

Is Sociobiology Methodologically Flawed?

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The argument between human sociobiologists and their critics is a case of competing paradigms. Two frequent criticisms of sociobiology are: 1) it is inherently dangerous to assume that biology has an important influence on behavior; and 2) the assumption of evolutionary adaptation is a methodological error. These criticisms are aimed at the underlying assumptions of sociobiology with the intent of demonstrating that sociobiology is fundamentally flawed. It is argued that the first criticism disregards examples of human suffering that have occurred because of an ignorance of biology and instead focuses exclusively on suffering that has occurred because of a misuse of biology, while the second criticism represents a misunderstanding of the nature of evolutionary biological research. Individual sociobiological arguments may be incorrect, but the research paradigm is not intrinsically flawed.

INTRODUCTION

Human sociobiology means different things to different people. The classic definition (Wilson 1975:2) states that sociobiology is "...the systematic study of the biological basis of all social behavior." Because it is recognized that an organism's biology evolved (as opposed to being specially created), sociobiology necessarily involves an application of evolutionary biological principles to the understanding of social behavior. There remains, however, an extreme diversity of views on sociobiology's goals, methods and accomplishments (or lack thereof, depending on one's perspective). This can be traced to the fact that sociobiology deals with something that no one can claim to be agnostic about. You may not, for example, have a vested interest in the truths of ceramic tile heat conduction, or of cloud formation, but you are likely to have some understanding of human behavior. Because humans are highly interactive social animals, one simply cannot afford to be ignorant of other people's behavior. To its severest critics, human sociobiology is seen as a dangerous and misguided attempt to speculate on the limits to human behavior; so dangerous and misguided, in fact, that they feel it should be rejected out of hand as a research paradigm. How valid is this claim?

In this article I will assess two of the most common *a priori* reasons for rejecting the sociobiological paradigm. The first criticism emphasizes the potential negative effects of faulty studies that attempt to detect/explain biological influences on behavior. This viewpoint ignores the other side of the coin, that there are serious negative consequences to the assumption that biology is irrelevant to behavior, *even as a working hypothesis*. The second argument, advanced by some evolutionary biologists, is that

sociobiology suffers from serious methodological flaws because it emphasizes a search for adaptations. As we shall see, however, this criticism betrays a profound lack of insight into how the field of evolutionary biology allows us to understand the world around us.

THE PURSUIT OF KNOWLEDGE

My basic argument will hinge on the fact that humans are severely limited in their ability to perceive and understand the complexity of the world around them. As scientists, we are confronted with a bewildering array of empirical observations which no human is able to comprehend as a single unit. In order to make sense of this knowledge, we have no option but to break it down into smaller, manageable pieces. We use hypotheses, or theoretical constructs (which in turn derive from our current scientific paradigm; Kuhn 1970) to guide our explorations. Whether the history of scientific understanding has proceeded in a tortuous and twisted route, as Kuhn (1970) has argued, or simply by a series of successive modifications of existing theories, it is clear that the process requires intermediate steps. Paradigms are constructed precisely because our search for understanding proceeds at a snail's pace through a series of intermediate steps. Paradigms serve not only to organize and make sense of the mass of empirical observations, but because they represent ways of perceiving the world, they also serve to guide future research. Paradigms define which questions "make sense" to ask; that is, which questions are likely to provide meaning when answered. Even "holists" (those who emphasize that the whole is more than the sum of its parts) reject the "...romantic notions that one can grasp the functional intricacies of complex systems without conducting

scientific and technological studies of individual components" (Soulé 1985:728). We simply cannot go from a position of complete ignorance to one of complete knowledge in a single step.

Human sociobiology is an attempt to explain behavior within an evolutionary biological framework, using exactly the same theoretical foundation that evolutionists have used to explain morphological variation. In this sense, it represents nothing more than a simple extension of a much larger research program. The diversity of opinions about the merits of sociobiology stem from an extremely basic dichotomy (a conflict of paradigms) in how people choose to study behavior. There are those who are fundamentally interested in differences between human groups, and consequently feel that cultural variability indicates human transcendence over biology; and there are others who see meaning only in common underlying behavioral patterns, and are consequently more receptive to biological explanations.

These two basic points of view define quite nicely (but obviously only on a very general level) the fundamental difference between the sociocultural anthropology paradigm and the evolutionary biology paradigm. No graduate student in sociocultural anthropology, for instance, could get away with claiming that the people she studied in her fieldwork in East Africa were for all practical purposes essentially the same as the Balinese. It is the nature of this field to emphasize uniqueness, and because of this, there is no unifying theme that ties the field together, save the omnipotence of culture. In contrast, it is the nature of evolutionary biology to emphasize commonalities, links and underlying threads. A graduate student in zoology could not get away with studying desert pupfish without putting them into an evolutionary framework. Evolutionary biology, like the rest of the natural sciences, is a field that attempts to explain the greatest number of differences with the least number of principles. Human sociobiology is nothing more than the application of evolutionary biological analyses to human behavior (Ruse 1985; Barash 1977), and therefore shares all the detriments as well as all the benefits of this larger paradigm.

THE DANGER OF BIOLOGY

Perhaps the most frequent criticism of sociobiology stems from the historical record of abuse of biology to support racist, ethnocentrist and sexist ideologies. The argument is that because there is, and has historically been, such a

potential for the abuse of biological ideas in political arenas, then any theories purporting to explain human behavior should operate under the assumption that biology is irrelevant. It is important to keep in mind that there are two basic types of errors that can be made when discussing behavior. The first error is to assume that biology is irrelevant when it is in fact relevant. The second error is to assume that biology is relevant when it is in fact irrelevant. Critics of sociobiology feel that this second kind of error is inherently more dangerous (and likely) than the first. They feel that it is safer to ignore biology in discussions of human behavior than to acknowledge it.

That this fear is central to criticisms of sociobiology is evidenced by the opening chapter of Kitcher's (1985) critique of sociobiology. In it he describes a policy in England which placed children into either academic or trade schools on the basis of psychometric tests given at age eleven. His point is that children were made to feel like failures if they did not pass these tests, and that this quite possibly scarred them for life. In a sense, he believes that the tests *created* the differences between children, rather than pinpointing existing differences. He feels that the risks of assuming a biological basis of behavior are greater than the potential benefits that such a belief might bring, and therefore we should always operate under the assumption that biology is irrelevant. Furthermore, he argues that we should hold research on such subjects to a higher level of scrutiny than other fields of inquiry. As Kitcher (1985) wrote:

If a single scientist, or even the whole community of scientists, comes to adopt an incorrect view of the origins of a distant galaxy, an inadequate model of foraging behavior in ants, or a crazy explanation of the extinction of the dinosaurs, then the mistake will not prove tragic. By contrast, if we are wrong about the bases of human social behavior, if we abandon the goal of a fair distribution of the benefits and burdens of society because we accept faulty hypotheses about ourselves and our evolutionary history, then the consequences of a scientific mistake may be grave indeed (1985:9).

There is nothing wrong with the argument that we should weigh the costs and benefits of implementing policies and doing research. The question is whether the second kind of error (being wrong in assuming that biological differences influence a particular behavior) is

inherently more dangerous than the first kind of error (being wrong in assuming biology is irrelevant to behavior). While Kitcher (1985) and other critics point to examples of the negative consequences when a biological influence on behavior was mistakenly assumed, it is equally possible to document cases where harm has occurred because biology was implicitly, if not explicitly, assumed to be irrelevant. One specific example is the situation with regard to lactose intolerance. Until recently, it was assumed (by scientists and policy makers of European ancestry) that all humans were essentially the same in their ability to digest the milk carbohydrate lactose as adults. However, it has become clear that Europeans, along with some populations in Africa, are abnormal with regard to most human groups (and mammals in general) in their ability to continue producing into adulthood the necessary enzyme (lactase) which allows them to digest lactose. "Lactose intolerant" adults suffer a variety of ailments upon ingestion of milk, including diarrhea (often severe) and other symptoms of a disturbed intestinal mucosa (Leininger 1978). These facts are now common in introductory textbooks in physical anthropology, but what is not stressed is that milk has been commonly sent as famine relief to needy countries where most of the population is lactose intolerant, such as Asia. Milk-induced severe diarrhea in malnourished individuals can be directly or indirectly fatal. Since it is unlikely that malnourished individuals will be as cautious about the foods they ingest as healthy individuals, the potential for serious complications is amplified. This demonstrates that behavioral differences (the lack of milk usage among most groups) may well have biological bases (lactose intolerance) and the ignorance of this possibility can and probably has led to unnecessary suffering and death.

While much attention is given to the Nazi atrocities carried out under the guise of "genetics" (e.g., Stein 1988), little mention is made of the devastation wrought in the Soviet Union because of a *rejection* of genetics. From the 1930's until the fall of Krushchev in 1964, Soviet genetic theory and research was directed by the agronomist T. D. Lysenko, who rose to supreme academic authority solely because his theories were tailored to be desirable to the prevailing political environment (Medvedev 1969). Lysenko's theories included a sort of bastardized version of Lamarck's theory of the inheritance of acquired characteristics along with an outright rejection of Mendelian genetics. He insisted on the indivisibility of the organism and maintained that it was never possible to separate environmental from hereditary influences, to the extent that the whole

field of genetics was decreed by him to be devoid of meaning (Lerner and Libby 1976). He was quoted as saying, "Just what is this gene? Who has seen it? Who has felt it? Who has tasted it?" (Medvedev 1969:257). For Lysenko, evolutionary change occurred in an organism when the environment changed, because the organism was nothing more than the sum of the environmental conditions (Brill 1975).

The scientific basis for Lysenko's theories was non-existent. "Scientific" articles supporting his claims consisted of various mixtures of extreme polemics, guilt by association (e.g., Mendel was a priest and therefore his laws were invalid), *argumentum ad hominem* (arguments that appealed to feelings and prejudices instead of intellect), a rejection of statistical analysis, and circular reasoning (certain results could be obtained only under particular conditions, which were defined as the conditions under which the results were obtained) (Lerner and Libby 1976). An incredible series of claims were made concerning the miraculous transformation of one species into another through purely environmental manipulation.

This fiasco had disastrous repercussions on Soviet agriculture. The minimum probable loss sustained in the Soviet Union due to its 20 year failure to adopt American hybridization techniques is estimated to have amounted to 30 to 50 billion kilograms of corn alone (Medvedev 1969: 180). Unfortunately, the consequences were not limited to agriculture. By the end of 1936 all research in human genetics was suspended because it was considered inherently dangerous, racist, degrading, and based on fallacious "bourgeois genetics". Those scientists who disagreed with Lysenko and his followers lost their jobs, were reassigned to lower positions, or were sent to work camps where an unknown number perished. The first book in Russian on human genetics was not published until 1964, which meant that twenty-five successive classes of physicians graduated from medical schools "...without the slightest notion of the laws of heredity" (Medvedev 1969:94). While researchers in other countries became increasingly aware that the severe behavioral effects of genetically based metabolic disorders could usually be avoided with special diets, Soviet doctors were forced to toil under a proscribed ignorance.

This ignorance led directly to unnecessary suffering. Research into phenylketonuria, for example, which is known to cause early mental retardation because of an enzymatic deficiency, began in 1934 and a special diet had been devised by 1953 (Plomin *et al.* 1990). Galactosemia, another enzymatic deficiency that also causes

mental retardation, was discovered in 1956 (Cavalli-Sforza and Bodmer 1971). In all, the specific enzyme deficiencies for some 24 different genetic conditions (11 of which are known to cause retardation or early death) were discovered prior to 1964, the year of Lysenko's replacement (Cavalli-Sforza and Bodmer 1971). If Soviet scientists had been allowed to research human genetics, it is likely that Soviet researchers would also have made significant discoveries. While we will never know the exact cost in human life of the rejection of genetics in the Soviet Union during this period, we can be sure it was not trivial.

Is it possible, then, to justify the position that it is always more humane to operate from a non-biological paradigm in the absence of more specific knowledge? Unfortunately, if we continue to operate from a non-biological mindset, the only way to obtain specific knowledge of biologically important influences on behavior will be to stumble blindly onto them. The Lysenko affair, along with the situation with regard to lactose intolerance, serves to remind us that severe costs have been paid as a direct result of ignorance. While neither situation involved a conscious conspiracy to cause harm, this did not make the costs any more palatable. It would have been easy to avoid such costs if the right questions had been asked. It will always be more prudent to investigate every possibility, including the possibility that biological differences influence behavior. This is not the same as stating that we should assume all behavioral variation is genetic. It is an appeal for more knowledge. If differences exist, it is essential that we understand them. Truly humane policies can only be derived from an understanding of both biological and environmental influences.

JUST-SO STORIES

In the post-Darwinian era, a reaction against uncritical acceptance of the selection theory set in, which reached its climax in the great days of Comparative Anatomy, but which still affects many physiologically inclined biologists. It was a reaction against making uncritical guesses about the survival value, the function, of life processes and structures. This reaction, of course healthy in itself, did not (as one might expect) result in an attempt to improve methods of studying survival value; rather it deteriorated into lack of interest in the problem -- one of the most deplorable

things that can happen to a science (Tinbergen, quoted in Clutton-Brock & Harvey 1979).

The second *a priori* objection to sociobiology arose from within the ranks of evolutionary biologists. Sociobiologists believe that behavior itself should be considered an adaptation, just as morphological characters, like the wings of birds, have been considered adaptations (Barash 1977). As a working hypothesis, an animal's behavior is not assumed to be the result simply of learning, in a sense "independently created" in each generation, but rather it is assumed to have a heritable basis and therefore to have been shaped by natural selection. This idea has been challenged primarily because of this emphasis on behavior as an adaptation (Lewontin 1979). Gould and Lewontin (1979) have been the primary critics of the way many biologists place exclusive emphasis on the delineation of adaptations in species. They argue that not enough attention is given to such questions as "to what extent are we justified in assuming a character (or behavior) is an adaptation?", "How should we define adaptation?" and "What other evolutionary forces besides natural selection are operating to produce the phenotypic and genotypic variation we see today?" In defense, adaptationists acknowledge these problems but argue that some starting assumptions are necessary for any evolutionary investigation (we do not *start* with perfect knowledge), and that there is no reason to assume that adaptationism as a working hypothesis (i.e., as a guide to future research) is invalid. In fact, as I will argue, the "adaptationist programme" (Gould and Lewontin 1979) is the only useful paradigm for evolutionary research. As a result, sociobiology cannot be rejected out of hand simply because it is "adaptationist".

How do evolutionary biologists define adaptation? Lewontin (1978) has defined it as a "process of evolutionary change by which the organism provides a better and better 'solution' to the 'problem.' The 'problem' is set by the external world, and the agent of change is natural selection" (1978:56). Function is therefore implicit in the concept of adaptation. Futuyma (1986) states that "the analysis of adaptations entails showing that the trait has been developed by natural selection, and specifying the nature of the selective agent or agents that have favored the trait" (1986:251). Clutton-Brock and Harvey (1979) have argued that the concept of adaptation should not be restricted to traits of known genetic origin, since ontogeny always involves the interaction of environment and genes. Any conceivable trait would therefore have to be divided

into adaptive (genetic) and nonadaptive (environmental) segments. By not restricting the definition in this way Clutton-Brock and Harvey (1979) acknowledge, however, that adaptations could arise from forces other than natural selection. Most workers reserve the term adaptation for those features specifically built for some function by natural selection (Williams 1966; Gould & Vrba 1982).

Gould and Lewontin (1979) argue that the common strategy among evolutionists is to: 1) atomize the organism into traits; 2) argue that the traits are optimally designed for some function by natural selection; and 3) argue that traits not perfectly adapted to some function are so because of the inability to optimize more than one trait without imposing expenses on others, such that a balance between opposing traits is reached. They find fault in this strategy for two main reasons. First, not enough care is given to the problem of how to atomize traits, or how to find what Lewontin (1979) calls "the 'natural' suture lines for evolutionary dynamics" (1979:7). Both Gould (1977) and Lewontin use the example of the human chin: it is not an adaptation but simply a result of two growth fields (alveolar and mandibular) that, in humans, have regressed at different rates (the former faster than the latter).

Second, they argue that the exclusive focus on the adaptive function of traits, the "adaptationist programme," obscures the fact that some traits may not be adaptations. They feel that one should not assume a trait is an adaptation even if it is clearly advantageous for the organism: "The mere existence of a good fit between organism and environment is insufficient for inferring the action of natural selection" (Gould & Lewontin 1979:592). Some evolutionists try one "adaptive story" after another until they find one they can live with. These explanations are dubbed "just-so stories" after Kipling's children's tales. Other evolutionists simply assume an adaptive explanation exists without considering alternative, nonadaptive explanations. Possible alternatives include: 1) pleiotropy, where the trait is simply one nonadaptive expression of a gene with many effects (these other effects may or may not be adaptive themselves); 2) multiple selective peaks of equal adaptiveness, such that chance determines which peak an organism happens upon first (e.g., one-horned Indian rhinoceros versus two-horned African varieties); 3) allometry, in which traits are unequally affected by developmental processes, so that an increase in the size of, for instance, cervine deer antlers is more than proportionately greater than the corresponding increase in body size; and 4) random gene frequency changes due to finite population size, in

which combinations conferring lower genetic fitness can even become fixed (if population and/or fitness differences are small enough) (Gould & Lewontin 1979).

Given these confounding variables, under what circumstances are biologists ever justified in advancing adaptationist arguments? Gould and Lewontin (1979) give no explicit guidance, but remark that they "would not object so strenuously to the adaptationist program if its invocation, in any particular case, could lead in principle to its rejection for want of evidence" (1979:587). What they object to is the use of adaptationism as a working hypothesis. They emphasize that biologists need to treat the organism as a whole entity, not a collection of discrete adaptations: "If selection can break any correlation and optimize parts separately, then an organism's integration counts for little" (1979:596). Lewontin (1979) states outright that "If sociobiological theory is to make a lasting contribution to our understanding of evolution, it must abandon the naive adaptationist program..." (1979:14).

This is a fundamental methodological issue, and to properly analyze it we must not forget how science proceeds. Adaptationism is simply one way of ordering the mass of empirical observations. It does not follow that we are unjustified in using it to guide our investigations simply because it might yield "incorrect" answers. In fact, nonadaptive arguments suffer from exactly the same theoretical problem. Adaptationalism and nonadaptationalism do not represent opposite ends of a spectrum (such as "high metabolism" versus "low metabolism") but rather the presence or absence of a phenomena. The opposite of "adaptive" is not "*less* adaptive", but "*not* adaptive". We just cannot know, *a priori*, which hypothesis is operational. But if we start with the assumption of nonadaptation, the quest for understanding is ended. Mayr (1983) makes this explicit: "As a consequence of the adaptationist dilemma, when one selectionist explanation of a feature has been discredited, the evolutionist must test other possible adaptationist solutions before he can resign and say: This phenomenon must be a product of chance" (1983: 326). We have no choice but to start from an assumption, *as a working hypothesis*, that a given trait is an adaptation if it confers some advantage to the organism. There can never be direct "proof" of nonadaptation, only a lack of adaptationist explanations that fit our observations.

Nonadaptive arguments therefore suffer from an intractable problem. Lewontin (1978) points out that "biologists are forced to the extreme adaptationist program because the alternatives, although they are undoubtedly operative

in many cases, are untestable in particular cases" (1978:169). This is *not* true of most adaptive arguments (Mayr 1983). As Clutton-Brock and Harvey (1979) point out:

Though many functional arguments are initially *post-hoc*, relatively few are *ad-hoc*: almost all claim generality of some kind and are consequently refutable by more detailed observation, by experiment or by examination of their validity in other groups of animals... The fact that they originated in *post-hoc* explanations is not an objection: this is an inevitable stage in any observational science. In fact we rather doubt that *post-hoc* explanations are more misleading than many cases where predictions are formulated and subsequently tested: it is seldom difficult to produce facts that are generally congruent with a theory, and the process can appear falsely conclusive (1979: 550).

It is instructive to note that in Gould's (1984) attempt to demonstrate nonadaptive variation in the shells of land snails in the genus *Cerion*, *he empirically invalidates the adaptive arguments he had previously advanced* (Gould 1969). He acknowledges that "some unexamined selective agent might be clinally distributed throughout the islands" (1984:235) that would account for the observed variation. In order to argue for non-adaptation, Gould himself implicitly recognizes that he must demonstrate that the adaptive hypotheses are inoperable. Thus, whether one operates from the adaptationist program or espouses nonadaptationist explanations, one is still obligated to test possible adaptive arguments.

THE CASE FOR ADAPTATIONISM

Aside from methodological issues, however, there are other arguments that support the adoption of adaptationism as an initial working hypothesis. Mayr (1978) points out that our world view is dominated by the knowledge that both cosmic evolution and biological evolution have proceeded under "more or less directional natural processes consistent with the laws of physics" (1978:47). Yet he goes on to state that biological evolution is fundamentally more complicated than cosmic evolution; that living systems are "far more complex than any non-living system" (1978:47). The tremendous complexity of living organisms points to the im-

portance of natural selection in evolution. While there have obviously been random, or nonselective, forces helping to shape organisms, such forces could not have been dominant. No one has been able to demonstrate how such complexity could arise without selection. In fact, Wright (1980) has argued that pure random drift (with no accompanying selection) must lead to degeneration and extinction. While Wright's adaptive landscape metaphor incorporates random factors, he is in fact arguing that adaptations superior to those produced solely by selection could be obtained from a mixture of selection and drift.

Experiments have demonstrated that tremendous changes can be induced in a population by artificial selection, given some genetic variation (e.g., Yoo 1980; and see Falconer 1981). Dawkins (1982) warns us that human subjective judgement can be quite unreliable in assessing just how unimportant weak selection may be to have any effect. Mathematical calculations by Haldane (1932) demonstrate selection pressure as weak as 1 in 1000 on an advantageous allele would lead to fixation in only a few thousand generations, given reasonable assumptions about population size. Lande (1976) has shown that, assuming the heritability we see in extant species has been constant throughout horse evolution, only about two selective deaths per million individuals would account for the observed changes in the paleontological record. Selection, therefore, can at least theoretically exert a tremendous influence on biological evolution.

The utility of these calculations on extant organisms to help us understand the past is limited because we do not fully understand the constraints imposed by developmental processes on traits. Allometry, of course, is one such developmental constraint. But allometric constants are not constant for all time. Dawkins (1982) points out that "the allometric constant is a parameter of embryonic development. Like any other such parameter it may be subject to genetic variation and therefore it may change over evolutionary time" (1982:33). Clutton-Brock and Harvey (1979) have noted that allometric constants vary between phylogenetic groups. It is certainly not inconceivable that these differences are due to selection. But even this can be tested: if no other major ecological or behavioral factor is correlated with increased antler size in relation to body size, for example, then we may confidently assert that the allometric constant, as far as we are able to judge, is nonadaptive. Clutton-Brock and Harvey (1979) found that large deer species tend to be strongly polygynous. Since males of polygynous species are likely to compete for access to females, they may well invest

more heavily in large antlers than the males of small, non-polygynous deer species. The acid test would be to see how much of the variation in antler size can be explained by these other variables.

There are evolutionary biologists that have no faith in their ability to make decisions about what constitutes an adaptation and what constitutes a trivial character before actually studying an organism. Cain (1964) remarks that, before studies by Sheppard and himself demonstrating selective forces operating on the snail species *Cepaea nemoralis* and *Cepaea hortensis*, "it had been confidently asserted that it could not matter to a snail whether it had one band on its shell or two" (1964:48). This remark comes frighteningly close to Gould's (1984) remark about variation in *Cerion*: "Are such small differences, each involving a simple variation in basic ontogenetic pattern, necessarily adaptive? Must they make a difference to a snail?" (1984:235). Dawkins (1982) notes that history seems to be on the side of the adaptationists, in that time after time aspects of organisms thought to be "trivial" have been found to be adaptive (1982:31). This does not mean that every trait must be an adaptation, but simply that "merely to fail on a casual inspection to see any selective significance in a particular variation does not license the observer to proclaim that there is none" (Cain 1964:48). Every question must be tackled afresh, on its own merits (Dawkins 1982).

Cain (1964) also calls into question the concept of neutral adaptation. What pattern of variation should we expect to find for truly neutral traits? He argues that we would find enormous variation. The example he cites is of fingerprints. Every human being has dermal ridges. This lack of variation in morphology suggests dermal ridges are functional (i.e., are adaptive). However, provided there are enough ridges to produce an adequate friction pad, and assuming they run in all directions so that the finger is not likely to slip in one direction more than another, "the exact pattern is immaterial and can be allowed to vary. The resulting variation is certainly tremendous, and this, and not relative constancy, is what we would expect of neutral characters" (1964:48). With this logic he maintains that ancestral traits that characterize major clades (like the aquatic phase of amphibians) are not merely neutral holdovers (as per Gould 1986), but represent adaptations to less specialized ways of life. If these characters were truly neutral and not soundly functional, they would vary wildly, especially given their antiquity (Cain

1964:37). This must be true, since mutations are continually occurring at all loci and would accumulate unchecked in neutral genes.

While it is true that adaptationists maintain that natural selection is inherently an optimizing process, this does not mean that they ignore constraints. Dawkins (1982), Clutton-Brock and Harvey (1979), Cain (1964) and Mayr (1983) all list essentially the same possible constraints on perfection. The difference is that adaptationists insist that we *test* for adaptations. This *requires* that we construct plausible "just-so stories". Adaptationists operate from the assumption that natural selection, given enough time, closely approaches the optimal solutions given the possible constraints. In sum, there is no reason to assume: 1) that nonadaptationism as a working hypothesis is most appropriate *a priori*; and 2) that adaptation and nonadaptation are mutually exclusive explanations of a trait: in order to test for nonadaptation one is forced to exclude (test for) adaptation.

CONCLUSION

Sociobiology is a research program aimed at understanding behavior as an evolutionary adaptation. As such it carries all the underlying assumptions of the field of evolutionary biology. But because every paradigm has underlying assumptions, this fact cannot be a criticism of sociobiology, but instead is a criticism of human limitations. The main reasons that have been proposed for why sociobiology should not be used as a research program simply do not hold water. Nonbiological explanations of behavior are not inherently less dangerous than biological ones. Human suffering has resulted from the uncritical acceptance of nonbiological explanations. Criticisms of adaptationism reflect a misunderstanding of evolutionary biological reasoning. Adaptationist hypotheses are an essential step in the process of gaining knowledge. Individual sociobiological explanations of particular behaviors may well be incorrect, but the sociobiological world view is not "wrong" *a priori*.

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REFERENCES CITED

- Barash, David P. (1977) *Sociobiology and Behavior*. New York: Elsevier.
- Brill, Henry (1975) Presidential address: Nature and nurture as political issues. In R.R. Fieve, D. Rosenthal, and H. Brill (eds.), *Genetic Research in Psychiatry*. Baltimore: Johns Hopkins University Press. Pp.283-288.
- Cain, A.J. (1964) The perfection of animals. In J.D. Carthy & C.L. Duddington (eds.), *Viewpoints in Biology*, volume 3. London: Butterworths. Pp.36-63.
- Cavalli-Sforza, L.L. and W.F. Bodmer (1971) *The Genetics of Human Populations*. San Francisco: Freeman.
- Clutton-Brock, T.H. and Paul H. Harvey (1979) Comparison and adaptation. *Proceedings of the Royal Society of London B* 205:547-565.
- Dawkins, Richard (1982) *The Extended Phenotype: The Gene as the Unit of Selection*. New York: Oxford University Press.
- Falconer, Douglas S. (1981) *Introduction to Quantitative Genetics*. London: Longman.
- Futuyma, Douglas J. (1986) *Evolutionary Biology*, 2nd edition. Massachusetts: Sinauer Associates.
- Gould, Steven J. (1969) Character variation in two land snails from the Dutch Leeward Islands: Geography, environment, and evolution. *Systematic Zoology* 18:185-200.
- Gould, Steven J. (1977) *Ontogeny and phylogeny*. Cambridge, Massachusetts: Belknap Press.
- Gould, Steven J. (1984) Covariance sets and ordered geographic variation in *Cerion* from Aruba, Bonaire and Curaçao: A way of studying nonadaptation. *Systematic Zoology* 33:217-237.
- Gould, Steven J. (1986) Of kiwi eggs and the Liberty Bell. *Natural History* 95:21-29.
- Gould, Steven J. and Richard C. Lewontin (1979) The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London B* 205:581-598.
- Gould, Steven J. and Elizabeth S. Vrba (1982) Exaptation -- A missing term in the science of form. *Paleobiology* 8:4-15.
- Haldane, J.B.S. (1932) *The Causes of Evolution*. London: Logman's Green.
- Kitcher, Philip (1985) *Vaulting Ambition, Sociobiology and the Quest for Human Nature*. Cambridge, Massachusetts: The MIT Press.
- Kuhn, Thomas S. (1970) *The Structure of Scientific Revolutions*, 2nd edition. Chicago: University of Chicago Press.
- Lande, Russel (1976) The maintenance of genetic variability by mutation in a polygenic character with linked loci. *Genetical Research* 26:221-235.
- Leininger, M. (1978) Some cross-cultural universal and non-universal functions, beliefs, and practices of food. In M. Leininger (ed.), *Transcultural Nursing: Concepts, Theories, and Practices*. New York: John Wiley and Sons. Pp.203-219.
- Lerner, I. Michael and W.J. Libby (1976) *Heredity, Evolution, and Society*. San Francisco: W.H. Freeman and Company.
- Lewontin, Richard C. (1978) Adaptation. *Scientific American* 239:156-169.
- Lewontin, Richard C. (1979) Sociobiology as an adaptationist program. *Behavioral Science* 24:5-14.
- Mayr, Ernst (1978) Evolution. *Scientific American* 239:47-55.
- Mayr, Ernst (1983) How to carry out the adaptationist program? *American Naturalist* 121(3):324-334.
- Medvedev, Zhores A. (1969) *The Rise and Fall of T.D. Lysenko*. Translated by I. Michael Lerner. New York: Columbia University Press.
- Plomin, Robert, J.C. DeFries and G.E. McClearn (1990) *Behavioral Genetics*, 2nd edition. New York: W.H. Freeman and Company.
- Ruse, Michael (1985) *Sociobiology: Sense or Nonsense?* 2nd edition. Boston: D. Reidel Publishing Company.
- Soulé, M.E. (1985) What is conservation biology? *BioScience* 35:727-734.
- Stein, George J. (1988) Biological science and the roots of Nazism. *American Scientist* 76: 50-58.
- Williams, George C. (1966) *Adaptation and Natural Selection*. Princeton, New Jersey: Princeton University Press.
- Wilson, Edward O. (1975) *Sociobiology: The New Synthesis*. Cambridge, Massachusetts: Harvard University Press.
- Wright, Sewell (1980) Genic and organismic selection. *Evolution* 34:825-843.
- Yoo, B.H. (1980) Long-term selection for a quantitative character in large replicate populations of *Drosophila melanogaster*. I. Response to selection. *Genetical Research* 35: 1-17.