Third, we need to develop theories of transition between organizational levels, so that knowledge of behavior on one level can be used to predict behavior on another level. Paradoxically, in all of this, there is a new danger of overemphasizing individuals as independent entities. Gains will be made when individual-level theorists remember that the adaptations of individuals are not independent nor are they dependent solely because of shared genes. The effort to understand the characteristics of groups and social systems beginning with a focus on individuals will need a better theory of "interest group" activities, where interest groups are defined by any form of fitness interdependence including control of access to strategic resources. Related to this is a need for incorporating social structure into coevolutionary models for human social behavior.

Finally, in addition to any understanding of the present gained from a coevolutionary view of the past, the insights from these endeavors should prove useful as tools for contemporary social change.

3. Evolution and Culture[1]

Richard D. Alexander

The basic argument developed by Darwin, and destined to become the central principle upon which all of biology rests, was two-part in nature. The first part was that all of life is continually and relentlessly subjected to a process of differential reproduction of variants, which Darwin termed natural selection or "survival of the fittest." The second was that all of the attributes of life are owing, directly or indirectly, to the cumulative effects of this process. No significant doubt has ever been cast on the first part of this argument, and the only alternatives to the second, advocated since 1859, have been divine creation and culture.

1 I thank Laura Betzig for allowing me to read an essay of hers which prompted me to begin immediately to develop and write down some of the ideas in this paper.

Concerning divinity

The effects of accepting both parts of Darwin's argument are that (1) the traits of modern organisms are, in terms of the environments of history at least, assumed to be means of maximizing genetic reproduction and (2) the patterns of long-term change observable from paleontological data are assumed also to be owing to natural selection. Creationists believe that unfilled gaps in the paleontological record imply creation, hence did not involve change by natural selection; and most thoughtful people would agree that some extensive changes during human history, evidenced in the archaeological record, are likely to have been unaccompanied by genetic change, hence also did not involve change by natural selection.

A degree of importance for natural selection has been granted by both creationists and the most radical adherents to the idea that culture and biology have been independent throughout human history. Thus, the organized supporters of creation as an alternative to evolution, such as members of the Creation Research Society (see the *Creation Research Society Quarterly),* have found it necessary to accept the process of natural selection, which they refer to as "microevolution" (e.g., Moore and Slusher 1970). They have established their line of defense chiefly against "macroevolution," which is their name for natural processes, supposed by others to account for the formation of "major organs" and for the origin of large changes or differences among organisms, such as exist between species or "major groups." The creationists argue that because the formation of major groups or major organs cannot be observed directly or studied by experiment, its analysis is outside science; and they argue that this process is best explained as creation. Understandably, they have remained indefinite about the precise nature of major groups and major organs, or the levels at which divine creation is unavoidable.

Many lines of evidence indicate that creationists are wrong in their efforts to distinguish long-term and short-term changes in evolution. Darwin offered a devastating critique of this view, and anticipated the small, cumulative effects of gene mutations as well, when he noted that major organs are the products of large numbers of small changes of the observable kind attributed by creationists to "microevolution." This fact is easily demonstrated by crossing organisms with variant forms of a given major organ or attribute. Darwin went so far as to offer the challenge that "If it could be demonstrated that any complex organ existed, which

could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down" (1967[1859]:189). A related class of evidence derives from laboratory or forced hybridization of different species or genera, a procedure which clearly shows that differences between such forms are also accumulations of small mutational changes of the directly observable kind (see also Alexander, 1978b).

Concerning humanity

Creationists thus deny that the second part of Darwin's thesis applies to humans by denying that the *earliest* of human attributes—i.e., those actually responsible for the designation "human"—originated through natural selection. Students of culture, on the other hand, tend to deny that the most *recent* of human attributes can be understood by reference to natural selection—i.e., the details of cultural patterns and differences—because they feel that the advent of traditionally transmitted learning signaled the end of any necessary relationship between behavior and the differential reproduction of alternative genetic elements.

Some recent authors have developed arguments, often explicitly about human behavior and culture, as alternative to natural selection in ways that may seem to cast doubt upon even the first part of Darwin's argument. Three such arguments seem most prominent.

Is Selection Tautological? The first argument is that the basic thesis of natural selection is tautological. Supporters of this view (e.g., Peters 1976) contend that we are unable to identify the "fittest" organisms or traits except retrospectively, and that, accordingly, we can only identify them as those which *have survived.* This argument ignores an enormous body of evidence confirming its falsity. Biologists, as well as plant and animal breeders, are continually able to identify as unfit individual organisms whose phenotypic attributes reveal ahead of time that their chances of reproducing are either nonexistent or relatively small (see also Ferguson 1976; Stebbins 1977). Success in such predictions is possible, as with the maintenance of adaptation, only to the extent that environments are predictable. But all environments of life have some predictable aspects. We can prove this directly, and the countless fashions in which organisms are marvelously and intricately tuned to their environments show that we are correct in assuming that the empirical evidence of environmental consistency is relevant to the process of evolution. Modern evolutionary biology depends upon an ability to generalize about adaptiveness, both across

genetic lines and across generations, and remarkable success is being realized from such generalizations, especially with attributes common to most or all organisms, like sex ratios, senescence, and parental investment, and others for which the social environment is crucial, like group-living, nepotism, and sexual competition (see references in Alexander 1977a, 1977b, and Alexander et al., this volume, chapter 15). In the first case more effective comparisons are possible; in the second, the winning strategies are more stable and more easily identifiable.

Criticisms that statements about natural selection are tautological only concern their predictive value, but some detractors have supposed that they also cast into doubt the existence or universality of the entire process. Even retrospective judgments, however, are entirely sufficient to demonstrate the inevitability of differential reproduction, whether or not humans are aware of its workings or capable of assessing its consequences.

The argument that natural selection is tautological is often linked with statements by prominent evolutionists, such as Mayr (1963) or Simpson (1964), that evolution is not a particularly predictive or predictable phenomenon, to suggest that evolution does not even qualify as a scientific theory. The misapprehension involved is failure to see that Simpson and Mayr were talking about our inability to predict or give the adaptive reasons for ancient or long-term phylogenetic changes because we are necessarily ignorant of the environments of selection during geological time. We are not so ignorant of the current and recent environments of selection, and our understanding of them grows constantly.

Organic evolution leads to patterns of change in morphology, physiology, and styles of life. Some of these patterns are reflected by fossil remains and some by the array of organisms present at any given time. Evolution also involves speciation, which results in irreversible divergences of different patterns of life. Pattern changes and speciation together lead to phylogenies or family trees that presumably, if the record were complete, could be reconstructed to illustrate the whole history of life. But phylogenetic patterns, although they are outcomes of evolution, are not the essence of the process. The essence of the process is differential reproduction, or, as Williams (1966) put it, the maintenance of adaptation. Phylogenies are reconstructed with little understanding of the selective forces that produced their patterns because the environments of long-term history cannot be reconstructed with the precision necessary to reconstruct the generation-by-generation effects of natural selection. Efforts to "predict" phylogenies, or the nature of species (i.e., to presage what will be discovered about either the past or the future when more complete informa-

tion is available) fail to the extent that we are ignorant about environments and the array of living organisms present at each time and place in history. They do not fail, as Peters (1976) suggested, because of the demonstrable independence between the causes of mutations and the causes of selection. Our inability to make long-term evolutionary predictions thus does not mean that the nature of the process yielding evolutionary patterns is itself to be doubted, or that evolutionary propositions are so tautological as to fail as scientific theory. Predictions about adaptiveness are most accurate when they concern short-term changes in the present, and there is every reason to believe that they fail increasingly with longer time spans, or when other eras are considered, simply because our information about environments is more incomplete in such cases.

Arguments about the relationship of long-term pattern changes during evolution to the process of natural selection, which is widely accepted as responsible for short-term changes, have relevance here because of the common failure to realize that long-term pattern-tracing (paleontology, archaeology) can be carried on without direct attention to or concern for the process responsible. In biologists' terms, the process of change is guided largely by natural selection. For anthropologists, it is probably fair to say that there is no universally accepted *guiding force* to account for the changes commonly called cultural evolution or for modern variations in culture. The question we must ultimately address is: what is the nature of this guiding force and to what extent has it been the differential reproduction of genes, realized through reproductive striving of individuals? In this question there is no implication that reproductive striving is consciously so directed.

Is Selection Often Impotent Because of Lack of Genetic Variation? The second argument seeming to cast doubt on the universality of natural selection is that genetic variations relevant to selective forces are not always present, rendering selection ineffective. But this argument only specifies rare and temporary situations. As any plant or animal breeder knows, even in genetic lines on which directional selection has been practiced for a very long time, genetic variants and combinations now and then appear which are relevant to a desired direction of change. Because of their unpredictability, the only way to take advantage of such variants is to maintain selection. This realization causes humans to practice artificial selection in a way that parallels the differential reproduction of organisms induced by natural environments, which is also inexorable whether or not the variations involved are heritable (and also ineffective when they are not).

For this reason we may assume that in natural populations most novel variants which increase reproduction spread and become characteristic of the population, and that this is the usual process of evolutionary change.

The reasons why natural selection is regarded as the guiding force of evolution are not commonly discussed, but they are obviously crucial (see Alexander 1977a, for a fuller discussion). The most apparent ones are the following: (1) altering directions of selection alters directions of change in organisms (probably always, even if there is sometimes delay owing to specialization as a result of previous selection), (2) the causes of mutation (chiefly radiation) and the causes of selection (Darwin's "hostile forces" of food shortages, climate, weather, predators, parasites, and diseases) are independent, (3) only the causes of selection remain consistently directional for relatively long periods (thus, could explain directional changes), and (4) predictions based on the assumption that adaptiveness depends solely on selection are met (e.g., consider the history of sex-ratio selection: Fisher 1958[1930]; Hamilton 1967; Trivers and Willard 1973; Trivers and Hare 1976; Alexander and Sherman 1977; Alexander et al., Chagnon et al., this volume).

The greatest constraints on selection occur then, paradoxically, in two opposite situations: when the change of selective direction is very great and when unidirectionality persists for a very long time. In the first case, specializations as a result of previous selection reduce the likelihood of adaptive changes in certain directions; thus, moles are almost certainly less likely than squirrels to evolve wings. In the second case, alleles causing change in the favored direction are apt to be fixed by selection faster than mutants arise; thus, after generations of selection for increased milk production, dairy farmers know that "management" (i.e., environment) is crucial but, obviously, they will continue to favor breeding stock from their best producers in the expectation that once in a while the differences will be heritable. Unlike many aspects of phenotypes, cultural variations of humans, which lack correlation with genetic variations, may nevertheless be heritable because of traditional transmission of learned behaviors. Thus, as is well understood, culture has the unusual property of being able to evolve cumulatively in the absence of genetic change. Rates of cultural change within historical times are clear evidence that massive cultural change does indeed occur without genetic change, or in its virtual absence. However, for cultural change to be independent of natural selection, the following hypotheses would also have to be true: (1) because directions and rates of cultural change are potentially independent of many or most human genetic changes, they are independent of the history of natural selec-

tion upon humans; and (2) genetic change through natural selection is not induced by cultural changes. Until very recently, both of these hypotheses have remained largely untested; should they eventually be rejected, as I believe likely, then even for human culture the second part of Darwin's argument will stand as stated above.

Does Evolutionary Theory Suggest Genetic Determinism? The third argument about the relationship of biology and culture is exemplified by the newspaper announcement of the British Broadcasting Corporation film "The Human Animal," which identified sociobiology as "The field of study built on the theory that behavioral patterns in humans are inherited through genes." This definition is, perhaps innocently, a version of the argument that efforts to invoke biological explanations of human behavior are efforts to defend the notion that behavior is "genetically determined." It cannot be denied that some statements by biologists also suggest this kind of naïveté. But there is equal naïveté in supposing that merely to consider genes as influences upon behavior (or any other aspects of phenotypes) means that one is automatically excluding the environment or underplaying its role. To argue that behavior is a product of a history of natural selection, however, is in no way an argument that behavior is determined by the genes. It is almost the opposite—a declaration instead that the behavior of each organism is determined, not by the genes, but by the genes and the developmental and experiential environment together. That the mere introduction of genes as influences on behavior is construed as an unsupportable kind of genetic determinism is indicated by the tendency to contrast explanations which include genes with explanations invoking learning. For so many years we asked: "Is this behavior learned or genetic?" Finally, we are coming to realize that the answer is always "Both." The consequence of this realization is not the exclusion of biology from considerations about human behavior but its appropriate reintroduction into them. (For fuller discussions see Alexander 1978a, 1977b, 1977c.)

Traits, Learning, and Genetic Variation To explain this paradox it is fruitful to consider still another question recently made prominent by self-professed critics of evolutionary approaches to the analysis of human behavior. What is a "trait"? This question seemingly has two aspects. First is the problem of how much or what part of the phenotype can be viewed as a unit in terms of function. In other words, upon what parts and amounts of the phenotype is selection acting in a given circumstance or environment? How much of the phenotype does a given kind or aspect of selection affect?

The second part of the question involves how the genes work together during ontogeny to create the phenotype—in other words, how do the genes in the genotype relate to the identifiable components of the phenotype? A history of natural selection suggests that in some sense these two problems resolve into a single one: How do the units within genotypes (genes, supergenes, chromosomes, etc.) interact (through epistasis, pleiotrophy, linkage, etc.) to produce the functional units (appendages, sensory devices, reproductive organs, etc.) of the phenotype?

This question relates to the genes/learning dichotomy because of a common confusion between (1) whether or not a particular behavioral variant characterizes a particular genotypic variant and (2) whether or not a particular *set* of behaviors characterizes a particular genotypic variant. If a particular behavioral act was learned, then its individual presence as a variant is clearly not a result of genetic variation. But genes are necessarily causal (together with their environment) in the production of all behavior; the only problem is to understand how. To reach this understanding we must consider entire sets of learned behaviors in the set of different individuals possessing the same set of genes influencing that behavior in the collection of environments in which the set of individuals developed. Ideally, such entire sets of learned behaviors would be compared with other sets of learned behaviors in other sets of organisms which do differ genetically. In a species with a great deal of immediate-contingency learning in the behavioral repertoires of individuals, then, the effects of genes on learned behavior can only be understood by analyzing the behaviors expressed by *numerous* individuals who *collectively* have experienced the array of environments in which the behavior in question has evolved, or the environments in which it has usually been expressed. Traits can only be identified by examining the variations in learned activities in the normal range of environments of learning. Genetic change could shift the ease of learning in such a group of organisms one way or another along one or more axes, or reduce or abolish certain possibilities. The adaptive or evolved aspect of learning traits so identified will be the nature or range of expression correlated with the usual environments of history, with non-adaptive, maladaptive, or evolutionarily incidental aspects represented by those appearing in novel or rare environments. Obviously, such "incidental" or non-evolved aspects of learning are crucial in understanding human behavior because of the extraordinarily rapid changes induced by culture and technology. What would be left is a set of learning abilities, the range and relative ease of which have been tuned by natural selection acting on the genetic makeup of the population. It is difficult for me to conceive of

any other relationship between learned behaviors and the process of natural selection.

Indeed, what I have just described is the general relationship between natural selection and all kinds of expressions of the phenotype, whether behavioral, physiological, or morphological. This is the reason why—even though learning, or variation resulting from environmental variation, is an explanation for observed behavioral variations which is alternative to an explanation based on genetic variation—cultural evolution is not an *alternative* to natural selection as a general explanation for the nature of human activities. Cultural patterns are, like all expressions of the phenotype, outcomes of different developmental environments acting on sets of genetic materials accumulated and maintained by natural selection. Culture differs from other aspects of phenotypes in the degree to which it can change without genetic change; but behavior in general differs from morphology and physiology in the same regard. This is the raison d'être of behavior. It is a way of responding to a greater proportion of the information available to the organism from immediate contingencies in its environments. Culture is a particular and elaborate system of behavior for doing the same. The questions we are led to ask about culture, after considering it in a biological context, are the same that would be asked from any other analytical approach: What forces influence its patterns? What do its expressions mean? The only distinctive aspect of a biological approach is that we are apt to ask these questions in relation to biological functions, or reproduction. This attitude may seem alien to social scientists, but the correct answers to questions about the significance of culture will be the same regardless of the manner in which they are approached.

Concerning culture: natural selection and culture theory

Probably because anthropologists and others tended to identify the possession of culture and the capacity for culture as peculiarly human traits, the concept of culture has acquired and retained a certain singularity: hence, perhaps, efforts to seek general or singular theories of culture; and perhaps also the assertion by investigators reluctant to see culture in this way that "Culture is dead"—that is, that it does not possess the singularity attributed to it and that truly general theories of culture are therefore unlikely. Others, still convinced about the generality of the concept of culture, have come to the notion that, in the absence of acceptable functional explanations, culture can only be explained in terms of itself, or as a set of arbitrarily assigned meanings or symbolizations (White 1949; Sahlins 1976b),

and specifically cannot be explained in terms of utilitarianism of any sort or at any level. White, for example, writes skeptically of man's "vaunted control of civilization" and of the fond belief that it "lies within man's power . . . to chart his course as he pleases, to mold civilization to his desires and needs."

Culture, such authors seem to be arguing, is something greater than humans collectively and almost independent of humans individually: It continues on courses perhaps unpredictable, and certainly swayed but slightly by the wishes of individuals, who are merely its "passive" transmitters. Sahlins comes very close to describing culture as an aspect of the environment of humans about which they can do little but accept it in just those terms, thereby almost paralleling the biologists' concept of the genotype and the phenotype as parts of the environment of selection of the individual genes.

But, 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" course to chart in the development of culture but rather a very large number of slightly different and potentially conflicting courses. In such event 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 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 inclusive-fitness-maximizing behavior (i.e., reproductive maximization via all socially available descendant and nondescendant relatives) of the entire collective of all humans who have lived. I here advance this as a theory to explain the existence and nature of culture, and the rates and directions of its change.

If this theory is appropriate, then aspects of culture would be expected to be adversary to some of the wishes of each of us; few aspects of it would be viewed with equal good humor by all of us; and in just this circumstance we would not expect grand utilitarian views of culture, general theories of culture, or efforts at purposeful guidance of culture to succeed easily. These are exactly the kinds of failures that have always plagued culture theorists. Yet, by this theory, the inertia of culture would exist *because* individuals and groups did influence its directions and shape, molding it—even if imperceptibly across short time periods—to suit

their needs, thereby incidentally increasing the likelihood that subsequent individuals and groups (a) could find ways to use it to their own advantages as well and (b) could not alter it so greatly or rapidly.

It would also be a source of confusion, in attempts to relate directions and rates of cultural change to utilitarian theories, that the reproductive efforts of individuals would not actually be directed at *changing* culture, as such; nor would such efforts lead to any particular directions of change in culture as a whole. The striving of individuals would be to *use* culture, not necessarily by changing it, to further their own reproduction. No necessary correlation would exist between success in the reproductive striving of an individual and the magnitude of the individual's effect on cultural change, or between the collective success of the individuals making up a group or society and the rate of cultural change. It would not matter if one were a legislator *making* laws, a judge *interpreting* them, a policeman *enforcing* them, a lawyer *using* them, a citizen *obeying* them, or a criminal *circumventing* them: Each of these behaviors can be seen as a particular strategy within societies governed by law, and each has some possibility of success.

Again, it would tend to be contrary to the interests of the members of society that cultural changes of any magnitude could easily be effected by any individuals except for inventions seen as having a high likelihood of benefiting nearly everyone. The reasons are that (1) changes, effected by individuals or subgroups in their own interests, would likely be contrary to the interests of others; and (2) once individuals have adopted and initiated a particular set of responses to the existing culture around their own interests, changes of almost any sort have some likelihood of being deleterious to them. These arguments not only suggest how anthropological interpretations of culture may be entirely compatible with the notion of reproductive striving principally effective at the individual (or genic) level, but also may explain the genesis of views that culture is somehow independent of individuals and groups and their wishes, and not easily explainable in utilitarian terms.

The Evolution of Culture

It is a fundamental characteristic of culture that, despite its essentially conservative nature, it does change over time and from place to place. Herein it differs strikingly from the social behavior of

animals other than man. Among ants, for example, colonies of the same species differ little in behavior from one another and even, so far as we can judge from specimens imbedded in amber, from their ancestors of fifty million years ago. In less than one million years man, by contrast, has advanced from the rawest savagery to civilization and has proliferated at least three thousand distinctive cultures [*George Peter Murdock, 1960b:247*].

If long-term changes in human phenomena, as evidenced for example in the archaeological record, are cultural, and were not induced by natural selection or accompanied by genetic changes relating to cultural behavior, then we should be interested in answering two questions: First, what has guided cultural evolution? What forces can account for its rates and directions of change? Second, what degrees and kinds of correspondence exist today between the patterns of culture and the maximization of genetic reproduction of the individuals using, transmitting, and modifying culture? Are the degrees and kinds of correspondence, and of failure to correspond, consistent with the forces presumed to underlie rates and directions of cultural change?

At one end of a spectrum lies the possibility that all of the cultural changes during human history have been utterly independent of genetic change, neither causing such nor caused by it. At the other end is the possibility that changes in human behavior have correlated with genetic change to approximately the same degree as changes in the behavior of other species, such as non-human primates. Observations within recorded history are sufficient to show that neither of these extreme possibilities is likely. As examples, cultural changes, such as eyeglasses and treatments for diabetes, obviously influence genetic change; and cultural changes clearly have accelerated tremendously in recent decades without any evidence of parallel acceleration in genetic change. At least, then, cultural changes do influence genetic change although there is apparently no clear evidence that genetic changes are causing cultural changes, or that there is any close correlation between cultural changes and genetic changes that specifically influence behavior in relation to culture. Now, it is easy to understand, on theoretical grounds, how culture can change cumulatively without accompanying genetic changes that relate to the behaviors involved—and easy to argue that numerous such changes have occurred within recorded history when strikingly different cultures merged. Therefore the significance of the

above two questions about the forces which change culture and the relationships of culture to maximization of reproduction by individuals is brought into an even sharper focus. We expect that the answers to these two questions will be complementary, and that the efforts to answer them should be conducted simultaneously and jointly.

Some changes in culture, such as those influenced by climatic shifts, natural disasters, and diseases, predators, and parasites (of humans and the plants and animals on which they depend), are beyond human control; others are explicitly under such control, although such control may be very direct (invention and conscious planning) or not so direct (resource depletion and pollution). The difficult question, in understanding the relationship between culture and our inevitable history of natural selection, is not in discovering the reasons behind cultural changes, as such, which are actually fairly obvious. Instead, it is in understanding exactly *how* such changes influence culture: What is done with them? What *direction* of change do they induce, and why? Those changes in culture which are consequences of human action appear to represent products of the striving of individuals and groups of individuals. Such changes, as with extrinsically caused changes, are also *responded to by changes* in the striving of individuals and groups of individuals. Inventions are seized upon. Pollution and resource depletion are lamented, and cause geographic shifts in population or efforts at inventions or practices which will either offset their effects on the lives of those showing the effort or allow them to take advantage of such effects. Attempts are made to predict and offset natural disasters and climatic shifts. All of these responses are easily interpretable as part of efforts by individuals, acting alone or in groups, to use culture to their own advantage in the fashion already suggested. But culture is not easily explainable as the outcome of striving to better the future for *everyone equally:* If that were the case, then surely conscious planning would quickly become the principal basis for cultural change, and it would be carried out with a minimum of disagreement and bickering (perhaps we shall actually be able to make our interests coincide to a greater degree by realizing that we have a background of competition in genetic reproduction, which may be less interesting to us once exposed to our conscious reflection).

It is possible to examine the problem of cultural change in a fashion parallel to that used for evolutionary change (e.g., Alexander 1977a). We can ask about the same five phenomena which characterize the process of genetic change (the most closely parallel argument is probably that of Murdock [1960b]).

1 *Inheritance:* Just as the morphological, physiological, and behavioral traits of organisms are heritable, given consistency in the developmental environment, the traits of culture are heritable through learning. They may be imitated, plagiarized, or taught.
2 *Mutation:* Like the genetic materials, culture is mutable, through mistakes, discoveries, inventions, or deliberate planning (Murdock's "variations," "inventions," and "tentations").
3 *Selection:* As with the phenotypic traits of organisms, some traits of culture reinforce their own persistence and spread; others do not, and eventually disappear for that reason (Murdock's "social acceptance," "selective elimination," and "integration"). (See also Campbell 1965, 1975.)
4 *Drift:* As with genetic units, traits of culture can also be lost by accident or "sampling error."
5 *Isolation:* As with populations of other kinds of organisms, different human societies become separated by extrinsic and intrinsic barriers; they diverge, and they may come into contact and remerge or continue to drift apart; items and aspects of culture may spread by diffusion (Murdock's "cultural diffusion" and "cultural borrowing").

Immediately, differences are apparent between the processes of change during genetic and cultural evolution. Unlike genetic evolution, the causes of mutation and selection in cultural evolution are not independent: Instead, there is a feedback between need and novelty. Most of the sources of cultural "mutation" are at least potentially related to the reasons for their survival or failure.

Some culture theorists have tended to deny utilitarian connections between the sources or causes of cultural change and the reasons for their survival or failure. I suggest that the reason for these denials is that such theorists have never sought function both in terms of reproduction and at the individual level, as biologists now realize must be the case in organic evolution. Some, such as Franz Boas and Ruth Benedict, have emphasized the individual; others, such as Bronislaw Malinowski and A. R. Radcliffe-Brown, have emphasized function as survival value—even, sometimes, to the individual. None, however, has seen function as reproductive value. Instead, most functionalists have either sought group-level utilitarian effects or have regarded survival, not reproduction, of the individual as crucial (for reviews of such views, see Hatch 1973; Harris 1968).

Some recent investigators, such as Cloak (1976), Dawkins (1976),

Durham (1976a), and Richerson and Boyd (1978), have concentrated on heritability of cultural traits (or cultural novelties or "instructions") and argued that their separate mode of inheritance thwarts the operation of natural selection of genetic alternatives. I regard this approach to the history of culture as similar to a view of the natural history of organisms that sees phenotypes in general (as opposed to no phenotypes) as essentially thwarters of natural selection. In one sense they are, since they necessarily render the action of selection on the genes less direct: Selection must now act through the phenotype. But this change had to have occurred because those genes that reproduced via phenotypes outsurvived their alternatives in the environments of history. So must it be with the capacity for culture, as the above authors for the most part acknowledge. Even if culture outraces organic evolution, creating blinding confusion through environmental novelties, to view the significance of its changes and its traits as independent of, or as mere thwarters of, natural selection of genetic alternatives, would be parallel to supposing that the function of an appetite is obesity.

The important question in cultural evolution is: Who or what decides which novelties will be perpetuated, and how is this decided? On what basis are cultural changes spread or lost? In other words, we are led to analyze exactly the same part of the process of cultural change as for genetic change. In cultural change the answer to this question of who decides, and how, actually determines the heritability of culture, since heritability of cultural items at least theoretically can vary from zero to 100 percent from one generation to the next, or even within generations. Any cultural trait, unlike a gene, theoretically can be suddenly cancelled and just as suddenly reinstated, in the population as a whole. Again, in theory at least, this can be done as a result of conscious decision based on what the involved parties see as their own best interests at the time. This reinforcing relationship among selection, heritability, and mutation in culture means that, unlike organic evolution, heritability of culture traits will not be steadily increased; nor will mutability be depressed because the majority of mutations are deleterious in the individuals in which they arise owing to the lack of feedback between mutational directions and adaptive value. Some cultural mutations appear (that is, are implemented, or translated from thought to action) because they are perceived to have value. Unlike evolutionary change, then, cultural change will acquire inertia to the extent that the interests of individuals and subgroups *conflict* (and have a history of conflicting), and whenever the distribution of power is such as to result in stalemates. In part this means that cultural change may be expected to continue accelerating, and this acceleration, I believe,

will not only make it increasingly difficult to interpret human behavior in terms of history, but will also increasingly become apparent as the source of novel ethical problems, bound to increase in numbers and severity as cultural change accelerates, because ethical problems derive from conflicts of interest and these are bound to become more complex (Alexander, in press a).

Most recent and current efforts to relate genetic change and cultural change, then, seem really to be efforts to divorce them—to explain why and how culture and genes came "uncoupled" during human history. These arguments generally assume that the uncoupling is essentially synonymous with the appearance of culture—that culture is, by definition, an uncoupling of human behavior from gene effects.

I think these are the reasons why virtually all efforts to understand culture in biological terms have failed. We can easily assume that the capacity for culture *allowed* (as an incidental effect) various degrees of uncoupling of human behavior from reproductive maximization. In modern urban society, for example, such uncoupling is rampant. But to assume that uncoupling is the (historical, biological, evolutionary) function of culture, or its basic significance or attribute, is, as already suggested, like assuming that the function of an appetite is obesity.

There is enough evidence, even in everyday life, to indicate that in general human social behavior is remarkably closely correlated to survival, well-being, and reproductive success. If one accepts this assumption then it is easy to agree that the real question is: What forces could cause the continued coupling between culture and genes? In effect, we must discover, for cultural as well as genetic evolution, the nature of the "hostile forces" (paralleling Darwin's "Hostile Forces" or predators, parasites, diseases, food shortages, climate, and weather [see Alexander 1977a] responsible for natural selection's effects on gene frequencies) by which variations in human social behavior and capacity are selected, by the adjustment of strategies or styles of life, consciously and otherwise, by individuals and groups.

Few people would doubt that positive and negative reinforcement (learning) schedules relate, respectively, to environmental phenomena reinforcing (1) survival and well-being and (2) avoidance of situations deleterious to survival and well-being. With ordinary physical and biotic stimuli this relationship is easy to understand: We withdraw from hot stoves, avoid poisonous snakes, seek out tasty foods, appreciate warmth in winter, dislike getting wet in cold rains, etc.

What about social stimuli? Should it not be the same? Should we

not seek social situations that reward us and avoid those that punish us? Should not the actual definitions of reward and punishment in social behavior, as with responses to physical stimuli, identify for any organism those situations that, respectively, improve or insult its likelihood of social survival and well-being, with appropriate connotations for reproductive success? Is it possible that Sheldon (1961) was right in suggesting that ". . . the reason why many pleasures are wicked is that they frustrate other pleasures"? That evil consists ". . . in frustrations, as the Thomist says, in privation of one good by another"? Is what is pleasurable, hence, "good" and "right," that which, at least in environments past, tended to maximize genetic reproduction?

Arbitrariness in culture

The symbolic or seemingly arbitrary nature of many aspects and variants of culture is commonly regarded as contrary to any functional theory, and especially to the notion that culture can somehow be explained by a history of differential reproduction by individuals. Of course, *seeming* arbitrariness may represent observer error based on failure to understand the significance of environmental variations. Arbitrariness may also be a consequence of the inertia to cultural change in the face of environmental shifts; of mistakes about what kind of behavior will best serve one's interests—especially in the face of the constant and accelerating introduction of novelty, primarily through technology. But, even if the assessment of arbitrariness is actually correct, it need not be contrary to a theory based on inclusive-fitness-maximizing, particularly if culture is explained as a product of the different, as well as the common, goals of the individuals and subgroups of individuals who have comprised human society during its history. Thus, however symbolism and language arose—say, because they were superior methods of communication—their existence, as the major sources of arbitrariness, also allowed the adjustment of messages away from reality in the interests of the transmitting individual or group. In other words, as abilities and tendencies to employ arbitrary or symbolic meanings increased the complexity and detail of messages, and the possibility of accurate transmission under difficult circumstances (e.g., more information per unit of time or information about objects or events removed in time or space), they also increased opportunities for deception and misinformation. It would be a consequence that arbitrariness could typify some of the different directions taken by cultural changes which were nevertheless crucial to their initiators and perpetuators.

Consider the relationship between status and the appreciation of fashion, art, literature, or music. What is important to the would-be critic or status-seeker is not alliance with a particular form but with whatever form will ultimately be regarded as most prestigious. If one is in a position to influence the decision he can, to one degree or another, cause it to become arbitrary. Fashion designers, the great artists, and the wealthy are continually using their status to cause such adjustments. In no way, however, does such arbitrariness mean that the outcomes are trivial or unrelated to reproductive striving. Precisely the opposite is suggested—that arbitrariness may often be forced, in regard to important circumstances, because the different circumstances involved represent important alternatives and because forcing arbitrariness is the only or best way for certain parties to prevail.

These various suggestions may simultaneously explain the genesis of "great man" theories of culture and their failure as general explanations. Great men do appear, and their striving, almost by definition, is likely now and then to have special influences; but, for reasons given above, not necessarily great influences and not influences leading to particular, predictable, overall changes in culture.

The old saw that "one hen-pecked husband in a village does not create a matriarchy" also emphasizes not only that individuality of striving occurs within culture but that it does not necessarily lead to trends. Similarly the argument about status and arbitrariness is a variant of the adage that "when the king lisps everyone lisps," and it bears on the notion of a "trickle-down" effect in stratified or hierarchical social systems. But it indicates that the "trickle-down" effect, rather than being a societal "mechanism for maintaining the motivation to strive for success, and hence for maintaining efficiency of performance in occupational roles in a system in which differential success is possible for only a few . . ." (Fallers 1973) is a *manifestation* of such striving, and a *manifestation of degrees of success.*

As already noted elsewhere in this volume, several recent studies have suggested that many aspects of culture, involving such items as patterns of marriage, inheritance, and kinship behavior, and varying in expression among societies, are neither arbitrary nor independent of predictions from a theory dependent upon inclusive-fitness-maximizing by individuals (Alexander 1977a).

Like learning theory and other theories that stop with proximate mechanisms, Malinowski's "functional" theory of culture, which was couched in terms of satisfying immediate physiological needs, did not account for the existence of those needs (Alexander 1977b). Thus, Sahlins

(1976a) was led to say that for Malinowski culture represented a "gigantic metaphorical extension of the digestive system." But Malinowski's theory would have made sense in the terms suggested here if it could only have been interpreted as seeing culture as a gigantic metaphorical extension of the *reproductive* system.

The ideas I have just suggested are alternative to recent efforts to explain the relationship of culture and genetic evolution—or, more particularly, their apparent lack of relationship—by suggesting that "cultural instructions" (Cloak 1975) or "memes" (Dawkins 1976) are selected in the same fashion as, and often in opposition to, genes or genetic instructions; or that two kinds of selection, often in opposition, are necessarily involved (Richerson and Boyd 1978). Arbitrariness, then, in fashion or any other aspect of culture, may not be contrary to the genetic reproductive success of those initiating and maintaining it, only to that of some of those upon whom it is forced, in particular those who are least able to turn it to their own advantage. To understand the reproductive significance of arbitrariness as a part of status-seeking, one need only understand the reproductive significance of status. One might suggest that there are *genetic instructions* which somehow result in our engaging in arbitrariness in symbolic behavior in whatever *environments* it is genetically *reproductive* to do so.

I suggest, then, that the rates and directions of mutability and heritability in culture are determined by the collectives and compromises of interest of the individuals striving at any particular time or place, together with the form and degree of inertia in the cultural environment as a result of its history; that the "hostile forces" that result in cultural change have tended increasingly to be the conflicts of interest among human individuals and subgroups in securing relief from Darwin's "Hostile Forces of Nature" (see above); and that, among these "Hostile Forces of Nature," increasingly prominent and eventually paramount have been what amounted to predators, in the form of other humans acting in groups or in isolation, with at least temporary commonality of interests (Alexander 1971, 1974, 1975a, 1977a).

By these arguments four outcomes are predicted: (1) a reasonably close correspondence between the structure of culture and its usefulness to individuals in inclusive-fitness-maximizing, (2) an even closer correlation between the overall structure of culture and those traits which benefit everyone about equally, or benefit the great majority, (3) extremely effective capabilities of individuals to mold themselves to fit their cultural milieu, and (4) tendencies for culture to be so constructed as to resist significant alteration by individuals and subgroups in their own interests and

contrary to those of others. If these predictions are regarded as important we shall be led to analyze the variations in culture potentially as the outcomes of different strategies of inclusive-fitness-maximizing under different circumstances, and the proximate or immediate physiological and social mechanisms whereby inclusive fitness is maximized as potential explanations of degrees and directions by which cultural patterns diverge from actual inclusive-fitness-maximizing behaviors when technological change and other events create novel environments outside the limits of those in which earlier behaviors functioned.

Concluding remarks

I think we may regard as settled the universality and inevitability of natural selection and the rarity of effective selection above the individual level, and as relatively trivial for social scientists the problem of the relative effectiveness of selection at the individual level as against some lower level. I also suppose that culture can evolve without genetic change, and that it does so frequently without diminution of inclusive-fitness-maximizing effects. It would appear that the immediate future in other areas of investigation will see concentration on two questions: (1) to what extent are cultural patterns actually independent of predictions from natural selection, and why, and (2) how could patterns of cultural behavior be consistent with natural selection in ways that do not do violence to our knowledge of the extent and nature of learning? The papers in this volume suggest this trend and indicate that in most cases the data, if they are to lead to convincing answers, will have to be gathered with these questions actually in mind.

The complexity of the picture developed by these arguments and conclusions indicates both the difficulty involved in extensive and thorough testing of an inclusive-fitness-maximizing theory of human sociality and the potential generality of such a theory. Such testing is the major challenge that lies ahead on the border between the social and biological sciences, together with the problem of dealing with the moral and ethical questions that arise along with any increase in understanding of human behavior and how to modify it. The tasks so identified are not likely to be easy or simple. But, then, no one who ever thought about human behavior in analytical terms is likely to have supposed that they would be.

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