy in the expanding economies characterizing these cultures. And the fortunes tend often to stay together because they have come to involve items like money and shares of stock which, unlike the farms and herds of old, can be inflated in value by extreme subdivision; and these are usually transmitted to the few members of immediate families rather than dispersed to enrich the power of growing clans.

Paradoxically, in this urban world of unprecedented novelty and fluidity, and also unprecedented human cooperativeness and competitiveness, the individuality we induce may also cause us to be unusually susceptible to the human brand of loneliness. I quote the cultural anthropologist, Anthony F. C. Wallace (1961), in a statement utterly consistent with the new evolutionary theory of human nature:

The humanist—the poet, the novelist, the dramatist, the historian—has tended to approach . . . with a sense of tragedy (or humor) . . . the paradox, so apparent to him, that despite the continuing existence of culture and the group, the individual is always partly alone in his motivation, moving in a charmed circle of feelings and perceptions which he cannot completely share with any other human being. This awareness of the limits of human communication, of the impossibility, despite all the labor of God, Freud, and the Devil, of one man fully understanding another, of the loneliness of existence, is not confined to any cult of writers; it is a pan-human theme.

And so, with our individualized sets of genes and our history of individualized interests, we humans write poetry, philosophize, seek adoption by surrogate kin groups, sometimes commit suicide, and travel on through history trying to decide where we should go from here, given what we seem to have found out about where we have been. A part of that finding out is the knowledge of the depth and nature of our conflicts of interest during history, measurable only by carrying our analyses to the level of the gene.

The other part of the finding out is the realization of the profundity and unpredictability of the consequences of the ever-accelerating introduction of real novelty into our environment. So far as I can see, the two ideas together put the lie to any ordinary meaning of the phrase "genetically determined" as applied to human behavior, and they cast much doubt on our ability to prognosticate the so-called "biological limits" of human nature or the most appropriate behavior or morality of the future. Surely we can take a lesson from those who naively tried to establish an all-wise eugenics as soon as genes were discovered. If someone argues that we must at all cost maintain the diversity of the gene pool, let him also

realize that without tolerance of a diversity of opinions about what ought to be—about moral codes and ethical opinions—gene diversity is an empty facade.

I will end by noting that the eccentric nature of our culture has not been lost on the more ancient and perhaps more properly human cultures that have had the misfortune to co-exist with it. Thus, an Eskimo version of the origin of our peculiar culture goes as follows: An Inuit girl (and I am told that Inuit means human), to the horror of her parents, accepted her father's dog as a mate. When the father realized how she had gotten pregnant he banished her to a small, desolate island where, true to his worst fears, she gave birth not to a single child but to a whole litter. The island was so small and poor that she could not support her half-human half-animal litter, and so she set them afloat in the only available boat, which happened to be a leaky one, hoping that they would somehow arrive at a better fate. According to the Eskimos, the restless, obsessive, ambitious, and boorish nature of the members of the culture deriving from this original litter is a consequence of their having been thoroughly infused with the necessity of bailing frantically and continuously to keep their leaky boat from going down (from Kurelek, 1978).

Maybe there is a better analogy than this one; then, again, maybe there is not.

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This volume is dedicated to George C. Williams, whose pioneering efforts to return our attention to the crucial question of what are the units of selection and whose ideas regarding that crucial question, applied to such areas of research as senescence, sterile castes in the social insects, reproductive effort, sexuality, sex ratios, among many others, in large part fostered the revolution responsible for the research presented here.