



---

The Adaptive Significance of Cultural Behavior: Comments and Reply  
Author(s): Eugene E. Ruyle, F. T. Cloak, Jr., L. B. Slobodkin and William H. Durham  
Source: *Human Ecology*, Vol. 5, No. 1 (Mar., 1977), pp. 49-67  
Published by: [Springer](#)  
Stable URL: <http://www.jstor.org/stable/4602390>  
Accessed: 01/12/2013 13:50

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at  
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Springer is collaborating with JSTOR to digitize, preserve and extend access to *Human Ecology*.

<http://www.jstor.org>

## The Adaptive Significance of Cultural Behavior: Comments and Reply

Eugene E. Ruyle,<sup>1</sup> F. T. Cloak, Jr.,<sup>2</sup> L. B. Slobodkin,<sup>3</sup>  
and William H. Durham<sup>4</sup>

The following comments and reply concern William H. Durham's article "The Adaptive Significance of Cultural Behavior," published in *Human Ecology*, Vol. 4, No. 2, April 1976.

### COMMENT

F. T. Cloak, Jr.

In "The Adaptive Significance of Cultural Behavior," William H. Durham's handling of methodological and factual materials is far more successful than his effort at theory building. A method of determining and/or predicting the costs and benefits to individual fitness of various behaviors (Durham, 1976a; 104) would be most worthwhile, both for cultural studies (*cf.* Durham, 1976a: 98) and for studies of human genetics. And I hope, with Durham (1976a; 96), that students of both sorts will agree to use "adaptation" and its variants to refer to fitness-enhancing outcomes of cultural behavior.

Durham's examples, his "supporting evidence" (1976a: 106-113), are well chosen, well handled, and quite convincing. I applaud his successful effort thereby to show, *contra* certain anthropologists, that culture does have causal relations to genetic fitness and, conversely, *contra* certain biologists and publicists, that pro-fitness behaviors may be acquired culturally and not genetically. [But

<sup>1</sup> Department of Anthropology, California State University, Long Beach, California.

<sup>2</sup> 1417 East Cook Street, Springfield, Illinois.

<sup>3</sup> Ecology and Evolution Program, State University of New York, Stony Brook, New York.

<sup>4</sup> Division of Biological Science and Society of Fellows, University of Michigan, Ann Arbor, Michigan.

his notion that people have an innate ability to recognize and adopt cultural features that are good for them and to recognize and reject cultural features that are bad for them (1976a: 97, 105) seems unintentionally to reintroduce a genetic determinism of culture.]

The essence of Durham's thesis, however, is that most cultural determinants of human behaviors tend to increase (or at least not to diminish) the number of children begotten or borne by the behavior and/or his/her relatives, i.e., they enhance his/her inclusive fitness.

*Of course they do.* The explanation, which Durham appears to have overlooked (1976a: 94), is quite simple: it is a near-universal contingent *fact* (not a theoretical principle) that human beings, as a rule, rear and enculturate their own children. Wherever that is true, a cultural instruction whose behavior helps its human carrier-enactor (or his/her relatives) to acquire more children thereby has more little heads to get copied into. Thus cultural instructions that enhance inclusive fitness propagate through populations as generations go by, until most extant cultural instructions have that effect. (For a more thorough discussion of cultural instructions, see Cloak, 1975: 162-169.)

Recognition of that simple explanation of Durham's "theory" leads to further observations:

1. As outlined, and despite "convention" (Durham, 1976a: 91), the process is simply one form of *natural* selection of *cultural* instructions (Cloak, 1975: 168-170). The reader can test that statement by substituting "gene" for "cultural instruction" and "genome" for "head," in the explanation above, starting after "true." The term "cultural selection" and its variants are redundant, here as elsewhere. [Marvin Harris's well-known thesis about India's sacred cattle excellently exemplifies this form of natural selection of cultural instructions — *not*, as Durham (1976a: 91) erroneously concludes, of genetic instructions.]
2. The process has absolutely nothing to do with what happens to the carrier-enactor's genotype. A cultural instruction which helped its carrier *adopt* children would be selected for in exactly the same way and be just as successful, yet it would in no way enhance the carrier's genetic fitness; indeed, it would probably enhance the fitness of the children's natural parents at the expense of the carrier's fitness. So the fact that successful cultural instructions often enhance genetic fitness is merely an accidental truth, an empirical generalization of no theoretical import. (A factual thesis more generally true than Durham's would be that most cultural determinants of human behaviors tend to increase, or at least not to diminish, the number of children *enculturated* by the behavior and/or his/her relatives.)
3. Nothing said here, or by Durham, theoretically precludes other cultural instructions being successful through other pathways, even though actually maladaptive (detrimental to carrier's inclusive fitness). [*Cf.* Feldman

and Lewontin (1975: 1166): “Our recent work indicates that . . . phenotypes acquired by learning or other modes of cultural transmission can spread through a population even though they lower the fitness of the individuals showing the phenotype.” Indeed, at least one successful *gene* is maladaptive — the *T* allele in the house mouse (Williams, 1966: 119).]

A maladaptive behavior may become widespread because the real unit of natural selection (*contra* Durham, 1976: 92) is not the organism but the unit that replicates itself — the genetic or cultural instruction. An instruction of either kind succeeds (proliferates) or fails in the environment in which it happens to occur, according to the effects on that environment of its behavior. There is no *theoretical* basis whatever for predicting that a certain *kind* of environmental effect, such as organism construction, maintenance, or reproduction, is more likely to lead to success than any other kind; to make such predictions, one has to make factual assumptions about environments-in-general (such as Durham’s apparent unconscious assumption about environments where humans are enculturated), or to make factual determinations about a particular environment in question.

[By the way, Durham (1976a: 105) misunderstands and misrepresents my remarks on the possibility of maladaptive cultural behaviors (Cloak, 1975: 171-172). I said “a cultural *instruction* is [not “culture evolves”] . . . like an active parasite.” I went on to say, “It may be in complete mutual symbiosis with the human host, in which case the behavior it produces has survival value for itself through the value it has for the survival/reproduction of the host.” From that statement, one surely could as well predict Durham’s Fig. 1C as his 1D (1976a: 103): We have no quarrel at all about the *facts*; for reasons of theoretical exposition, however, I emphasized maladaptive instructions.]

4. Theoretically, then, instructions are primary, and their phenotypic products are secondary, mere *instruments* by which instructions succeed (if they succeed). Such instruments include organisms and modifications thereof: genetic instructions (genes) build organisms, and genetic and cultural instructions modify them, and the instructions thereby succeed. Some cultural instructions modify (or program) humans to build artifacts and social forms, again instruments of the instruction’s success — probably, but not necessarily, through their contribution to the instruction-carrier’s survival and/or reproduction. (Just *how* instructions cooperate to produce structures of marvellous complexity, efficiency, and beauty is of course a fascinating subject of empirical inquiry, as are the questions of how they compete and how they exploit and domesticate each other and each other’s products. Here, however, we are concerned with *why* they do so, when they do.)
5. Another result of the organism-modification process is the construction of the physiological (neural and humoral) bases of “wants” and “needs”—what Campbell (1965: 41) has perceptively called vicarious selection sys-

tems. Those want-and-need instructions, through their products, control the environment in which other instructions succeed or fail. As a rule, of course, they favor instructions whose behavior contributes to their success, usually by contributing to their carrier's fitness.

### Summary

Fundamentally, theoretically, there is only one process underlying genetic and cultural evolution: natural selection. Organism fitness-enhancement ("adaptive significance") is one of its practical mechanisms; group formation and maintenance is another, often but not always through fitness-enhancement; and need-fulfillment is still another. If Durham can accept that formulation, and switch from "organism-thinking" to "instruction-thinking" (Cloak, 1975: 178), he will free himself from two handicaps: First, he can forget his worries about "reductionism" and "determinism" (1976a: 100, 101). Under this general theory of natural selection, cultural evolution *is* biological evolution, continued by "other" (nongenetic) means. Second, he will spare himself the appearance of anthropomorphism, mentalism, and wishy-washiness attendant on his discussion of kinds of "significance," other than adaptive "significance," of cultural behaviors (1976a: 102-106, 115).

### Conclusions

Every instruction's success (or failure) depends on its environment, which includes every other instruction in its biotope — cultural or genetic — and the phenotypic outcomes thereof, including organisms, behaviors, artifacts, and social forms. (For example, the genetic and cultural instructions that cause people to rear and enculturate their own children are a very salient part of the environment of all cultural instructions which follow Durham's route to success.) Thus the theoretical relation Durham seeks is not a simple complementarity between one thing called "human biology" and another thing called "culture," but something far more complex: it is an *ecological* relation (*cf.* Cloak, 1975: 175) among a myriad of individual instructions. We *do* need "a general theory for the coevolution of human biology and culture" (Durham, 1976a: 116); we will find it, however, not by prejudging the relevance of instructional products to the survival and reproductive needs of individual organisms *or* groups thereof, but by tracing the pathways, *wherever* they lead, by which instructional products meet the survival and replicative needs of the instructions, genetic and cultural, that produced them. In other words, attempting to explain a behavior, one should ask not "What does this behavior do for the organism's fitness?" but "How does this behavior help make places, in this environment, for the genetic and cultural instructions that it expresses?"

## COMMENT

Eugene E. Ruyle

Durham's recent article in this journal (1976a) is a valuable contribution to the growing literature on biological interpretations of cultural evolution. There are three areas where I feel Durham is on the right track. First, I was pleased by his stress on natural selection at the individual level (incorporating the concept of inclusive fitness, a concept which is not as new as sometimes thought; see Haldane, 1966: 131) as the decisive force in biological evolution, particularly since this point is weakened in the recent, widely acclaimed work of Wilson (1975). Second, I was pleased to see Durham's criticisms of the sometimes rather casual application of the concept of natural (genetic) selection to the explanation of cultural phenomena (Wilson, again, has been criticized in this regard; see Allen *et al.*, 1975). Third, I found Durham's use of cost/benefit analysis stimulating, particularly in pointing out the relative freedom of low-cost activities.

However, I cannot accept Durham's rejection of the satisfaction criterion for cultural selection, nor can I accept his suggestion (pp. 97-99) that "humans tend to behave in ways which maximize the propagation of their genes." I find Durham's position in this regard both inelegant and untenable. My remarks are directed toward this point.

Both biological and cultural evolution are characterized by adaptation, if this term is used in its broad sense of referring to a "fit" between an organism and its environment. This fit, however, is maintained by quite different mechanisms. In the case of biological or genetic evolution, the mechanism is natural selection, or the differential reproduction of individuals. This selective mechanism leads to the selective criterion, inclusive fitness. Since offspring obtain their genetic materials more or less unchanged from their parents, it is axiomatic that those genetically based traits that improve the relative reproductive efficiency of individuals will tend to increase proportionately in the gene pool. This process of natural selection is adaptation, in the strict sense of the term (*cf.* Harris, 1960).

In the case of cultural evolution, however, the selective mechanism is quite different. Offspring may and in most cases probably do derive much of their cultural repertoire from their sociological parents (who may or may not be their biological parents), but (1) other social agents such as friends, "big men," and schools are also important in the enculturation process, and (2) cultural evolution can occur even within the life span of an individual, in contrast to the necessarily cross-generational nature of genetic evolution. This means that the test of adaptation in the strict sense (but not the broad sense) is lacking, unless one posits, as Durham in fact does (p. 97), the existence of internal structural rules which guide the selective retention of cultural traits according to the criterion of inclusive fitness. I find this rather dubious but note that, even were such

internal rules present, they would operate, as Durham notes, by providing “pleasurable sensory reinforcements” for certain behaviors, that is, by making these behaviors satisfying.

Therefore, unlike the case in genetic evolution, it is not axiomatic that those individuals with the most offspring make the greatest contribution to the culture of succeeding generations. What is axiomatic in cultural evolution is that individuals behave in ways that are pleasurable (satisfying) to them. This is axiomatic since the test of satisfaction is the behavior of individuals, just as the test of fitness is the leaving of offspring. People do things because they are, for whatever reason, satisfying, just as genetic traits increase because they contribute, for whatever reason, to differential reproduction. In other words, the satisfaction criterion, like the fitness criterion in genetic evolution, is tautological, and therefore irrefutable. Its value lies in the fact that it forces us to explain how a particular trait contributes to the satisfaction of individuals (and, indeed, who these individuals are, what their needs are, and how these needs are formed), just as the synthetic theory of bioevolution forces us to explain how a particular trait contributes to the differential reproduction of individuals (*cf.* Harris, 1968: 240-241).

Now, this concept of satisfaction subsumes the concept of inclusive fitness. Durham, unfortunately, misunderstands my argument (Ruyle, 1973) when he claims that “the satisfaction criterion . . . is scarcely adequate for explaining cultural patterns of fertility control by abstinence or infanticide” (p. 106), and “the general standard suggested for the selective retention of cultural traits (satisfaction) could easily result in noncomplementary, nonadaptive hedonism” (p. 116). But satisfaction as a selective criterion leads to adaptation in the broad sense of the term simply because it is rarely satisfying to be maladapted. Square wheels, crooked spears, and sickly children are unlikely to provide much satisfaction. The raising of viable offspring and grand-offspring is almost universally satisfying for human beings. Once these facts are taken into account, Durham’s objections must disappear. Satisfaction is the mechanism which maintains adaptation and, in most cases, inclusive fitness, in cultural evolution. To insist on inclusive fitness as Durham does is to hold to an approximate and partial explanatory tool instead of a more direct and complete one.

Durham acknowledges this by noting that the concept of inclusive fitness is *a* tool to aid our understanding of human behavior, not necessarily *the* tool or even the *best* tool for all human behaviors (p. 102). Durham seems to imply, however, that supplementary explanations are limited to low-cost activities (p. 115), but this is untenable. In most cases, I suspect, there is no contradiction between inclusive fitness and satisfaction, but there is abundant evidence that, where there is, satisfaction wins out. For example, for the sake of his political convictions Karl Marx endured a poverty so bitter that it caused the death of several of his children. If Marx had been behaving in a way to maximize the propagation of his genes he could easily enough have followed an orthodox

legal career and reared a larger family, but had he done so his influence on subsequent cultural evolution would have been nil. Similarly with Lenin, who consciously decided not to have children in order to devote himself to the revolution. The subsequent growth and spread of communism in the twentieth century have been based on massive self-sacrifice and nonpropagation of genes by individuals. Presumably all this was ideologically and politically satisfying to the individuals concerned, even though it entailed considerable cost. Cultural evolution is quite simply inexplicable without understanding such phenomena, examples of which could easily enough be multiplied.

A final point. Durham's attempt to shackle cultural evolution to an essentially mechanistic process ignores the most significant aspect of humanity. Cultural behavior is the conscious, purposeful, and meaningful activity of human beings, who create ideas in order to satisfy their own needs. (This is not to deny the force of custom, nor that human activity is often short-sighted and often leads to unanticipated results.) This human characteristic was created by the "blind" forces of biological evolution. However, it makes cultural evolution fundamentally different in kind from biological evolution, in which genes are created and altered by biochemical forces and selected according to an essentially mechanistic criterion. This difference opens the way for considerations of human happiness and even progress in cultural evolution, considerations which are quite properly excluded from the study of biological evolution as irrelevant. The gulf between humanity and other creatures, in short, is as great as the gulf between life and nonlife, and any theory of cultural evolution which fails to grasp this is doomed to failure.

## COMMENT

L. B. Slobodkin

There is a curious but quite definite distinction between "advantageous" and "having selective advantage." An advantageous behavior or morphology confers some benefit on an organism where the concept of benefit is defined by arbitrary agreement and may even include an improvement in the organism's likelihood of being an ancestor. "Having a selective advantage," by contrast, refers to a very tightly defined evolutionary situation in which the genetic properties of some particular class of organisms within a population in some particular environmental context confer on their possessors the capacity to increase the relative frequency of their type of genes in the population concomitant with a relative diminution of other types of genes.

Therefore, as Durham points out, the demonstration that a particular behavioral property would have selective advantage if individuals of differing geno-

type differed in that behavior does not in any way demonstrate that in fact it does have selective advantage in any usual evolutionary sense. This is of absolutely central importance. In fact, this criticism is at the heart of the current controversy over the doctrines of Alexander, Wilson, and Trivers. That is, the general argument which Durham is criticizing and which must be very seriously criticized is “If we can show a cultural trait or property (usually rather loosely defined) to be the kind of thing that would have selective advantage *if* it were in any way genetically determined, then, since so many things are, at least in part, genetically determined, there probably really is some genetic basis for the behavior. We may not have discovered it yet. There is a kind of parsimony in saying that that behavior represents the outcome of a long-term selective process.”

As Durham points out, there are several things wrong with this argument. If someone were to say that the behavioral differences between sparrows in New York City and sparrows in the countryside were genetic, we would demand that certain experiments be done to demonstrate this genetic basis. We would not be generally satisfied by a plausibility argument which says that so many things are genetic that this must be genetic, too. Are we to be satisfied with less definitive data and theory with regard to human behavioral differences or regularities?

It is possible to say that we cannot experiment with people the same way as with sparrows and therefore we deal with a kind of likelihood assertion. But, really, what kind of likelihood is it?

There are well-known and clear-cut examples of genetic differences between persons altering their behavior in significant ways, so that persons suffering from various metabolic deficiencies (say, Tay-Sachs disease or porphyria) may behave in a curious fashion (Ehrman and Parsons, 1976). The well-analyzed cases of human behavioral genetic difference do not involve the kind of traits that are considered by Alexander, Wilson, and Trivers.

Dr. J. Sohn has pointed out to me an interesting statement in Maimonides' *Guide to the Perplexed*, Chapter 49:

It is well known that man requires friends all his lifetime . . . . When man is in good health and prosperous he enjoys the company of his friends. In times of trouble he is in need of them. In old age when his body is weak he is assisted by them. This love is more frequent and more intense between parents and children and among other relations. Perfect love, brotherhood and mutual assistance is only found among those near to each other by relationship. The members of a family united by common descent from the same grandfather, or even some more distant ancestor, have towards each other a certain feeling of love, help each other and sympathize with each other . . . .

It is the apparent contention of Alexander, Wilson, and Trivers that these feelings, modulated by distance of relationship, represent a deep genetic property of man and that somehow it is genetically natural for man to feel this way. No explicit genetic analysis has been made. It is of interest that Maimonides did not consider this to be instinctive, because his passage continues: “To affect

this [sense of love and mutual assistance] is one of the chief purposes of the Law." That is, one cannot rely on men to naturally feel this way. One imposes laws which encourage this feeling, and the remainder of his passage is concerned with the rules of divorce, fidelity, and the relationship between married persons and families. The idea that cultural institutions such as law are the *cause* of these warm feelings is refutable by saying that cultural institutions are reflections of the genetically based feelings themselves. It should be apparent by now that one can build vast polemical structures on this subject without any particular end.

Note the claim by Wilson (1976) that the time has come "for ethics to be removed temporarily from the hands of the philosophers and biologicized [*sic*]" and that "The question that science is now in a position to answer is the very origin and meaning of human values from which all ethical pronouncements and much of political practice flow."

Even relatively simple-sounding assertions about the genetic basis of human traits other than the grossly morphological or biochemical are at the moment extremely controversial (*cf.* Kamin, 1974). One may ask why are suppositions about frankly nonexistent genetic analyses being presented as if they represented scientific communication? That question is probably impossible to analyze satisfactorily in what is meant to be a brief comment on another article. I will simply note the possibility that it is related to the oracular role that has been imposed on scientists in the popular imagination and the temptation to fulfill that oracular role in response to an ever-present, eager audience.

The presentation of loose plausibility arguments as if they were fact, or as if they had the weight of normal scientific theory, is not particularly dangerous in, for example, the study of the evolution of bryozoans or bryophytes, but it is, curiously enough, precisely in such fields as the evolution of bryozoans that the most rigid of scientific standards are applied before a work is permitted to be published and promulgated. In the area of human behavioral evolution there is a tendency to be looser, rather than more stringent, in the intellectual criteria applied, as if the depth of our ignorance about human behavior required us to say something at all cost rather than to remain silent. This is an extremely dangerous state of affairs from both the political and the social standpoint (see Allen *et al.*, 1975).

Durham very properly dissociates himself from this curious kind of analysis but then substitutes an analogy between the process of cultural change and that of evolutionary change, which does not rely on any assumed genetic infrastructure.

He introduces a theory of complementarity between biological and cultural evolution in which the process of cultural evolution seems to involve selective retention of particular cultural properties and in which the coupling between biological and cultural evolution is by a fitness criterion. That is, it is considered to be highly unlikely that there would be selective retention of a cultural property which tends to lower fitness.

If there were real fitness differences in the genetic sense between individuals or between groups within cultures or even between cultures, then we would anticipate that there would not be selective retention of cultural traits which tend to lower such fitness unless they are appealing for some other reason. The arguments of Alexander, Wilson, and Trivers would say that people would have a genetic tendency to avoid the appeal of such cultural properties. I suspect that this implies that eventually we will have a genetic aversion to cigarette smoking but I am not at all sure. I am certainly not sure enough to feel that I have gained a deep insight of human behavior by considering the problem in this way. In the absence of any documentation that culturally significant behavior is dependent on observed genetic differences, Durham's statement that "people are not likely to harvest energy either in a way or in amounts that would cause them reduced fitness" is not very meaningful.

In his conclusions, Durham states: "I do not believe . . . behaviors are controlled by genes whose frequencies were increased by natural selection." Curiously enough, I do. That is, I am almost certain that in the process of development of the primates there were at one time changes in behaviorally significant genes as a consequence of natural selection. This in no way says that that process is going on at the present time. In fact, one can quite readily build a model of extremely high behavioral flexibility in which the flexibility itself is a genetic property, and, if that flexibility is sufficiently high, it becomes almost impossible for gene frequencies to be materially altered by specific environmental pressures unless these are of extremely long duration and extremely great force. I develop this argument at greater length elsewhere (Slobodkin, 1977a,b). Durham continues: "Rather . . . this correlation may largely result from a complementary process of *cultural selection* which influences the retention of cultural traits according to the same criterion as natural selection (i.e., inclusive fitness) . . ." I do not believe that he has developed the details of this analogy sufficiently to permit us, for example, to use any of the more formal theories of population genetics as paradigms for cultural evolution, and, until it is developed in that way, it becomes very difficult to criticize more explicitly. Perhaps the clearest item in the conclusion is that there exists a spectrum ranging from complete genetic control to complete nongenetic control in behavior and that any theories which attempt to assign 100% genetic control or 100% nongenetic control are empty at best.

There is a complex evolutionary theory which addresses itself to the question of what are the genetic mechanisms which determine the amount of environmental vs. genetic control (Waddington, 1957; Bradshaw, 1965). This type of evolutionary theory may provide a biological basis for the fact of complementarity in human systems. For the moment, however, the genetic component of anthropological theory remains obscure. Durham performs a service in denying one class of simplistic assertions. His planned substitute analysis is an improvement but obviously must be more fully developed in later studies.

## REPLY

William H. Durham

With the publication of E. O. Wilson's book (1975), *Sociobiology: The New Synthesis*, the relationship between human biology and culture has once again emerged as a major issue in the public and academic press. Unfortunately, it does not appear that the relationship has been clarified to any great extent by the recent attention. Sociobiology, defined as the study of the biological basis of social behavior in any animal species, proposes that many forms of human cultural behavior are genetically inherited and therefore a product of natural selection. Far from being the new synthesis we were waiting for, this is really only a more sophisticated brand of the disciplinary chauvinism we suffered before. There is still not adequate allowance for nongenetic factors in the making of adaptive human phenotypes.

Now more than ever, I feel I must point out the dangers inherent in human sociobiology and I must reemphasize the conceptual differences of the theory I have proposed. In the first place, disciples of sociobiology in anthropology and biology must bear in mind the following:

1. The demonstration that a trait is *adaptive* (i.e., fitness-enhancing) for human beings by no means proves it to be the result of natural selection and genetic inheritance. Because culture has been the more important means of human adaptation in recent millennia (a point agreed upon by Wilson and others), we have no reason to postulate a predominantly genetic basis for a given behavior until cultural mechanisms of adaptation are shown insufficient to explain the frequency and distribution of the character.
2. The demonstration that a trait is *universal* or *almost universal* among human societies also tells us nothing about its having a genetic basis or not. Similar behaviors in a variety of societies can easily result from *cultural* means of adaptation. A practice can become widespread through either independent cultural evolution or diffusion, and may even be retained for different reasons in nonsimilar habitats.
3. Even the demonstration of a phylogenetic history of a trait cannot be accepted as unconditional proof of its genetic origin in human beings. First, there is good evidence that the adaptations of other primates, for example, include an important amount of learning (Kummer, 1971). Second, *even if* a given social behavior in another primate society is shown to have genetic transmission, this does nothing more than suggest the *possibility* that the behavior evolved primarily in the same way in humans.

In short, good sociobiologists will not continue to argue or advocate the hypothesis that behavior *X* has a genetic basis, *not even* when they know it to be adaptive and widespread. Instead, they will present sound evidence that requires rejecting the null hypothesis that behavior *X* is not genetically acquired. Curiously, *none* of the evidence marshalled by sociobiologists to date has made possible a convincing rejection of the null hypothesis for *any* form of human social behavior. Actually, this may not be so surprising as it seems — there are good reasons why cultural processes probably account for the origin and maintenance of more forms of human social behavior than genetic processes (see Durham, 1976a, pp. 100-101).

The major differences between hard-line sociobiology and the theory I propose are two. First, I argue that the observed consistencies between human behavior and biological theory may largely result from a complementary process of *cultural* evolution. The process I envision would promote the adaptation of human beings to their social and physical environments by cultural means, but it would still be adaptation in the biological sense. Second, I do not suggest that all human activities make perfect sense in terms of fitness. As a general rule, the utility of fitness arguments for understanding a given human behavior is expected to increase in proportion to the behavior's phenotypic costs to the behavior. Customary high-cost behaviors are expected to be fitness-enhancing almost without exception. Low-cost behaviors may very well have no important relation to fitness. In the case of human beings, the adaptiveness of a trait is therefore not necessarily its most important feature.

When I first formalized the thoughts behind "The Adaptive Significance of Cultural Behavior" into a manuscript, I was afraid these points were almost too self-evident to publish. The earnest and thought-provoking comments of these reviewers suggest otherwise, and their criticisms deserve to be carefully considered.

The major comment by Eugene Ruyle is that satisfaction, not fitness, is the most direct and complete explanatory tool for human behavior. His position follows logically from the axiomatic assertion that human beings always behave in ways that are pleasurable or satisfying to them. Since pleasurable activities are not always fitness-enhancing (a point we agree on), fitness will therefore not be as useful a measure as satisfaction.

This argument, Ruyle declares, is tautological and therefore irrefutable. What makes it tautological is the meaning that "satisfaction" takes on for not being explicitly defined. If the test of satisfaction is postulated to be the (repeated) behavior of individuals, then satisfaction must logically be defined as "*whatever* leads individuals to repeat a behavior." This of course is not a particularly satisfying notion of satisfaction. It *does* include everything, it *is* complete, but it also tells us *nothing*. If Ruyle really wants to say something more profound, he will have to define satisfaction explicitly and describe for us a few of the properties he wishes it to have. Unfortunately, I suspect that this is neither a trivial request

nor a simple oversight on Ruyle's part. Within any sound definition of satisfaction will be implied answers to a number of tricky questions concerning the operation of selective retention. For example, if a human being is faced with a choice between a number of alternative cultural practices, will he or she generally choose the *most* satisfying? Can satisfactions always be quantified or at least rank-ordered as that would imply? What happens if the alternatives are satisfying in different ways? What happens if one is more satisfying in the short term and another in the long term? If Ruyle wants to use a selective retention model for cultural evolution, he will have to explain satisfaction more carefully — in a way that makes possible its use as a yardstick for comparing alternative practices.

At times I get the feeling that Ruyle wants satisfaction to mean something other than its implicit definition. He suggests, for example, that he means satisfaction in the sense of pleasure. If so, that is, if Ruyle really wants pleasure to be his criterion, then his argument is no longer tautological and irrefutable. "*Whatever* leads individuals to repeat a behavior" is not necessarily pleasurable sensory feedback. His proposition thereby becomes a hypothesis which requires testing just like any other: "people tend to behave in ways that produce pleasurable sensory reinforcement." In this case, he should not ask us to accept the truth of his assertion. Our task should be to test it.

That brings me to another point. Ruyle argues that satisfaction is a more encompassing and therefore more basic or complete criterion of selective retention than fitness. This claim is derived from his observation that "it is rarely satisfying to be maladapted." If the latter is true, and if people always behave in satisfying ways, then people will rarely counter their fitnesses, he continues, in all the various satisfying things they may do. I wonder if Ruyle has ever backed up one more step to ask *why* is it rarely satisfying to be maladapted? *Why* is it that "Square wheels, crooked spears, and sickly children are unlikely to provide much satisfaction"? I submit that the theory that can answer these questions, not just assume them as given "facts," is more basic and complete. My hunch is that square wheels, crooked spears, and sickly children are unlikely to provide much satisfaction because they are unlikely to provide much fitness.

The relationship between adaptation and satisfaction can probably be explained as follows. Presumably throughout the organic evolution of hominids there was a persistent (genetic) selective advantage for the coupling of sensory reinforcements with acts likely to enhance fitness and for coupling unpleasant or painful feedback with potentially dangerous behaviors. Presumably the capacity for culture began evolving when there was already some coupling of this kind. Since we may assume that this capacity for culture evolved for its adaptive benefits, culture would be very unlikely to uncouple completely or indeed to reverse the association of fitness-enhancing activities and satisfactions. As explained in my article, it is reasonable to suggest that that this association has be-

come appreciably looser with the influence of culture (e.g., there certainly exist pleasurable low-cost activities which contribute essentially nothing to fitness, Fig. 1C in Durham, 1976a). Still, we would not expect to find satisfaction resulting from grossly maladaptive cultural behaviors.

Therefore, I agree with Ruyle when he says, "In most cases, I suspect, there is no contradiction between inclusive fitness and satisfaction," but I believe that this correlation *and its limits* are actually predicted by fitness and that they are not predicted by satisfaction. For this reason, I maintain that fitness is the more complete measure, and I suspect it will also prove more useful for the analysis of high-cost behaviors. On the other hand, I absolutely agree that fitness may often be indirect and unnecessary for explaining low-cost activities. When satisfaction is properly defined, Ruyle's theory should be very useful in the lower left-hand corner of Fig. 1C of my article.

Finally, I see neither "abundant" nor compelling evidence that where fitness and satisfaction arguments really are at odds (i.e., in the case of high-cost behaviors) "satisfaction wins out." At the risk of gross injustice to Karl Marx in these few paragraphs, let us reconsider Ruyle's proposed counterexample. In the first place, Ruyle suggests that the life of Marx himself is a good example that the pursuit of satisfaction may lead people to behave in ways that do not maximize their fitnesses. Before discarding the fitness hypothesis on these grounds, we must always remember that any given individual case can neither make nor break a general, statistical prediction of tendency. As a matter of fact, if a chosen counterexample is widely recognized for being unusual or exaggerated, the exceptional case may ironically support the general tendency. I wonder, then, if the unusual dedication of Marx to his cause (perhaps that of Jesus Christ as well) doesn't actually reinforce my argument for the general case. (In this discussion I will ignore along with Ruyle the reproduction of Marx's relatives and any possible manipulation by his parents.)

Second, in reference to *Marxism*, I must say that, again, I do not find the compelling contradiction that Ruyle implies. While this may not be the best way to interpret Marxism, I believe it is fair to say that Marxists realize that existing social structures generally serve to maintain and even increase the reproductive and related advantages of the rich at the expense of the poor (see Meek, 1971). In a sense, Marxism seeks to deflect the perpetration of such inequity, and Marx realized, as do his followers, that considerable self-sacrifice may be necessary to effect that change. Before we leap to any conclusion about "massive self-sacrifice and nonpropagation of genes" behind this behavior, it would be good to remember (1) that the poor may have relatively little to lose and potentially much to gain (either of fitness or of its supporting resources) and (2) that individual sacrifices are often seen as worthwhile for the benefits expected to follow for one's descendants. In this light, perhaps even the extreme sacrifice of Marx himself becomes understandable. In the article, I briefly discussed the possibility of cultural inertia in the event of an environmental change. It is clear that I should have included cultural forecasting as

well. Marx might be considered an outstanding example of the human potential to modify behavior in anticipation of predicted environmental changes. His behavior will seem altruistic only to those who do not anticipate such changes.

I believe that the remaining points Ruyle makes are simply elaborations and restatements of propositions already included in the text (e.g., the contrast between purposeful cultural evolution and blindly mechanistic biological evolution is a point I make, albeit with less fanfare, in the section on Determinism).

Turning now to F. T. Cloak's comments, I find "instructional thinking" to be a new and more sophisticated formulation of the older, complete analogy between biology and culture (see Murdock, 1956, for example). This analogy proposes that alternative forms of cultural instructions compete for representation in the total pool of instructions just the way that genes do. Those instructions that successfully replicate more copies than do other variants will ultimately increase in frequency — a process that Cloak considers *natural* selection, no more, no less. By this reasoning, what has fitness is not the carrier organism but the instruction itself; instructions are therefore expected to maximize their own reproductive success.

With respect to biological evolution, instructional thinking is normally equivalent to organism thinking for the simple reason that the replication of instructions occurs through the reproduction of the organism. On the other hand, the transmission of cultural instructions is not restricted to that act of fertilization, as we all know. An organism can *continually* acquire new cultural instructions and from a wide variety of sources. This is where the problems begin.

Despite the appearance of complete analogy and therefore complete accord between biological and cultural processes, instructional thinking predicts the existence of common cultural traits that actually impede their carrier's survival and/or reproduction. For example, it is possible in instructional theory for a cultural trait that spreads quickly through a population, while at considerable expense to each carrier, to achieve a higher "instructional fitness" than one which spreads more slowly although it enhances organism fitness (I assume this is what Feldman and Lewontin, 1975, refer to). This argument, while plausible, presents Cloak and the rest of us with a challenge — to find definitive examples of such traits. The appropriate place to begin looking is in the lower right-hand corner of my article's Fig. 1C — what I consider to be the hypothetical "black hole" of cultural behaviors.

I must confess that I have been unable to find even one good example. When I first began ruminating on this topic several years ago, a number of anthropologist friends suggested to me that primitive warfare was an excellent subject area in which to look for behaviors that are culturally maintained though biologically maladaptive. One Michigan faculty member insisted that Mundurucú headhunting would be the very case to dissuade me of my illusion. I took their suggestions, went to work in the literature, and tried to show that the null hypothesis (Fig. 1D) cannot be rejected. The only problem is that, to date, I have found no compelling evidence that participation in intergroup aggression in primitive so-

cieties is maladaptive (Durham, 1976b). Indeed, Mundurucú headhunting proved to be one of the best examples that where first appearances are to the contrary, we may simply not have looked hard enough.

While we await other, definitive counterexamples, I would like to reiterate what I believe to be the critical oversight in the biology/culture analogy suggested by Cloak and others. We must remember, as Cloak says, that “Every instruction’s success (or failure) depends upon its environment, which includes every other instruction in its biotope — cultural or genetic — and the phenotypic outcomes thereof, including organisms, behaviors, artifacts, and social forms.” I am skeptical of Cloak’s arguments for the simple reason that the ongoing evolution of cultural instructions takes place in an environment which includes previously evolved instructions of all kinds. In these terms, my article essentially proposes that the human environment in which culture propagates has, from preexisting instructions, an inherent differential selectivity for traits that enhance organism fitness. The medium, so to speak, is not passively receptive to just any smart new cultural instruction that comes along. Rather, I believe the medium comes with a strong bias or selection pressure against variants deleterious to human fitness.

Actually, Cloak hints that he may agree with this as a general feature of the environment — but he sees it as a *fluke*, an “accidental truth” that stems from the curious *fact* that adults generally rear and enculturate their own children. Two comments must be made here. First, it should be obvious from what I have said that I do not consider this “near-universal contingent *fact*” to be the sole source of any bias the medium may have. Indeed, I believe there may exist three different classes of influences on our receptivity to new cultural instructions: (1) enculturated or learned biases (parents, teachers, and friends may in many cases teach new carriers to be selective), (2) biological or genetic biases (as I say in the article, I am open to the possibility that there may be a structural basis to our selectivity for certain kinds of cultural instructions), and (3) circumstantial biases (arising as Cloak suggests from properties of residence and kinship systems). Of course, I am in no position to guess at the general, relative importance of (1), (2), or (3) behind the “genotypically selfish” selective retention I propose.

Second, as with Ruyle, I simply cannot let Cloak get away without examining the very “near-universal contingent *fact*” on which his argument rests. Indeed, by the fifth paragraph this fact creates a serious contradiction that seems to call his entire argument into question. There Cloak says that, according to instructional thinking, “A cultural instruction which helped its carrier *adopt* children would be selected for in exactly the same way and be just as successful [as the instruction for rearing one’s own].” We must then ask him why adoption is not more prevalent within human societies. How did this practice of rearing one’s own offspring get to be a “near-universal contingent *fact*” if instructional thinking is correct in implying that adoption should be

just as successful? It certainly was not through small sample size and drift! Cloak's own argument on adoption strongly suggests that there is no "accident" involved if cultural instructions often enhance fitness. I fear that his own example boomerangs to support my point — but I would hope in any case that some interested reader will take the hint and seriously reinvestigate human (and/or nonhuman) adoption practices, asking when (under what circumstances) do people adopt children, and why.

Having said all this, I have a confession to make. My own arguments actually do allow the existence of a class of cultural instructions that serve their own reproductive ends more than our own. However, in contrast to Cloak, I suggest that organism thinking actually predicts what kind of cultural instructions these are likely to be. The best place to look for "active parasites" should be the lower left-hand corner of Fig. 1C.

Slobodkin and I apparently have few disagreements regarding the relationship between biology and culture. Once or twice I get the feeling he misunderstands some of my arguments, but that may not be very serious. For example, he claims my predictions about the harvest of energy are not very meaningful "in the absence of any documentation that culturally significant behavior is dependent on observed genetic differences." I hope it is clearer to other readers (1) that my comments *do not require* a genetic basis for culturally significant behavior either in this case or in any other (the confusion here probably stems from the customary practice in population genetics of measuring fitness differentials between *genotypes* rather than between *phenotypes* as required in a cultural theory), and (2) that the idea of cultural selection actually suggests we would find variations in human social behavior to be much more dependent on cultural than genetic differences (the reader is again referred to the section on Determinism).

Also, I am not sure that I agree with Slobodkin about the importance and priority to be given plasticity theories that explain "the genetic mechanisms which determine the amount of environmental vs. genetic control" of human behavior. If I am correct in asserting that our cultural and biological attributes have coevolved in a complementary fashion, the question of the relative importance of genes and learning is really much less interesting and much less important than understanding both the possible adaptive significance of these attributes and the limitations of this approach. I fear that the refinement of models for environmental vs. genetic control might now only get us further embroiled in instinct vs. learning polemics.

This is perhaps an appropriate place to insert a few words of self-criticism about the theory I have proposed. First let me say that I believe the theory's strength is its ability to explain the evolution of adaptive cultural behaviors without presuming a genetic basis or predisposition for everything we do. I believe the theory is also adequate for predicting its own limitations and I reemphasize that it does not say everything we do is best explained by fitness arguments. On

the other hand, I believe my arguments are weakened by several problems beyond those suggested by these reviewers:

1. The theory in its present formulation overemphasizes the behavioral aspects of culture. Attention must be given to beliefs, attitudes, thoughts, and emotions before a holistic understanding will emerge. Although not emphasized in the text, these are clearly key features of human adaptation and adaptability.
2. The idea of a selective retention process for cultural evolution presupposes the existence of distinct and identifiable units of culture called "cultural traits," "practices," "instructions," etc. I am not sure that the analogy of particulate transmission is entirely appropriate for cultural inheritance which lacks the discrete physical manifestation that genetic units have.
3. I have not given sufficient emphasis to the critical distinction between "selfishness" as it is commonly understood and "genotypic selfishness" used as a shorthand abbreviation in the article. In no way am I prescribing a universal tendency for wanton selfishness, nor can such behavior find justification in the theory I propose. On the contrary, it must be re-emphasized that sharing, reciprocation, give-and-take, and cooperation are generally more adaptive and more common than pure selfishness in the social environments of human beings.
4. Likewise, I failed to emphasize that "adaptation" need not imply acceptance of and adjustment to a given social and natural environment. In particular, a coevolutionary perspective does not imply, as does sociobiology for example, that existing social structures are part of an immutable "natural order" to which individuals must adjust or lose out. Rather, it implies that these structures must be viewed as an outgrowth of our cultural history, which in turn must be seen, in part, as the chronicle of struggles for access to and control of life's sustaining resources. In the course of these struggles, there are times when adaptation may require *changing* the environment.
5. It is not always clear that I ascribe no conscious intention and no deliberate calculation to the behavior of individual human beings as they supposedly go about tending to maximize their fitnesses. It bears re-emphasis that such an ambition is assuredly the last thing on our minds most of the time. In fact, this may be an important part of happiness and peace of mind.
6. I apologize for any "mentalism and wishy-washiness" in my discussion of the limitations of fitness analysis for our understanding of cultural evolution. I now realize that only a small handful of my colleagues ever confused the adaptive significance of human behavior with its total significance.

## REFERENCES

- Allen, E., Beckwith, B., Beckwith, J., Chorover, S., Culver, D., Duncan, M., Gould, S., Hubbard, R., Inouye, H., Leeds, A., Lewontin, R., Madansky, C., Miller, L., Pyeritz, R., Rosenthal, M., and Schreier, H. (1975). Against sociobiology. *N.Y. Rev. Books* 22(18): 43-44 (November 13).
- Bradshaw, A. D. (1965). Evolutionary significance of phenotypic plasticity in plants. *Adv. Genet.* 13: 115-155.
- Campbell, D. T. (1965). Variation and selective retention in sociocultural evolution. In Barringer, H. R., Blanksten, G. I., and Mack, R. W. (eds.), *Social Change in Developing Areas: A Reinterpretation of Evolutionary Theory*, Schenkman, Cambridge, Mass., pp. 19-49.
- Cloak, F. T., Jr. (1975). Is a cultural ethology possible? *Hum. Ecol.* 3: 161-182.
- Durham, W. H. (1976a). The adaptive significance of cultural behavior. *Hum. Ecol.* 4: 89-121.
- Durham, W. H. (1976b) Resource competition and human aggression. Part I: A review of primitive war. *Quart. Rev. Biol.* 51: 385-415.
- Ehrman, L., and Parsons, P. A. (1976). *The Genetics of Behavior*. Sinauer Associates, Sunderland, Mass.
- Feldman, M. W., and Lewontin, R. C. (1975). The heritability hang-up. *Science* 190: 1163-1168.
- Haldane, J. B. S. (1966). *The Causes of Evolution*. Cornell University Press, Ithaca, N.Y. (originally published 1932).
- Harris, M. (1960). Adaptation in biological and social science. *Trans. N.Y. Acad. Sci.* 23: 59-65.
- Harris, M. (1968). *The Rise of Anthropological Theory*. Thomas Y. Crowell, New York.
- Kamin, L. J. (1974). *The Science and Politics of IQ*. John Wiley and Sons, New York.
- Kummer, H. (1971). *Primate Societies: Group Techniques of Ecological Adaptation*. Aldine, Chicago.
- Meek, R. L. (ed.) (1971). *Marx and Engels on the Population Bomb*. Ramparts Press, Berkeley, California.
- Murdock, G. P. (1956) (rev. 1971). How culture changes. In Shapiro, H. C. (ed.), *Man, Culture, and Society*. Oxford University Press, New York, pp. 319-332.
- Ruyle, E. E. (1973). Genetic and cultural pools: Some suggestions for a unified theory of biocultural evolution. *Hum. Ecol.* 1: 201-215.
- Slobodkin, L. B. (1977a). Is history a consequence of evolution? In Klopfer, P., and Huxley, *Advances in Ethology*. Plenum Press, New York.
- Slobodkin, L. B. (1977b). The peculiar evolutionary strategy of man. *Trans. Boston Colloq. Philos. Sci.* (in press).
- Waddington, C. H. (1957). *The Strategy of the Genes*. Allen and Unwin, London.
- Williams, G. C. (1966). *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton University Press, Princeton, N.J.
- Wilson, E. O. (1975). *Sociobiology: The New Synthesis*. Belknap Press, Cambridge, Mass.
- Wilson, E. O. (1976). Quoted in *Science* 191: 1153.

## ERRATUM

An unfortunate error was made in the citation of Richard Alexander's paper "Incest, Culture, and Natural Selection" in my paper "The Adaptive Significance of Cultural Behavior" (Durham, 1976a). The error was introduced without my knowledge by changes made after I had read and returned the proofs.