The Biology of Moral Systems

Richard D. Alexander
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When a biologist publishes a treatise with a title like *The Biology of the Amphibia*, *The Biology of the Mountain Bluebird*, or *The Biology of the Gene*, he means “everything about the life and natural history” of the group or unit in question, as seen through the eyes of a biologist. That is precisely how the title of this book should be translated. I have tried to discuss everything about the life and natural history of moral systems, as seen through the eyes of a biologist.
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Richard D. Alexander
To my children

And theirs
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Thoughtful people seem increasingly to agree that our society—indeed, world society as a whole—has entered into a crisis of unprecedented magnitude, and with potential consequences almost too horrible and irreversible to contemplate. This deepening crisis arises from the interaction of several contributing factors. First, is an accelerating technological alteration of the environment and, concomitantly, of our social structures and ourselves. Second, is an accelerating depletion of the world’s resources, and an accompanying interest among the more powerful nations in manipulating and competing over those less powerful who possess the scarce resources they need. Third, is an elaboration and proliferation of weapons now so terrible as to assure, for the first time in history, that almost no imaginable alternative is worse than their employment. Finally, coincident with the rise of weaponry, there has been an effective shrinking of the social brain that controls it. No matter how many millions of citizens may exist in a given nation-state, no matter how hideous its weaponry, the decision regarding use of that weaponry eventually comes down to about the same small number of individuals, or even to the calculations of a single brain. At least as a final step, it takes only one finger to push a button that could bring on what might aptly be termed the ultimate holocaust. Moreover, modern nations are now so large and complex that internal differences of interests and the possibilities for deception may allow small, special-interest groups to promote the international arms race at the cost of the rest of the society, and even of the world as a whole (including, ultimately, even if inadvertently, themselves). It may be appropriate to characterize the so-called great nations of the world today as the most enormous, most awesomely weaponed, smallest-brained “dinosours” of all time.

Even if I have exaggerated its seriousness (the growing public clamor suggests otherwise), the crisis is undeniable. Just as undeniably, the crisis arises out of our social activities: out of the nature and consequences of our personal and group interactions around the world; out of the nature and consequences of our beliefs, individual and collective, with respect to right and wrong; out of our attitudes and actions in the realm that we call ethics and morality, whether at international, national, local, or even family levels. Discords that bear strong resemblances to one another permeate the entire hierarchy of social organization, from the smallest social groups right through to the largest. These
discords are invariably centered on moral and ethical enigmas. It is
difficult to avoid the impression that some common problems underlie
the solutions to all of them.

During 1977–1978, I participated in a series of conferences at the
Hastings Institute in New York, charged with a search for the "founda-
tions" of ethics. These conferences, which together with an earlier series
gave rise to five published volumes (Engelhardt and Callahan,
1976–1980; Callahan and Engelhardt, 1981), were organized as a result of
the flood of new ethical questions arising out of technology: abortion,
euthanasia, the right to reject certain kinds of technological prolongation
of life, etc. The Hastings Institute itself was organized for the same
general reason, in 1969, and it has become widely known for its
examination of the questions involving medical ethics and bioethics.
More than anything else, the Hastings conferences set me to thinking
and reading about the general background of human ideas about
morality. I read all of the reports published by the Hastings Institute and
entered the philosophical literature on the same topics. As a result, I
began to puzzle over what I saw as an incompleteness or inconclusive-
ness, not only of the collection of Hastings reports and the discussions
in the conferences in which I had participated, but, indeed, of all general
arguments on ethics. I found myself sharing the attitude expressed by
the philosopher, Alasdair MaClntyre (1981a), in a question in the title of
his final paper in the Hastings Center conference series: "A crisis in
moral philosophy: Why is the search for the foundations of ethics so
frustrating?"

Even if quick and decisive solutions to ethical and moral problems are
simply not possible, I find myself thinking that in all of the arguments
something is missing. Indeed, I believe that something crucial has been
missing from all of the great debates of history, among philosophers,
politicians, theologians, and thinkers from other and diverse back-
grounds, on the issues of morality, ethics, justice, right and wrong. Why
have the greatest minds throughout history left such questions seemingly
as unresolved as ever? Why is it that, as MaClntyre (1981b) put it, debates
about morality "apparently can find no terminus"? Why should it be that,
despite our most intense and sincere efforts, we are not really prepared
to deal with the crises that our own activities bring about, even though
we cannot but admit that they now have the potential, incredibly, to
cause the destruction of life, or at least civilization, on our planet?

Part of the answer is that those who have tried to analyze morality
have failed to treat the human traits that underlie moral behavior as
outcomes of evolution—as outcomes of the process, dominated by
natural selection, that forms the organizing principle of modern biology.
This omission is not really the fault of those who have studied ethical and moral systems. The science of biology has been so vague about how to apply natural selection that not until the last two decades have biologists themselves been able to use it to analyze social systems.

Discussions of moral issues seem invariably to end up confronting a core of unanalyzable mystery. Sometimes this mystery is acknowledged, or dealt with, by relegating moral decisions to the supernatural—by asserting, for example, that the answers to moral questions come only from God. Sometimes the mystery is simply what is left when a philosopher or other intellectual has wrestled through an issue—like the conflict between seeking what is best for one’s self and seeking to bring "the greatest good to the greatest number"—and failed to explain how the issue can be resolved by referring to the concept of morality. Sometimes the mystery seems to represent all that we do not understand about human nature or motivations.

Part of my purpose here is to see if this core of mystery can be dispelled by re-examining human striving, using new information and ideas from the discipline of biology. Although I may not have succeeded, at least I believe I have demonstrated that the undertaking is reasonable. I think I have shown that evolved human nature and morality are compatible; that morality as generally conceived, and possibly even as seen by idealists from philosophy and theology, is neither contrary to biologists’ understanding of evolution by natural selection (as thought by T. H. Huxley, 1896) nor independent of selection, requiring a divine origin (as thought by Lack, 1957, 1965).

Moral problems involve the interests of people, and biology gives good reasons for expecting different individuals to behave as if their interests are unique, and thus as if interests conflict among individuals to some degree almost all of the time. Regardless of the value of insights provided by individuals, then, only the collective—directly or through representatives—is likely to serve the collective’s interests. Arguments from biology support those from other sources which indicate that, for many conflicts of interest, compromises and enforceable contracts represent the only real solutions. Appeals to morality, I will argue, are simply the invoking of such compromises and contracts in particular ways. Moreover, the process of natural selection that has given rise to all forms of life, including humans, operates such that success has always been relative. One consequence is that organisms resulting from the long-term cumulative effects of selection are expected to resist efforts to reveal their interests fully to others, and also efforts to place limits on their striving or to decide for them when their interests are being “fully” satisfied.
These are all reasons why we should expect no "terminus"—ever—to debates on moral and ethical issues. But they are not reasons for supposing that the mystery underlying the concept of morality is inevitable or that practical solutions to moral questions cannot be devised that will lessen the social and political problems of the world.

Biologists do not typically talk much about morality, and I have often heard people express disappointment and frustration because biologists seem always to stop short of explaining how Darwinian evolution might help in the search for ideas on how to turn our social behavior into more positive and less terrifying channels. As a student once said to me, "What good is a theory about human behavior that cannot help us with our worst [moral and ethical] problems?" Although this is a serious and useful question, I am convinced that biology can never offer what most such people seem to expect: easy or direct answers to the questions of what is right and wrong. I explicitly reject the attitude that whatever biology tells us is so is also what ought to be (David Hume's so-called "naturalistic fallacy"), as offered by such biologist-philosophers as Julian Huxley (1947) and Wolfgang Wickler (1972). Contrary to Wickler's arguments, biologists do not have special abilities to assess what is ethical; and, contrary to the implications of Huxley, there are within biology no magic solutions to moral problems.

The opinion seems to be widespread that for evolutionary biology to be important to humans it has to provide quick and dramatic solutions to specific problems. It is not my experience that such solutions are likely. Some are possible, as in the discovery, from applying evolutionary theory, of means for telling which disease symptoms of a host aid the disease organism and which aid the host (Ewald, 1980). This approach may enable one to decide the highly practical question of which symptoms of human disease to alleviate by palliatives, and which to leave alone. Generally speaking, however, the great value of evolutionary understanding lies in its guidance in developing appropriate and useful ideas and hypotheses about human activities and tendencies. Evolutionary understanding changes attitudes, therefore it may affect almost anything we do, but sometimes quite indirectly and only after considerable delay. Scarcely any reasonable person exposed to Darwin's theory would deny that it has significantly altered human existence. But the exact ways in which evolutionary knowledge participates in solutions to human problems are usually subtle and difficult to evaluate. For the very reason that evolutionary understanding affects nearly everything humans think about themselves, most
people would be hard-pressed to explain or summarize its effects adequately.

Biology provides a broad source of information about humans that has no substitute. It clarifies long-standing paradoxes. It shows that some things have indeed been missing from the debates about morality, and they have been missing because the process of organic evolution that gave rise to all forms of life has been left out of the discussions. Knowledge of the human background in organic evolution can provide a deeper self-understanding by an increasing proportion of the world's population; self-understanding that I believe can contribute to answering the serious questions of social living.

These are reasons why I regard it as a responsibility of biologists—in the tradition of Charles Darwin, Thomas Huxley, Sir Arthur Keith, David Lack, Theodosius Dobzhansky, George G. Simpson, and a few others—to develop a better "natural history" of moral and ethical attitudes and beliefs. They are reasons why I think it useful to examine the biology of moral systems.

This book may be regarded as continuing the arguments in my 1979 book, *Darwinism and Human Affairs*; the first chapter of that book is a useful introduction to what follows here. In the present book there are five chapters. The first takes up biological issues that underlie the theoretical positions, and deals with some concepts and problems that have in the past made it difficult for biologists, philosophers, and social and political scientists to understand one another. I do not think all of the biology in this first chapter is required to follow my arguments, but the more of it that is absorbed the better the reader will understand my positions.

The second chapter develops the theory and discusses its application to human actions, the human psyche, and the ontogeny of moral ideas. The third reviews arguments of moral philosophers, philosophers of biology, and biologist-philosophers on several moral issues. This review is mainly critical, trying to show how philosophers' arguments have been affected by leaving out concepts and facts essential for understanding the strivings of organisms. I have not tried to review the voluminous history of philosophical writing or even to trace the development and priority of ideas; rather, I have chosen a few prominent authors that seem representative of modern philosophical discussions of morality and discussed aspects of their writing that seem most important in illustrating my arguments.

The fourth chapter considers the consequences of applying a biological approach to morality. It includes an effort to interpret the human
psyche in evolutionary terms and a review of problems associated with
the international arms race. The fifth chapter briefly reviews conclu-
sions, and the epilogue is, in part, a brief abstract of the entire book.

I am sincerely of opinion that the views . . . propounded by Mr. Darwin
may be understood hereafter as constituting an epoch in the intellectual
history of the human race. They will modify the whole system of our
thought and opinion, our most intimate convictions.

T. H. Huxley, 1894

Richard D. Alexander
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Should a traveller give an account of men who were entirely divested of avarice, ambition, or revenge; who knew no pleasure but friendship, generosity, and public spirit, we should immediately detect the falsehood and prove him a liar with the same certitude as if he had stuffed his narration with centaurs and dragons.

David Hume, 1772, *Essays and Treatises*

A hydrogen bomb is an example of mankind’s enormous capacity for friendly cooperation. Its construction requires an intricate network of human teams, all working with single-minded devotion toward a common goal. Let us pause and savor the glow of self-congratulation we deserve for belonging to such an intelligent and sociable species.

Robert S. Bigelow, 1969 *The Dawn Warriors*

The self-extinction of our species is not an act that anyone describes as sane or sensible; nevertheless, it is an act that, without quite admitting it to ourselves, we plan in certain circumstances to commit.

Jonathan Schell, 1982 *The Fate of the Earth*
INTRODUCTION

Moral systems are societies with rules. Rules are agreements or understandings about what is permitted and what is not, about what rewards and punishments are likely for specific acts, about what is right and wrong. Although moral rules are somewhat different from legal rules, or laws, the two are not unrelated and frequently overlap.

Moral behavior, in general, consists of following the rules—of not "cheating." But this is where the problems begin, rather than where they end. Few would accept that following the rules that prevail in society at any particular time is necessarily the most moral thing that one can do. Rules change. They are sometimes imposed by tyrants. There is probably no rule that everyone agrees with.

Moreover, we have come to regard morality—in the sense of concern for others—as something above and beyond rules per se, an ideal to be striven for even if there is no real hope of achieving it in its purest form. Many people believe that morality is an absolute, that there are general rules of moral behavior that are unchanging, and even that such rules are "natural laws" or God-given. I wish to examine such seeming absolutes, how they might have arisen, how hard we really strive toward them, what are the consequences of our striving, why we have failed so far, and how all of these questions are affected by an evolutionary viewpoint.

I will argue that the concepts of moral and ethical arise because of conflicts of interest, and that—at least up to now—moral systems have been designed to assist group members and explicitly not to assist the members of other competing groups. Because between-group competition and aggression are major concomitants of within-group cooperativeness, moreover, I will also argue that moral "advances" are not necessarily related to the philosophical ideal of morality as either indiscriminate or self-sacrificing beneficence or producing the greatest good for the greatest number. Although not necessarily denying the
feasibility of achieving or approaching such ideals, I will argue that failing to distinguish them from what has really been going on in the world has been—and still is—the main source of confusion and mystery with respect to moral and ethical considerations.

If there had been no recent discoveries in biology that provided new ways of looking at the concept of moral systems, then I would be optimistic indeed to believe that I could say much that is new. But there have been such discoveries. They are the advances in evolutionary theory developed principally by William D. Hamilton (1964), George C. Williams (1966b), and Robert L. Trivers (1971). These refinements, which were systematically reviewed in *Darwinism and Human Affairs* (Alexander, 1979a; see also Dawkins, 1976; Alcock, 1984; Chagnon and Irons, 1979; Symons, 1979) have been incorporated into the research and teaching of hundreds of young biologists active in fields like ecology, animal behavior, and population biology (e.g., see Alexander and Tinkle, 1981; Clutton-Brock and Harvey, 1978; Hunt, 1980; Krebs and Davies, 1981, 1984; Trivers, 1985; and biological journals like *The American Naturalist, Animal Behaviour, Ecology, Evolution, and Behavioral Ecology and Sociobiology*). They have also been used by a small group of biologists and social scientists, probably fewer than 100 so far, in renewed efforts to apply evolutionary biology to the human understanding of humans (Alcock, 1984; Alexander, 1979a; Alexander and Tinkle, 1981; Betzig, 1986; Cavalli-Sforza and Feldman, 1981; Chagnon and Irons, 1979; Daly and Wilson, 1983; Dawkins, 1976, 1982; Hull, 1978; Lumsden and Wilson, 1981; Pulliam and Dunford, 1980; Ruse, 1979; Strate, 1982; Symons, 1979; Trivers, 1985; Wilson, 1975, 1978. See also, especially: *Ethology and Sociobiology, Current Anthropology, American Anthropologist, Journal of Social and Biological Structures, Human Ecology*).

The interpretations of different authors with regard to the recent advances in evolutionary theory often vary considerably. Aside from the pages that follow, my own views are most completely expressed in the first chapter of *Darwinism and Human Affairs*. With respect to humans my views probably coincide most closely with the general statements of Alcock (1984), Daly and Wilson (1983), Irons (1979), Symons (1979), and Trivers (1985). Otherwise, I recommend that the reader return to the original writings of Hamilton, Williams, and Trivers, which have now been reprinted many times (e.g., Clutton-Brock and Harvey, 1978; Krebs and Davies, 1981; Hunt, 1980). The central point in these writings, separated from all of its consequences and ramifications, is that natural selection has apparently been maximizing the survival by reproduction of genes, as they have been defined by evolutionists, and that, with respect to the activities of individuals, this includes effects on copies of
their genes, even copies located in other individuals. In other words, we are evidently evolved not only to aid the genetic materials in our own bodies, by creating and assisting descendants, but also to assist, by nepotism, copies of our genes that reside in collateral (nondescendant) relatives.

During the past few years, I have heard several people suggest that the above-mentioned refinements of evolutionary theory represent the greatest intellectual advance of the century. I agree, in the sense that significant improvements in the theory that explains our underlying nature must always command special attention. I think that almost every concept relevant to human sociality (such as rationality, conscience, guilt, consciousness, altruism, and egoism) has its meaning changed—or made more precise—by applying the new refinements of evolutionary theory. I also feel that the true realization of intellectual advances in biological theory comes from their eventual application to human conduct: from their effect on humanity’s view of itself, and, in turn, the effect of changes in self-views on human conduct and, consequently, the future of all existence. In this case the changes in self-views involve principally two items: First, is a more precise awareness of the nature of the long-term history that has shaped our life interests, most especially the idea of fulfillment through relatives and their surrogates. Second, is the realization that ethics, morality, human conduct, and the human psyche are to be understood only if societies are seen as collections of individuals seeking their own self-interests (albeit through use of the the group or group cooperativeness, and given that, in historical terms, the individual’s self-interests can only be realized through reproduction, by creating descendants and assisting other relatives). In some respects these ideas run contrary to what people have believed and been taught about morality and human values: I suspect that nearly all humans believe it is a normal part of the functioning of every human individual now and then to assist someone else in the realization of that person’s own interests to the actual net expense of those of the altruist. What this “greatest intellectual revolution of the century” tells us is that, despite our intuitions, there is not a shred of evidence to support this view of beneficence, and a great deal of convincing theory suggests that any such view will eventually be judged false. This implies that we will have to start all over again to describe and understand ourselves, in terms alien to our intuitions, and in one way or another different from every discussion of this topic across the whole of human history. It is also a goal of this book to contribute to this redescription and new understanding, and especially to discuss why our intuitions should have misinformed us.
A major illustration of what this redescription means involves the resolution of the problem of duality (selfishness and altruism) in human nature, paradoxical to the earliest philosophers and not resolved in any writings that do not take modern biology into account. We have every reason to believe that our view of human nature can now be reunified, with David Hume's (1750) "elements of the serpent and the wolf" referring to the serving of our own interests by assisting ourselves at others' expense, and his "particle of the dove" representing the serving of our own interests through (1) relatives who carry our genetic materials and (2) friends and associates who may be expected to reciprocate our kindnesses with interest.

Only six authors (Alexander, 1979-1985; Campbell, 1972-1983; Singer, 1981; Mackie, 1978, 1982; Ruse, 1979-1986) have previously made extensive attempts to apply recent evolutionary theory to the study of ethical questions, although several (e.g., see Barash, 1977; Boehm, 1979; Caplan, 1978; Dawkins, 1976, 1982; Stent, 1978; E. O. Wilson, 1975, 1978; Richards, 1982-1986) have discussed the topic briefly. One author, Kitcher (1985), criticizes extensively what he sees as E. O. Wilson's (1975, 1978) and Lumsden and Wilson's (1981) views on evolution and ethics (and their and my more general views of how evolution has affected human behavior). Flew (1967) and Richards (1986a,b) review a good part of the literature on evolution and ethics that preceded the recent refinements of evolutionary theory (see also Ebling, 1969). I see the outstanding efforts by older authors to relate evolution and ethics as those of Darwin (1871), Thomas H. Huxley (1896), and Sir Arthur Keith (1947) (see pp. 168-177).

SOCIobiology and Ideology

A caution is necessary, especially for the nonbiologist audience. As I see it, the greatest distortions of the recent advances in evolutionary biology are discussed under the label "sociobiology," whether by its most enthusiastic supporters or (more especially) its most severe critics. These include implications that behavioral causation can sometimes be reduced to genetic factors alone; undue emphasis on the sterile dichotomy of innate versus acquired (or genetic versus learned, social, or cultural); suggestions of identifiable but unchangeable limits on human learning in the conduct of social and ethical activities; implications that one or another brand of social Darwinism deserves reviving; casual, careless, or otherwise flawed imputations of function; and arguments for some version of the naturalistic fallacy (see pp. 165-168). Opponents
of sociobiology argue that most or all evolutionary biologists support these errors and fallacies.

Some people asked why I did not use the label of sociobiology in my 1979 book; the main reason is that distortions by both proponents and opponents, which are involved in most so-called sociobiological writings about human behavior, detract from the real issues. The other reasons are: (1) outside biology the label is more closely associated with certain views of behavioral ontogeny and ethics (which I often do not share—see Alexander, 1979a), than with advances in evolutionary theory per se; (2) those efforts to apply evolution specifically to analyses of human behavior, which parade the adjective “sociobiological,” have sometimes been the least scholarly (especially in the sense of distinguishing hypotheses from conclusions or “explanations”); and (3) even if sociobiology were to be accepted as simply “the study of the evolution of social behavior” (rather than someone’s view of the developmental or genetic background of behavior), the label does not suggest any clear or logical boundaries for a discipline. Thus, it is not easily seen to include applications of evolutionary theory to apparently “nonsocial” topics like senescence, sex ratios, and life histories. I believe it is confusing to suggest that refinements of evolutionary theory create new disciplines, that they can be restricted to something like social behavior, or that they are properly part of one particular approach. This confusion has contributed to the term sociobiology becoming a target of derogation and ridicule by nonbiologists, and this has almost certainly delayed the acceptance and use of evolutionary principles by human-oriented scholars (Alexander, 1987). The attachment of labels like sociobiology to advances in evolutionary thinking that explicitly concern human behavior tends to create ideologies and to divide the intellectual world into proponents and opponents. Too many of those involved in the ensuing “debates” do not trouble themselves to understand the underlying issues, drawing their conclusions instead from the popular literature and what they (or popular writers) see as the political or social implications. This is characteristic of ideological as opposed to scientific arguments.

The label “sociobiology” also seems to have suggested to some social and political scientists, and philosophers, that there is an easy shortcut into a deep understanding of biology. If that is true, one only needs to examine the rash of publications by nonbiologists under the label of sociobiology to see that very few have discovered the shortcut. I believe, instead, that the route to appropriate understanding of organic evolution is through a broad understanding of basic biological principles, and that significant curricular revisions will be required, introducing biology
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where it is now often completely absent, in the training of human-oriented scientists, lawyers, philosophers, and others. It is this general absence of deep understanding of biology that has caused most of the controversies about "genetic" determinism, and about the relationship of evolution by natural selection to behavioral development, learning, and culture (cf. Flinn and Alexander, 1982; Irons, 1979). Nonbiologist readers may view the first section of this book as something that can be skipped over, in order to get directly to the topic of moral systems. On the contrary, I believe that unless the arguments in this chapter, and those in the first chapter of Darwinism and Human Affairs, are understood thoroughly, what I say in the latter parts of this book is virtually certain to be misinterpreted.

Paradoxically, within biology, terms like sociobiology are not particularly controversial. This is partly because most biologists understand genetics, development, and physiology well enough not to make the naive mistakes of both critics and enthusiasts from outside biology. And it is partly because no one is very upset if someone is wrong about the developmental basis of behavior in a frog, a bird, or an insect. To be similarly wrong about humans, however, can have decidedly pernicious effects.

Three decades ago Konrad Lorenz also tried to name a "new field" which he also said consisted of the evolutionary study of behavior. The label he used, "ethology," also came to be associated with his particular views concerning the physiology, development, and inheritance of behavior and as a result eventually became obscure and less frequently used. The label "sociobiology" appears to be suffering a similar fate; and I suspect that the causes of evolution, biology, and especially humanity's understanding of itself, will thereby be served. The reason is that whatever arguments from biology are useful in understanding human behavior will then melt more easily into the human-oriented disciplines and not be held outside in an artificial subdiscipline, thus perpetuating hostilities and impeding the flow of understanding.

MEANINGS AND MISINTERPRETATIONS

It is necessary that I comment further on definitions, because even the words in the title of this book have some likelihood of being misinterpreted.

Biology and Biological

The word "biology" has diverse meanings, especially for people from different disciplines. For many (especially in the social sciences, philos-
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...ology, and medicine) biology translates as "genetic" or "physiological," and is contrasted with "psychological," "social," or "cultural." I do not so mean it, and, indeed, I reject these usages. People who have fallen into this erroneous and, I believe, harmful dichotomy are often those who search for ways to alter human behavior. In their professions they are required to ask more or less continually: can I alter this behavior by changing only the psychological, social, or cultural environment, or must I (by some other means) alter the internal physiological, chemical, or hormonal environment, or even use a genetically different individual to get a different behavior? It is understandable that this kind of problem leads them to ask whether or not a behavior is "biologically" determined. But the dichotomy is misleading. Biologists also study what social scientists call "psychological" and "cultural" aspects of behavior, even in nonhuman organisms, and not merely physiological and genetic aspects: examples may be found in nearly every paper published in journals like Behaviour, Animal Behaviour, Zeitschrift für Tierpsychologie, and Behavioral Ecology and Sociobiology. Biologists, moreover, have no justification for being more deterministic than others in their view of behavior, or for neglecting ontogenies, plasticity, or psychological, social, and cultural stimuli and causes. Learning, after all, is essentially universal among animals, and prominent behavioral variations in even simple organisms—such as those of the different castes of social insects, and indeed the morphological and physiological uniqueness of the castes—are determined by environmental not genetic variations.

My dictionary defines biology first as the science of life, and the central question of this science is the evolutionary background or adaptive function of traits and tendencies. I mean to ask: How can biology, the science of life, contribute to our understanding of moral systems? What procedures, information, concepts, and theories from the science of biology may be useful to human-oriented scholars? In what ways are moral and ethical questions related to our background in organic evolution? What has been the natural history of moral systems? One aspect of this usage that distinguishes it from the use of "biology" by many nonbiologists is that it explicitly includes environmental as well as genetic effects, and, indeed, it always includes the interaction of genes and environment. When the Harvard paleontologist Steven J. Gould said on the television news program "60 Minutes" (broadcast on April 22, 1984) that the human mind is so flexible and the potential scope of human behavior so broad that "it scarcely behooves us to consider biology at all," he was obviously using "biology" as many nonbiologists use it—to refer to genetic variations. If he interpreted biology, as I do, to mean evolutionary background (i.e., to refer to the more or less common
heritage of genes and culture given to us across all of history), he would surely have been hesitant to make the same comment. Similarly, Lewontin et al. (1984) state (p. 7) that "Biological determinism (biologism) has been a powerful mode of explaining the observed inequalities of status, wealth, and power in contemporary industrial capitalist societies, and of defining human 'universals' of behavior as natural characteristics of these societies." Deterministic views have undoubtedly so been used, but biologists, whether they are dealing with humans or nonhumans, are in no way restricted to universals or to variations that correlate with genetic variations: natural selection also fixes genes that lead to environmentally alterable traits. Whether or not they are deliberate efforts to do so, I believe that such narrow references to biology tend to denigrate and illegitimize a scientific discipline by synonymizing it with particular approaches or with ideologies.

"Biological" is often used in the popular press to refer to the relationship between parent and offspring, siblings, or other genetic relatives (e.g., "the biological father . . . "). By itself this usage is not as misleading as that implying "physiologically or genetically determined"; but the two usages are allied and that indicating relationship undoubtedly abets the restriction of "biological" to genetic or physiological backgrounds of traits. In either case "genetic" or "physiological" rather than "biological" is the correct adjective that does not mislead.

As a consequence of the general ignorance of biology, many discussants of human behavior fail to realize that nearly all traits of organisms are variable or plastic. Those traits that in usual environments are not so plastic, and that still reflect genetic variation within the human species (like eye color, nose shape, ear lobe attachment, and hair patterns on the back of the hand), are actually rare and probably will require special explanations. Many such traits in humans are involved in individual and kin recognition (Alexander, 1979a). As such they are valuable only when unequivocal and not too common, and so (1) they will tend to be rigid in their expressions and (2) the relative frequencies of the alleles (alternative genes) giving rise to their alternative expressions will fluctuate and tend not to go to fixation (i.e., no allele is likely to eliminate all others: each time any becomes common its value in recognition will diminish; see Lacy and Sherman, 1983). But alleles that behave this way—and traits determined in this fashion—appear to be less the rule than the exception.

Modern authors who consider how biology might contribute to human social enterprises seem to divide into two camps. The first group supposes that biology will be principally useful in locating a core of "basic" or essentially unalterable behaviors that will tell us how far we
realistically can go in adjusting human social behavior. Such people see specific physiological and genetic mechanisms as the link between the biological and social sciences. A second group, of which I am a part, sees biological information as, rather, a means of altering human social behavior—of rerouting it so as to avoid such things as devastating wars or pathological conditions that develop because of faulty self-images. This second group uses as its chief inspiration the elaboration of predictive and explanatory subtheories from general evolutionary theory, not the elucidation of particular physiological or hereditary mechanisms (as important as they may be in many cases), and not patterns of social behavior shown by nonhuman species. This enterprise depends on evolution being a more or less singular process with long-term cumulative effects (which it is, evidently in large part as a correlate of the universality of DNA as genetic materials). It also depends upon a thorough understanding of adaptive trends as relative success in reproduction, and of flexibility in social strategies as an adaptive trend. As knowledge of the physicochemical underpinnings of human social behavior becomes extensive and detailed, the value of evolutionary theory in guiding our understanding of ourselves will necessarily diminish. But, currently, we are far from being able to discard such guidance without severe loss.

I am not optimistic about the usefulness of searches for unalterable or "basic" human social behaviors, as a method for solving our problems, because I see human social life evolving as flexible strategizing. The relevant environment of human social success is the collection of flexible strategies employed by other human individuals or groups. Inflexibility or preprogramming would be the worst possible strategy in the face of conflicts of interest, competition, the importance of cooperation, and other aspects of sociality. Understanding the relationship between human sociality and the environment is not like understanding how organisms survive, for example, winters or earthquakes, for in social behavior the winter and earthquake equivalents are not passive but have their own interests (i.e., are chiefly other humans) and may be expected to seek them. I will argue that human social behavior is even more unusual, in that the environment of its evolution is a within-species phenomenon to a greater degree than perhaps for any other form of life. Social behavior evolves as a succession of ploys and counterploys, and for humans these ploys are used, not only among individuals within social groups, but between and among small and large groups of up to hundreds of millions of individuals.

The value of an evolutionary approach to human sociality is thus not to determine the limits of our actions so that we can abide by them.
Rather, it is to examine our life strategies so that we can change them when we wish, as a result of understanding them.

The difficulty I have in dealing with the "biological constraints" approach to human behavior could not be illustrated more starkly than by the subtitle to Mel Konner’s (1982) book, *The Tangled Wing: Biological Constraints on the Human Spirit*. Taking Konner’s usage of “biological” as “physiological” or “genetic,” the phrase making up the subtitle seems to me internally contradictory, in an intriguing and perhaps enlightening way. If one translates “spirit” roughly as “imagination,” he sees immediately that only a nonhuman (presumably extraterrestrial) being could identify constraints on the human spirit that existed because of biology, for only a nonhuman could imagine things that humans are incapable of imagining. Whatever flights of fancy any or all human spirits, or the collective human spirit, may be capable of, are realities because of our evolutionary heritage, and included are all flights of fancy having to do with what it is imagined the human spirit cannot imagine.

I made a similar argument in the epilogue of *Darwinism and Human Affairs* (pp. 279–280). Kitcher (1985, p. 283) dismissed it as “specious” because “Not only can we identify limits on our cognitive abilities without specifying the content of things that we cannot come to know (as, for example, when we find out that the answers to certain questions will forever be unobtainable or that our brains are too small to carry out certain kinds of computations), but we are perfectly able to recognize things that we cannot learn to do.” Kitcher’s view is narrower than mine, in that I would include computations conducted with devices constructed deliberately and explicitly to enable us to carry out computations we found we wanted to do but could not, and others that would enable blind people to do the equivalent of seeing or deaf people to hear. Many questions that have seemed forever unanswerable, moreover, were not. Kitcher’s quote of my statement also stopped at the point where the statement began to make his criticism less reasonable. [This comment is not restricted to this particular argument of Kitcher’s; the tendency is also evident in his criticism of my argument (pp. 59–60) that Darwin provided useful falsifying operations for his theory and his implication (p. 188) that I present “the idea that rape violates the sexual rights of a male with a proprietary interest” as if it were ethically appropriate rather than by way of suggesting reasons why rape laws seem to have been constructed as if their goal were something other than justice for women.]

The question of “biological constraints” is not trivial. Therefore, I have repeated the central paragraph in the epilogue of *Darwinism and Human Affairs* so that the reader can judge the argument himself. Some
of the qualifying phrases that may otherwise not be given sufficient attention are italicized:

As it concerns *social* behavior, human nature would seem to be represented by our learning capabilities and tendencies in different situations. The limits of human nature, then, could be identified by discovering those things that we cannot learn. But there is a paradox in this, for to understand human nature would then be to know how to change it—how to create situations that would enable or cause learning *that could not previously occur. To whatever extent that is so*, the limits of human nature become will-o'-the-wisps that inevitably retreat ahead of our discoveries about them. *Even if this is not true in all respects, I believe that it must be true in some of the most important and practical ones.* I regard it as illusory to identify social behavior far outside present human capabilities (or interests) and then suggest that one has somehow said something significant about the limits of human nature, and similarly illusory to note any current human failure in social matters and regard it as unchangeable.

The question is not one of whether or not humans can learn any and all things with equal ease; they cannot. It is not a question of whether or not they can learn new things; they can. Moreover, one finds out how to teach or learn new things by playing around with "old" behaviors that come closest to the desired or perceived new possibilities. One thus finds out how to surpass the "border" of learning, or learning ability, as previously perceived. If there are any truly unalterable limits to human social learning (and I am not willing to admit that there are), then I would still contend that (1) they have not been identified, and to do so would be extremely difficult, and (2) they are of little significance to anyone. In this sense, the questions of *identifying* and *using* any such limits cannot be divorced from the question of their existence.

Just as biological scientists cannot ignore environmentally induced plasticity, social scientists are not justified in viewing any activities or attributes of humans as independent of this influence of the genetic materials. Such independence is a logical impossibility. Evidence from every quarter indicates that learning is not "writing-on-a-blank-slate," and if it were in some organisms at some times, it would only be appropriate to hypothesize that this too is either directly or indirectly a result of natural selection.

It follows that my use of the word biology in no way implies that moral systems have some kind of explicit genetic background, are genetically determined, or cannot be altered by adjusting the social environment. Nor am I about to espouse a Social Darwinist view of morality or claim that organic evolution offers a means of identifying proper modes of behavior. I mean simply to suggest that if we wish to understand those aspects of our behavior commonly regarded as
involving morality or ethics, it will help to reconsider our behavior as a product of evolution by natural selection. The principal reason for this suggestion is that natural selection operates according to general principles which make its effects highly predictive, even with respect to traits and circumstances that have not yet been analyzed, or perhaps even encountered by scientists.

In summary, the widespread hostility toward efforts of biologists to analyze human behavior appears related to the manner in which the adjective “biological” is used outside of biology. Because the problems of human behavior are of such immense proportions, and because I believe that biology has definite and unique contributions to make, I cannot dismiss this misuse as trivial (see also Alexander, 1985a, 1986a).

Moral Systems and Morality

By the phrase “moral systems” in my title, I mean to refer to what philosophers imply by this term: systems of ethics or normative conduct—the question of how agreements or contracts about right and wrong are generated and maintained within human societies, and why they differ. As the philosopher, Ralph B. Perry (1954) stated, “... a morality or moral value system is some kind of action guide, some kind of standard for conduct, character formation, and life . . . .”

If the concept of “moral systems” is an easy one, the same is not true of “morality.” On the meaning of this term even Perry (p. 86) is less confident: “... there is something . . . in the world to which it is appropriate to give the name 'morality'. Nothing is more familiar; nothing is more obscure in its meaning . . . .”

Aside from its reference to values, the concept of morality implies altruism or self-sacrifice. Not all moral acts call for self-sacrifice, however, and not all self-serving acts, by any means, would be termed immoral. On the other hand, I suspect most would agree that a moral life will inevitably call for some acts with net cost to the actor. Similarly, many acts with a net value to the actor would be judged immoral because alternative courses of action of value to others are available at the time but are not taken. Generally speaking, then, immoral is a label we apply to certain kinds of acts by which we help ourselves or hurt others, while acts that hurt ourselves or help others are more likely to be judged moral than immoral. As virtually endless arguments in the philosophical literature attest, it is not easy to be more precise in defining morality.

But this is our central problem: to find out what people mean when they speak of moral and immoral actions, how they make the distinc-
tion, and then to relate all of this to our history of evolution by natural selection. My approach is initially descriptive or analytical rather than normative. I am interested, first, not in determining what is moral and immoral, in the sense of what people ought to be doing, but in elucidating the natural history of ethics and morality—in discovering how and why humans initiated and developed the ideas we have about right and wrong. I am interested in unravelling and understanding the fabric of human sociality right down to the smallest threads of interaction. I trust that appropriateness in norms, however defined, will be enhanced as knowledge about moral issues becomes detailed and is widely dispensed. My reasons for this assumption are partly that I expect collective interests to be better served when decisions are made with more information and by a larger proportion of the people involved, and partly that I expect deception to be more difficult as knowledge about morality is enhanced. By this, of course, a normative view is suggested—namely, that we ought to study evolution and we ought to dispense as widely as possible whatever we learn about human actions as a result. This is a point to which I will later return.

PROXIMATE CAUSES AND THE REDUCTIONISM OF EVOLUTIONARY BIOLOGY

To social scientists, humanists, medical people, lawyers, and philosophers—all of the investigators most closely concerned with humans—biology inevitably implies reductionism of some kind. I will argue, however, that there is more than one form of biological “reduction” (or explanatory simplification), and the one employed here does not (extensively) involve the common meaning of reduction to proximate mechanisms (or proximate causes or physically identifiable components). Seeking proximate-mechanism reduction is what Mayr (1961) called answering the “How?” question. It is partly a concentration on this “How?” meaning of reduction that causes human-oriented scholars to contrast “biological” and “social.” As suggested above, the implication of “biological” in this case is that it refers to structural or physiological components or mechanisms—nerves, muscles, or hormones—or to variations in such attributes. The extreme version of this kind of reductionism asks: “Is that trait (variant) genetically determined?” At the very least students of human behavior who deal in this form of biological reductionism, which might be called the search for partial or proximate causes, must continually keep on their guard against unnecessary or unjustified assumptions of determinism or preprogramming.

The second kind of biological reductionism, which forms the theme of
this book, is not typically employed by human-oriented scholars in the form that biologists use it. It is most easily understood as the development of general evolutionary principles, and is usually referred to as the search for *ultimate causes.* Mayr termed it the "How come?" or "Why?" question (see Tinbergen, 1951; Daly and Wilson, 1983; Alcock, 1984; Wittenberger, 1981. Evidently Baker, 1938, originated the terms *proximate* and *ultimate* as I am using them—see Lack, 1954, and Hailman, 1982). Physicists tend to use the term "unification" for the process of principle generation, and biologists frequently use "synthesis." My use of reduction for this process may be novel, but I believe it is useful, for the reasons given below.

To establish principles is indeed reduction (or simplification), but not the kind of reduction that primarily seeks partial or proximate causes. Rather, the "Why?" approach seeks generalizations explaining phenomena that, in the absence of such generalizations, appear more complex as well as (sometimes) more mysterious. Rather than seeking to identify individual physiological, structural, or genetic contributions, each partly explaining some complex phenomenon, the "Why?" approach seeks broad generalizations about, for example, the goals of humans, or, in the most general sense, human motivations. These principles are necessarily sought in the evolutionary process that has given rise to all of our traits and tendencies, or at least to the potentials for them. One seeks general formulations that explain how natural selection has shaped, for example, sex ratios, senescence, differences between the sexes, parental behavior, or the length and nature of juvenile life. (Evolutionists tend to assume that there are multiple possible proximate routes by which similar evolutionary adaptations may occur. Because of this assumption they often postpone the study of physiological, ontogenetic, or other proximate mechanisms.) The perhaps unique applicability of this kind of reduction to living forms causes it appropriately to be termed *evolutionary reductionism.* The reason for this appropriateness is that formulating simplifying principles that apply to life is an effort to analyze the cumulative effects of the long-term operation of natural selection. This is done so as to predict or understand the effects in different environments of the collections of genetic materials now present in living things. The histories of nonliving phenomena are not as complex as those of living things, and the simplifying principles of physics and chemistry are as a result almost nonhistorical. In contrast, the principle of natural selection is dramatically simplifying primarily because of its relationship to the cumulative history of life. Because this aspect of reductionism in the evolutionary approach has not been generally recognized or accepted outside evolutionary biology, previous
discussions of proximate and ultimate mechanisms have not fully elucidated the reductionism of evolutionary biology. One consequence is that the kind of reduction practiced by evolutionary biologists is erroneously regarded as simply the invoking of genetic mechanisms as proximate causes. This is another way in which the approaches of biologists to human behavior are seriously misrepresented and underestimated.

Consider, as an example, a hungry human male. He has an immediate goal of eating. To achieve this goal he may leave an office and walk or drive his automobile some distance to his home, or to a favorite restaurant or a grocery store, and proceed appropriately. Or he may pick up his spear, say farewell to his family, and vanish into the bush. Carrying out either of these procedures involves an uncountable combination of contributing proximate causes or operations—the actions of nerves, muscles, hormones, sense organs, and thought processes. Each of these contributing proximate mechanisms may also function in many contexts other than hunger. Quite different sets of such proximate mechanisms may lead to what appears to be the same goal in different individuals, or to different goals in the same individual at different times and in different circumstances. With no understanding of the concept of hunger, and of the modes of its satisfaction, we might have great difficulty inducing the singularity of function (assuaging of hunger) from the multiple proximate parts or aspects of the activities relating to hunger.

Because confusion about the two kinds of reductionism lies at the heart of so many controversies about human behavior, the contrasts between them deserve further attention. The “How?” or partial causes approach is most likely to evoke criticism (1) because understanding is sometimes better achieved by dealing with the original whole (e.g., the effort to assuage hunger rather than the underlying morphological and physiological components of the effort), (2) because it is noticeable that similar ends may be achieved by many different kinds of subordinate or contributing mechanisms (causing the individual mechanisms to be less important), and (3) because of the likelihood that something important may be missing when reconstitution of the dissected phenomenon is attempted. All three realizations cause us to regard even essential contributing proximate phenomena as usually more trivial than the functional results of their collective and cooperative interactions.

In contrast, the “How come?” or ultimate cause approach seeks to simplify, explain, or “reduce” complex phenomena such as human activities by hypothesizing directly that they are parts of even grander sets or combinations of actions. Thus, merely to identify a complex set of activities by a hungry human as an effort to eat is a step in this kind
of reduction; another step is to see that effort as part of a lifelong effort to build (as a juvenile) and maintain (as an adult) a soma (phenotype, self) in the further interest of using it in the reproduction of one's genetic materials. This reduction by generalizing, because it seeks the adaptive significance of acts, also tends to identify the larger contexts within which specific acts or functions are carried out, and as a result identifies likelihoods of compromise or adjustment in the act that would not be obvious from any other approach. Without knowledge of food or ingestion, for example, we might be puzzled about failures to optimize other observed uses of lips and teeth like kissing, biting, or speaking. Similarly, without generalization from evolutionary reductions (principles), we could not easily predict that a hungry adult human might give all of its food to a mate or an offspring; nor could we develop a reasonable hypothesis about such behavior if we observed it. Discussions of proximate and ultimate mechanisms usually do not explain that reduction by generalization can profitably be carried much further. Thus, biologists proceed as if the lives of all organisms can be understood better by seeing them first as predictable patterns of somatic and reproductive effort (see pp. 40ff.). In the hierarchy of explanatory principles governing the traits of living organisms, evolutionary reductionism—the development of principles from the evolutionary process—tends to subsume all other kinds.

Proximate-cause reductionism (or reduction by dissection) sometimes advances our understanding of the whole phenomena. This happens when the mechanism discovered or elucidated is unique or new, has a special kind of practical application, or itself represents a simplification through generalization. Discovering that diseases are caused by microorganisms, that cancer results from mutated genes, or that the genetic materials of all life are likely to be deoxyribonucleic acid are obvious examples.

When evolutionary reduction becomes trivial in the study of life it is for a reason different from incompleteness; rather, it is because the breadth of the generalization distances it too significantly from a particular problem that may be at hand. For example, if a group of political scientists or physicists meeting to avert an imminent nuclear disaster were presented with a discussion of the general principles of conflict strategies and confrontations throughout the history of life (nonhuman as well as human), they might think that someone had changed the subject. Even if they realized that this was background material they should have had available to them to make the best decisions, there might be no time to review or absorb it. 

As a second contrast, reduction by dissection, or the seeking of partial
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causes or mechanisms, involves the discovery and examination of smaller and smaller units. In biology, this is the kind of reduction that leads to Nobel Prizes in physiology and medicine. It depends to some extent on new techniques and equipment, and does not frequently yield new information bearing directly on the analysis of complex human social behaviors (although when it does there is likely to be great excitement—as, for example, when someone discovers how to eliminate a problem that correlates with a specific genetic background, such as diabetes or Down’s syndrome).

Reduction by generalization, on the other hand, depends more upon new ideas, and quite commonly influences our interpretations and understanding of even the most complex human behavior. Indeed, as critics have frequently pointed out, the greatest weakness of reduction by generalization is not that it is likely to be trivial but that errors are probable through unjustified leaps from hypothesis to conclusion, by either those who generate hypotheses or those who hear about them.

Critics such as Gould and Lewontin (1979) and Lewontin et al. (1984) seem to condemn all evolutionary approaches to human behavior by arguing as though students of the evolutionary background of human behavior always talk in terms of unverified conclusions rather than going through the process of generating and testing hypotheses. These critics imply that evolutionists who write about human behavior are, like Kipling, constructing “just-so” stories. Either consciously or unconsciously they have tended to publicize the worst cases, almost invariably already criticized and dismissed within evolutionary biology. They ignore or condemn by implication those they cannot as easily criticize.

They also typically ignore the best work in the areas they are criticizing. For example, Levins and Lewontin (1985), in a long diatribe against the “adaptationist program,” direct their criticism at the notion of adaptation as perfection or optimization of traits, cite only two modern authors they say use this criterion, and fail to cite any modern evolutionist discussing or defending the concept of adaptation. Thus, they do not mention Williams (1966a), although his argument that adaptation means only better versus worse in the immediate situation is widely accepted, and Williams is almost certainly the most widely cited author on the concept. The omission may be considered all the more surprising because Lewontin (1966), in a review of Williams’ book on adaptation, wrote “… I believe that Williams’ book is excellent in its totality and that it is 95 percent correct. Most of the characteristics of organisms, including social behavior, must be the result of differential fitness at the level of individual genotypes.”

Critics such as Gould and Lewontin (1979) and Lewontin et al. (1984)
also do not acknowledge that the method of science—of progress in understanding in this as in other fields of endeavor in which knowledge is cumulative—is to identify the core of accuracy and correctness in the works of all writers in a field, excise the flawed portions, and then build from the best that is left. Rather, they give the impression that their mission is to locate and emphasize the weakest parts of the arguments of individuals they are criticizing, then use those weakest parts to declare that the entire enterprise with which those parts are connected must be discarded—i.e., that the weakest components in an intellectual edifice can be used to prove that there is no core of accuracy and correctness, no possibility of a cumulative growth of knowledge. This approach is reminiscent of the humanities, where rhetoric is the methodology (Raymond, 1982), there is no cumulative growth of knowledge only a cumulative change of attitude or sophistication in regard to meaning, and criticism is to a greater degree partitioned around the efforts (or “projects”) of individuals (Alexander, 1988). Sahlins (1976) and Kitcher (1985) argue similarly, but unlike Gould and Lewontin they do not have backgrounds that suggest to the reader that they are arguing in the manner of scientists.

Critics such as Gould and Lewontin also fail to acknowledge that they are capitalizing on difficulties in analyzing humans that are universal whatever the approach—namely, that we are analyzing ourselves and therefore must (1) use the attributes to be analyzed to do the analyzing, (2) avoid letting our own personal biases or interests influence the results, and (3) collect data from subjects whose best interests may be served by giving inaccurate or false information (and who, unlike most other organisms, are expert at deceiving other humans). They imply wrongly that all evolutionary biologists necessarily make the same mistakes. They do not discuss the facts that (a) all students of human behavior (not just those who take evolution into account) run the risk of leaping unwarrantedly from hypothesis to conclusion and (b) just-so stories were no less prevalent and hypothesis-testing no more prevalent in studies of human behavior before evolutionary biologists began to participate. Indeed, many of their examples predate the last two or three decades of modern evolutionary biology. It is one thing to criticize studies of human behavior because they do not meet current (or past) standards in the field, and quite another to reject them unless they meet some kind of Popperian ideal of procedure that has never previously been achieved. One wonders if such critics believe that merely to pursue knowledge about human evolution may yield undesirable directions of change in human society; I expect that this belief is held by many, including some whose views of “undesirable” would conflict dramati-

As a third contrast, investigations of proximate causes are typified by controlled laboratory experiments, and their practitioners are likely to criticize investigations of ultimate causes as being oversimplified, imprecise, or incomplete. Students of ultimate causes, on the other hand, are more likely to be theoretical and philosophical in their approach, and to use a broadly comparative method to secure answers. As already noted, they are also likely to see an identified proximate cause as one of several or many possible routes to realization of an ultimate function, therefore (in philosophical if not practical terms) as less vital as a first step to understanding.

Evolutionary reduction, when it is successful and accurate, tends to deepen our understanding of all of our immediate and primary behaviors, motivations, and emotions because their evolutionary significance and the involved compromises are almost never a part of our conscious knowledge before we pursue them deliberately. It changes our perceptions of nearly all that is dear to us. Unfortunately, it does not lead to dramatic “quick fixes” of serious human problems, although, and even more unfortunately, those who embrace it with inadequate understanding all too often act as though it does. The value of evolutionary generalization is difficult to grasp because it consists primarily in suggesting hypotheses. We forget that without considerable guidance in hypothesis construction our research efforts—indeed, our efforts at satisfactory day-to-day living—would nearly always be impotent.

Feinberg (1970, p. 5) followed a long line of philosophers in unknowingly connecting the general problems of moral philosophy directly to evolutionary reduction when he said that “... 'pleasure' and 'happiness' [are] the leading candidates, historically speaking, for the status of supreme goods or ultimate goals,” and (p. 7) “It is plain that finding one large genus for the analysis of all our enjoyment-idioms as they apply to the multifarious things we are said to enjoy will be no easy task.” Finding this “one large genus,” however—namely, discovering that our history of evolution by natural selection has been one of tuning “enjoyment idioms” (or proximate mechanisms) in the service of survival of our own genetic materials, via reproductive success in all its guises—is precisely what evolutionary reductionism has accomplished.

Humans are not accustomed to dealing with their own strategies of life as if they had been tuned by natural selection. As Maynard Smith
(1982) points out, one consequence is that game theory, designed for economics, has been applied with more difficulty to humans than to nonhuman organisms. But I do not share Maynard Smith's reluctance to accept that "financial rewards, the risks of death and the pleasures of a clear conscience" (the economists' "utility") can be turned into a supposition that humans too can be understood as products of the maximizing of "Darwinian fitness." Maynard Smith sees Darwinian fitness, as applied to nonhuman organisms, as providing "a natural and genuinely one-dimensional scale" for the employment of game theory, arguing (1974) that:

A major difficulty in applying game theory to human conflicts lies in the need to place a numerical value, or "utility," on the preferences the players place on the possible outcomes. How for example does one put the utilities of financial reward and of injury or death on the same numerical scale? This difficulty does not arise, at least in principle, in applying game theory to animal behaviour. In human conflicts, strategies are chosen by reason, to maximize the satisfaction of human desires—or at least it is in those terms that they are analyzed by game theorists. Strategies in animal contests are naturally selected to maximize the fitness of the contestants. Thus apparently incommensurable outcomes can be placed on a single scale of utility according to the contribution they make to reproductive success. This equivalence between utility and contribution to fitness is the main justification for applying game theory to animal contests. (p. 212)

It seems to me that Maynard Smith is not describing a special difficulty, in principle, of applying game theory to humans but simply an inadequacy so far of efforts to do so. To compare fitness, investigations of nonhuman strategies must also calculate the costs of deaths and risks and the value of resources gained or lost. The fact that such investigations ignore motivations or "desire" equivalents in nonhuman organisms does not mean that these do not exist but that they can (at least, for the moment) be safely ignored. Some might argue that they cannot be ignored in humans because we have introduced so much evolutionary novelty so swiftly into our environments. But novelty also exists in the environments of nonhumans. The difference is at least one of degree only, and to understand ourselves we simply have to deal with the problems of novelty anyway; even the particular nature of our responses to novelties is only likely to be understood as a result of evolutionary knowledge.

I believe that failure by biologists and others to distinguish proximate- or partial-cause and evolutionary- or ultimate-cause reductionism (and to use the latter) is in some part responsible for the current chasm between the social and the biological sciences and for the resistance to
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so-called biological approaches to understanding humans. Anyone who sees science as solely a matter of seeking partial causes by laboratory experimentation is very likely to regard the hypothesis-seeking and comparative and cross-cultural studies of evolutionary biologists as nonscientific, or even as useless speculation. If those with this bias were to have their way, however, a good deal of the direction would be eliminated from the investigation of both proximate and ultimate causes in biology. This direction is provided by the predictive value of principles derived from knowledge of the process of organic evolution, i.e., by evolutionary or ultimate-cause analysis, or reduction. Both approaches are essential to progress in biology and the social sciences, and it would be helpful if their relationship, and that of their respective practitioners, were not seen as adversarial.

THE PROBLEM OF CULTURE

Any claim that biology holds important keys to understanding ourselves will be viewed skeptically by those who believe that culture has somehow liberated us from our history of natural selection. Such skeptics would note that the human arms races and resource competition proceed through cultural and not genetic change, and therefore are, as I have indicated, merely parallels to changes that proceed as a result of natural selection (see Alexander, 1979a, p. 66 ff., for a fuller exposition of the views discussed here). But such skeptics often view the process of natural selection too narrowly. Natural selection has two effects (Flinn and Alexander, 1982). First, it sorts among existing genetic variations that produce different phenotypic effects or traits, saving some and eliminating others. Cultural change can occur without such genetic change, and may do so massively and for many generations. Cultural change, however, is never independent of the second effect of natural selection, which is to accumulate and maintain genetic units that in particular environments lead to particular effects (or traits or phenotypes), and in other environments lead to other such effects—in other words, to accumulate and maintain genetic units that yield functional plasticity. Every organism, including ourselves, is a bundle of effects from such accumulated and maintained genetic units having realized one or another potential in one or another environment, and in some sense no organism can be understood otherwise. The very concept of "phenotype" or "individual" connotes plasticity because the evolutionary raison d'etre of the phenotype is that it gives genes flexibility in dealing with the environment. As suggested earlier, variations in the phenotype that correlate (within species) only with genetic variations
require more special explanation than do those which vary according to environmental cues.

That plasticity of the phenotype is an inevitable consequence of the most basic facts about organic evolution is too often forgotten or ignored. To accept it is to realize that biologists are in no way restricted to studying species-wide traits, and that phenotypic variations need not be demonstrably correlated with genetic variations before traits can be assumed to be relatable to a history of natural selection. It is a main effect of natural selection to eliminate genetic variation associated with phenotypic variations that correlate with environmental variations. Stated differently, when trait differences correlate directly with genetic differences the reproductively inferior trait is maximally vulnerable to elimination by selection. Genetic backgrounds producing traits that can be varied to match the circumstances, on the other hand, are expected whenever circumstances vary unpredictably among predictable alternatives, as they do continually in the environments of living forms. It is not reasonable to use the demonstrated existence of a predicted effect of natural selection—plasticity associated with phenotypic variations in the absence of genetic variations—to deny the potency or relevance of natural selection. Some people, unfortunately, still try to do that.

There are some further points of great importance, I believe, in understanding the widespread failure of even educated and open-minded people to recognize the significance of an organic evolution guided principally by natural selection. First, an absence of heritable variations in phenotypic traits that track environmental changes virtually precludes identifying any part of the genetic underpinnings of the trait: genetic backgrounds of traits are identified only by studying heritable variations in the trait. So both strong directional selection (leading to homozygosity) and selection favoring plasticity (concealing heritable variations) lead to the impression of much phenotypic variation without any genetic correlates. At the same time, electrophoresis and other modern methods have revealed heretofore unsuspected amounts of genetic variation within populations. These genetic variations are uncovered by methods that do not relate them to particular traits. Moreover, genetic variations that persist are expected to relate either to persisting environmental variations (also not revealed by the methods used to locate the genetic variations) or to have neutral or relatively trivial effects on the phenotype. On the one hand, we are presented with great amounts of phenotypic variability that cannot be related to genetic variability, and indeed for which the genetic underpinnings are presently inscrutable. On the other hand, we observe large amounts of genetic variation that are not only unrelated to the observed phenotypic
variations but are believed to be trivial in their effects. The two seem unconnected. Anyone willing to give natural selection its due, however, must realize that all of these conditions would be predicted in complex, changing environments in which cues to the changes are potentially available to the evolving organisms. Because of the prevalence (or universality) of such environments, conditions they are expected to produce cannot be used to deny the significance of natural selection as the principal guiding force of evolution.

Even if culture changes massively and continually across multiple generations, even if our problems and promises arise out of the cultural process of change, even if there are no genetic variations among humans that significantly affect their behavior, it is always true that the cumulative history of natural selection continues to influence our actions by the set of genes it has provided humanity. Our learning biases and emotional responses, for example, are not random or manufactured from thin air; they are the products of the unbroken process of evolution by natural selection that extends across the whole of history, into our prehuman past, and millions of years before that. This is why even a seemingly "purely cultural" phenomenon, such as an arms race, may be most effectively dealt with from a perspective that includes a thorough understanding of our history of natural selection. This is true even in the case of rapid introduction of environmental novelties (such as excess amounts of sugar or drugs, birth control devices, and almost any other result of technology) because the particular nature of our response to the novelty, whether reproductively adaptive or maladaptive, will be most predictable to those with knowledge of our selective (adaptive) history. Moths fly to their deaths around electric lights; this maladaptive response to an environmental novelty is understandable, and likely would have been predictable, only by knowing the nocturnal behavior of moths prior to the introduction of electric lights. Given the seriousness of current world problems deriving from human social behavior, and the impasses in our confrontations that are paraded daily in the news media, are there really reasons for believing that we can understand ourselves well enough without finding out about novelties in our own environment and their significance; without examining our long-term as well as our short-term history; without analyzing our cumulative genetic history as a part of the reason for our cumulative cultural history?

People are sometimes comfortable with the notion that certain activities can be labeled appropriately as "purely cultural" because they also believe that there are behaviors that can be labeled "purely genetic." Neither is true: the environment contributes to the expression of all behaviors, and culture is best described as a part of the environ-
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ment. The often-used axis of genetic versus cultural, in respect to human behavior, is inappropriate because it omits all noncultural aspects of environment and suggests wrongly that there are behaviors at the two ends of the spectrum which lack, respectively, environmental and genetic input (Lumsden and Wilson, 1981; Flinn and Alexander, 1982).

Harris (1979) provides an excellent example of this confusion about culture, and about evolutionary analyses of human behavior, partly because he makes some assumptions that even many biologists make. He discusses Dickemann's (1979) evolutionary analysis of female infanticide as an example of "... the lack of parsimony and the redundancy involved in the behavior scaling version of sociobiological theory." Involved is female-biased infanticide among elite castes in stratified societies. Harris cites the evolutionary prediction (Alexander, 1974; Trivers and Willard, 1973) that female preferential infanticide is more likely among women married to high-ranking men and less likely among women married to low-ranking men, and notes that when male infants can be reared with confidence, their fitness (i.e., number of offspring) will tend to exceed that of females, since men in polygynous societies can have more "reproductive episodes" than women.

Hence in elite castes and classes, where males have an excellent chance of surviving because living conditions are good, the maximization of reproductive success of both male and female parents will be achieved by investing in sons rather than daughters. On the other hand, in the low-ranking castes and classes, where male survival is very risky, reproductive success will be maximized by investing in daughters, who are likely to have at least some reproductive episodes rather than none at all. To complete the model, elite men can be expected to marry beneath their station, while lowly women can be expected to marry up if their parents can provide them with a dowry to compensate the groom's family . . . .

Harris says that the "cultural materialist" explanation for this phenomenon does not require that the pattern has been selected for "genetically," or that it is part of a "genetic program" that is activated as a result of either poverty or wealth, respectively. He suggests that men are more valuable because they dominate the "political, military, commercial, and agricultural sources of wealth and power"; he argues that this domination is a result of cultural rather than genetic selection.

Sons have the opportunity to protect and enhance the elite family's patrimony and political-economic status. But daughters, who have access to significant sources of wealth and power only through men, are an absolute or relative liability. They can only be married off by paying dowry. Therefore, preferential female infanticide is practiced by the elite groups to avoid the expense of dowry and to consolidate the family's wealth and
power. Among the subordinate ranks, female infanticide is not practiced as frequently as among the elites because peasant and artisan girls can readily pay their own way by working in the fields or in cottage industry.

Harris argues that all of this has to do with efforts to maintain and enhance power and wealth, and not "the struggle to achieve reproductive success." He says the proof lies in the fact that high-status males marry beneath their station, such marriages taking the form of concubinage and not bestowing the right of inheritance upon the offspring. He says elites thus "systematically decrease their inclusive fitness by failing to provide for their own children." He thinks the whole system is a way of preventing elites from having too much reproductive success, so as to "maintain the privileged position of a small number of wealthy and powerful families at the top of the social pyramid."

Harris believes that the reason models based on reproductive success have "a degree of empirical validity" is that the factors which promote reproductive success

... do so through the intermediation of biopsychological benefits that enhance the economic, political, and sexual power and well-being of individuals and groups of individuals. The exploitation of lower-ranking women by higher-ranking men, for example, is the kind of stuff out of which theories of reproductive success can easily be spun. But exploitation confers much more immediate and tangible benefits than genetic immortality on those who can get away with it. Because of the bias toward reproductive success, the principle of behavior scaling [=evolved phenotypic plasticity] leads away from the most certain and powerful interests served by infrastructure toward the most remote and hypothetical interests served by having genetic survivors.

First, evolutionary models for female-based infanticide among elites do not call for the survival of males necessarily to be in doubt in lower class families (Alexander, 1974; Dickemann, 1979). Rather, because males in polygynous societies have more difficulty than do females in securing mates (and high-quality mates or multiple mates a fortiori) the question is the likelihood of one's son reproducing successfully or not rather than surviving or not. Because status correlates with desirability as a mate in stratified human societies, high-status males are more valuable reproductively if polygyny is permitted.

As Harris states, sons are also more valuable in protecting and enhancing the elite family's patrimony and political-economic status—in consolidating its wealth and power. On this point Harris, Dickemann, and the evolutionary biologists are, I think, in perfect agreement.

The second difficulty arises when Harris says that this means that "The genesis of the system lies in the struggle to maintain and enhance
differential politico-economic power and wealth, _not_ in the struggle to achieve reproductive success” (emphasis added). To clarify the difficulty let us suppose that someone argued that humans are interested in sex because of the pleasure associated with it and _not_ because of procreation. Sexual intercourse in humans may (unlike nearly all or all other organisms) have acquired significance beyond fertilization of eggs per se (e.g., in long-term pair bonding) but this cannot detract from the facts that (1) historically it has been the only way babies were created, (2) the creation of babies is the only reason for our continued existence, and (3) those of us alive today carry in preponderance the genes of those who produced and raised the most babies.

Happiness and its anticipation are thus proximate mechanisms that lead us to perform and repeat acts that in the environments of history, at least, would have led to greater reproductive success. This is a central hypothesis in evolutionary biology. Paralleling it in importance is the hypothesis that control of resources is the most appropriate route to reproductive success (the juvenile lives of all organisms represent a process of increasing control of resources up to the point—through growth and development—that reproduction becomes possible). Similarly, I presume that status is typically a vehicle toward resource control and an outcome of it. If these ideas are correct, then humans should always experience pleasure when they gain in status or increase their control of resources (unless they do so at large expense to close relatives or spouses), and they should experience some converse feeling when they lose status or resource control (except, sometimes, when they transfer it to relatives or spouses).

Harris’ analysis takes economic or “productive” ends as ultimate rather than as means to the end of reproductive success. Such analyses are like those which take pleasure and happiness as ultimate ends. They cannot explain why the proximate mechanisms of pleasure and happiness (Harris’ “bio-psychological benefits”) operate as they do, or even why they exist. Evolutionary theory from the science of biology does have the possibility of such explanations, whether or not in particular cases its individual practitioners err in their testing or interpretations, and whether or not contemporary humans actually use their striving for resource control to enhance their reproductive success (Vining, 1986, summarizes evidence that they often do not; but see Betzig, 1986, Hill, 1984, Alexander, 1988; reviews of Vining following his article). Harris implies that reproductive success, representing “remote and hypothetical interests,” is somehow an _alternative_ explanation to more proximate “bio-psychological benefits” as “the most certain and powerful interests served by infrastructure.” He sees the “struggle to maintain and
enhance differential politico-economic power and wealth" as opposed to "the struggle to achieve reproductive success." In the sense of comprehensive explanation, however, the relationship between such proximate and ultimate factors is not adversarial. Rather, neither can be explained without the other. The real problem that this aspect of Harris' discussion may be used to emphasize is that of determining the degree to which the exercise of proximate mechanisms may produce consequences different from those that led to their establishment and their present forms. Regardless of the answer to this question, I cannot imagine how cultural materialist explanations of human behavior and institutions can ever make real or complete sense except in light of a continuous history of natural selection of genetic alternatives.

Harris says that the proof of the accuracy of his opposing reproductive and economic success lies in the fact that elites "systematically decrease their inclusive fitness by failing to provide life-support systems for their own children." He is referring specifically to children of hypogynous marriages or via concubines. He ignores the essential certainty, however, that polygyny by elite males is a way of increasing inclusive fitness by adding children; that additional children, even poorly provided for, can be more reproductive than no additional children; and that it is more reproductive to concentrate parental investment on children of higher-ranking spouses because of their greater opportunities to join or remain in the elite than to distribute it evenly among offspring whose likelihoods of success vary greatly for reasons more or less beyond the elite polygynous father's control (Dickemann, 1979).

Even if males in elite castes and classes are sometimes more likely to survive, it is the rank they inherit socially that will make them likely to outcompete others in sexual and parental matters and thus likely to produce more offspring as well as to maintain and consolidate resources (Alexander, 1974; Betzig, 1986). This outcome explicitly requires the male dominance and polygynous tendencies that Harris implies associate only with a cultural materialist model. When Harris argues that male dominance is a matter of cultural rather than genetic selection we have to suppose that he means not only that males are not dominant over females because of male–female genetic differences but that, as well, variations among societies are not owing to genetic variations. (Males are not more politicoeconomically dominant in hierarchical polygynous societies because they are genetically different from the less dominant males of other societies.) No biologist I know would disagree with the second point; but probably none would say, either, that male–female genetic differences within societies are uninvolved in tendencies for
males to dominate females, or that "genetic selection" has had nothing to do with male–female power asymmetries or their variations. There is no reason to doubt that the genetic selection that led to the physical ability of males to dominate females, thus to the whole system under consideration here, had its genesis in differential reproductive success among males of differing strength, power, and status (Alexander et al., 1979). In no way am I implying that such ability justifies its use, any more than any unusually powerful individual necessarily has a "right" to use his strength to deny others access to resources.

Dowry is paid, at least partly, to secure a higher-ranking mate for one's daughter than would otherwise be the case, this, in turn, having probable beneficial effects on the status of the daughter's family (Dickemann, 1979). All of this is of questionable value for elites, who already have high status, so avoidance of dowry payment seems a doubtful reason for female infanticide by elites (who are also likely to be wealthy). Rather, females are not as valuable to elites, so investing in males what would have been invested in females is reproductively more profitable; there are other possible factors, such as that the necessity of marrying a daughter hypogamously may cause her to detract from the family's status sufficiently (when hypergamy cannot be accomplished because of the high rank of her family) to offset the value of her reproduction. In Harris' argument status would not be a commodity of great reproductive value; the argument from biology is clearly the reverse.

Harris thus (1) unduly restricts the nature of the hypotheses from the science of biology; (2) mixes biologists' hypotheses with his own, often confusingly; (3) asserts (but does not demonstrate) that efforts normally enhancing reproductive success are not involved in social stratification and hypergamy; and (4) treats proximate and ultimate factors as alternatives rather than as complementary and mutually dependent. Harris also states:

Sociobiologists propose that human beings are preprogrammed to switch from infanticide to mother love; from cannibalism to vegetarianism; from polyandry to polygyny; from matrilineality to patrilineality; and from war to peace whenever the appropriate environmental conditions are present. Cultural materialists also maintain that these changes take place whenever certain infrastructural conditions are present. Since both cultural materialists and sociobiologists take the position that the enormous diversity represented in the alleged genetic scaling of human responses is at least genetically possible—within the "envelope"—the need for the scaling concept itself seems gratuitous. The focus in both strategies has to be on the question of what kinds of environmental or infrastructural conditions are powerful enough to change human behavior from war to peace, polygyny
to polyandry, cannibalism to vegetarianism, and so forth. To the extent that sociobiologists sincerely pursue this issue, they will inevitably find themselves carrying out cost–benefit analyses that are subsumed by the infrastructural cost–benefit analyses of cultural materialism. (p. 139)

On the contrary, I would argue, the cost–benefit analyses of cultural materialism are necessarily subsumed under those which take into account the history of human strategies of reproductive success and analyze the effects of technological and other novelties in that light. The reason it is not gratuitous to consider the nature of phenotypic plasticity (or “behavior scaling”) very carefully is that the evidence is overwhelming that it is not random in its expressions. The only theory with a possibility of understanding why comes from biology. Harris’ analysis suggests that we will always end up doing those things that are beneficial to us, regardless of environmental change; evolutionary theory from biology does not, and it can be uncannily predictive about the kinds of errors we will make. It is a central problem in biology and the social sciences, and one of the most exciting prospects in these disciplines, to explore the question of the evolutionary-historical basis for the kinds of plasticity that are expressed in cost–benefit analyses such as those discussed above.

The argument is common that selection cannot be effective if the situation in which a particular trait is favored appears only infrequently, and this argument has been made to me with respect to female-biased infanticide in elites, menopause, and other human traits. Using menopause to illustrate, if, throughout most of history, women had on average died before the usual age of onset of menopause, then, the argument goes, menopause could not have been favored by selection. The first question that has to be asked is what proportion of reproduction is affected by the event in question? How much effect on reproductive success occurs after the event (in the case of menopause, how much is overall, long-term reproductive success affected by a postmenopausal woman turning all her attention to tending the offspring she has already produced, as opposed to starting additional offspring she has low probability of rearing)? Without this qualification we might be led to the conclusion that if, say, only one in a thousand individuals reached adulthood, selection on adults could not be effective. In the case of female-biased infanticide the question has been asked: How could such a tendency be favored if only a tiny fraction of individuals in a small proportion of the societies of the world ever become elites in a polygynous stratified society? The question implies that infanticidal elites are genetically different from noninfanticidal elites or nonelites and betrays precisely the simplistic view of the development of behavior
in the individual and the evolution of sociality in humans that I am trying to dispel. Thus, it is only necessary to hypothesize the obvious—that humans have evolved keen abilities to learn how to observe and mimic success in others and to avoid or "anti-imitate" failure (Flinn and Alexander, 1982).

Like Harris, Kitcher (1985) uses Dickemann's (1979) analysis of infanticide as a principal vehicle for criticizing evolutionary analyses of human behavior. Most of Kitcher's argument is virtually the same as that of Harris, although he does not cite Harris; the remainder does not oppose proximate and ultimate factors or culture and "biology," hence is not appropriate to the question discussed here (see Alexander, 1987).

THE PROBLEM OF RESISTANCE TO SELF-UNDERSTANDING

Consider the differences and similarities between two scientific searches. First, within the past decade theoretical physicists have begun to construct what they call the Grand Unifying Theory of the Universe (see Georgi, 1981; Ross, 1985). This activity entails the identification and characterization (sometimes in the reverse order) of ever more fundamental units in the physical structure of the universe, until those known and confidently predicted come to account for every event and effect relevant to the effort. This search is concerned almost entirely with items and events beyond our human senses, and even beyond the limits of the knowledge and imagination of most of us—a search conducted primarily by exotic and indirect means, guided by predictions sufficiently complex to allow complete characterization, in some cases, of phenomena still unencountered. It is a search necessarily involving language so arbitrary as to be whimsical: charmed quarks, colored gluons, etc. It is a search about which most of us can only marvel, without feeling competent to be skeptical, or even desiring to be skeptical, although the actual proof of its stepwise progress is essentially beyond our comprehension. It is also a search that has no significance for our social life proximate enough to generate interest in that context (even though it may affect one's religious views or self-understanding if these had previously called for particular conditions with respect to the physical universe and its origin). As a consequence the theoretical physicists are able to proceed in their awesome and all-encompassing task, involving the physical universe, without hostility or negative intervention from those who either fully or only partly understand.

Now contrast this search with that involving the sources and bases of human sociality—seemingly a simpler investigation, yet in some respects far more difficult. This search begins not with particles or forces
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beyond our senses but with the everyday and directly observable. More than that, it begins with phenomena that we are all expert in dealing with already, and about which we probably regard ourselves as more expert than we really are. The search proceeds from everyday phenomena, in not one direction but two; on the one hand, toward still unobservably small yet astonishingly intricate and somehow powerful genetic units, and the mysteries of their performance in different environments; and, on the other hand, toward the massively complex and in some sense also unobservable social phenomena that involve the combined minds, wills, and purposes of thousands, millions, and even hundreds of millions of human actors. This too is a search guided by predictions about the unknown, but one that simultaneously is seen as explaining the familiar; and one that, paradoxically, may provide directly and immediately the means for changing what it analyzes. Sometimes, even inadvertently, the search causes social alterations before the analysis is complete; and it is quite possible for erroneous hypotheses about human behavior, either seen as correct or desired to be so when they are not, to cause alterations in society that otherwise would not have occurred.

The search for the bases of human sociality, unlike those for the physical basis of the universe, affects nothing so much as it does our social lives and futures, individually and collectively. It is chapter one of the search for the foundations of ethics, the chapter missing, I believe, from the grand search as it has been conducted before this time in our history. It is a quest that, again unlike that of the theoretical physicists, leads not merely to skepticism but to hostility, fear, resistance, and even bitter and vituperative rejection. These emotions are aroused, I think, because the effort to understand the social universe involves ourselves, because it is seen as threatening to affect our everyday lives. Indeed, as I shall argue below, it threatens to affect our individual rights and opportunities to seek happiness and success in our own individual fashions. We do not hesitate to call the efforts of the physicists "science," but we are more apt to ridicule and dismiss the efforts of the behavioral scientists who study humans. In all the universe, the only topic we literally do not wish to be too well understood is human behavior (including, necessarily, our own) even, it would seem, if that kind of understanding represents the only clear way to diminish the threat of self-extinction. The reason for this resistance, and for the threat mentioned above, is that human behavior involves conflicts of interest. Anyone who understands some aspect of it very well will likely be able to use the knowledge to serve his own interests and thwart those of others. Social research, for example, does not flourish when its results
threaten the policies of the government that furnishes its financial support. Nor are those people viewed with favor who speak of seeking to understand human behavior so as to “manipulate” or “control” the actions of the populace in respect to as yet unspecified goals. By resistance to self-understanding, then, I mean not resistance to knowing about ourselves personally, or to understanding others (both of which we seem to approach with relish), but rather resistance to the concomitant condition of being understood by others.

Despite these negative aspects, I believe that to respond effectively to the crisis into which our world of dwindling resources, changing sociality, and devastating weaponry is moving requires the kind of self-analysis that must begin with deep biological understanding. Only then can the findings from the two “ultimate” kinds of searches—those of the theoretical physicists and the social behaviorists—be combined to enable us to improve the lot of humanity. Only then, perhaps, will we be likely to restrict technology largely or solely to developing widely or universally shared ways of enhancing human life, and to resist its use in developing more efficient ways of destroying human life.

Obviously I have been assuming all along that the reader agrees that there has been a process of organic evolution, guided principally by natural selection, and that this process stands alone as responsible, in some sense, for the traits and tendencies of all organisms, including the behavior of humans. In Darwinism and Human Affairs I argued at length why this assumption seems presently to be the only reasonable one and, I believe, showed that the myth of evolution as a nonfalsifiable proposition can be destroyed—even by referring back to Darwin alone. (Kitcher, 1985, criticizes my 1979 argument. He does so, however, by citing only a single falsifying procedure discussed by me, and by stopping his discussion short of my description of several reasons for the value of that one proposition. Anyone interested in my examples can locate nearly all of them under “Evolution, falsifying propositions” in the index of Darwinism and Human Affairs.) I caution again that I do not mean that any traits of any organisms are owing alone to the genes and gene combinations that natural selection has saved. I do mean that none of the traits of life can be produced without genes, as well as, of course, environments. Learning does not occur without genes, nor without environments. Intelligence does not occur without genes, nor without environments. Moral judgments cannot be made without genes, nor without environments.

The concept of hunger, used above to explain evolutionary reductionism, is obvious to us because it is a conscious part of our everyday lives. It is a major thesis of this book, however, that there are concepts
associated with morality that are neither obvious nor entirely conscious. To use such concepts to help understand and adjust our everyday behavior sometimes requires hard intellectual effort and is not always pleasant. But the consequence of ignorance about ourselves is no longer merely a vague uncertainty or uneasiness. I am by no means alone in believing that it is quite likely to lead us to self-extinction.

My concern in this first chapter has been to introduce the problems in understanding morality, and their importance, and to suggest the kind of approach I intend to take toward their solution. The next few chapters analyze in turn each of the items that I have indicated to be important, turning first to the crux of the matter, the nature of human interests and their conflicts.

Human Interests and Their Conflicts:
What Lifetimes Are About

Moral and ethical problems and questions exist solely because of conflicts of interest; moral systems exist because confluences of interest at lower levels of social organization are used to deal with conflicts of interest at higher levels.

To analyze conflicts and confluences of interest—therefore, morality and moral systems—a theory of interests is required.

A theory of interests is a theory of lifetimes—how they are patterned and what they are designed (by evolution) to accomplish.

What we are seeking to do and must do in a civilized society is to adjust relations and order conduct in a world in which the goods of existence, the scope for free activity, and the objects on which to exert free activity are limited, and the demands upon those goods and those objects are infinite. To order the activities of men in their endeavor to satisfy their demands so as to enable satisfaction of as much of the whole scheme of demands with the least friction and waste has not merely been what lawmakers and tribunals and jurists have been striving for, it has also been put . . . by philosophers as what we ought to be doing.

Today, in my judgment, the most important problem which confronts the jurist is the theory of interests. . . . I should define an interest . . . as a demand or desire which human beings either individually or in groups or in associations or in relations, seek to satisfy, of which, therefore, the ordering of human relations must take account. . . . It is not group demands or desires, but the strivings of men in (or perhaps one should say through) groups and associations and relations to satisfy certain demands or desires. . . . Conflicts or competition between interests arise because of the competition of individuals with each other, the competition of groups or societies of men with each other, and the competition of individuals with such groups or societies, in the endeavor to satisfy human wants.
... in determining scope and subject matter of the legal system we have to consider five things: (1) we must take an inventory of the interests which press for recognition and must generalize them and classify them; (2) we must select and determine the interests which the law should recognize and seek to secure; (3) we must fix the limits of securing the interest so selected ... (4) we must consider the means by which the law may secure interests when recognized and delimited, that is, we must take account of the limitations upon effective legal action which may preclude complete recognition or complete securing of interests which otherwise we seek to secure, as, for example, in the case of the rights of husband and wife to consortium as against each other; (5) in order to do these things we must work out principles of valuation or interests.

Roscoe Pound, 1941, pp. 251, 259, 261.

WHAT ARE HUMAN INTERESTS?

In some sense, conflicts and confluences of interests are the warp and woof of the fabric of society. Those who agree cooperate; those who disagree conflict or compete; and those who cooperate also use their enhanced abilities from cooperation to compete with those with whom they have conflicts of interest. Conflicts and confluences of interest are reflected at every level in society from the most closely related and intimately associated individuals to globally distant nations with populations of hundreds of millions.

What is implied is that the world is filled with people who are following their own interests. I suggest that this is true, and that they do it individually, and, when their interests overlap or coincide, they do it collectively in groups and coalitions of every imaginable size, shape, and description. They do it in families and clans and neighborhoods, and in unions, guilds, syndicates, cooperatives, corporations, tribes, municipalities, partnerships, nations, and even coalitions of nations. That people are in general following what they perceive to be their own interests is, I believe, the most general principle of human behavior. It is obviously not a new idea, but its current interpretations and consequences are different from those in previous developments of this idea, and not all of them are intuitively obvious.

Presumably, if all humans everywhere shared precisely the same interests there would be no ethical or moral problems. Our goals would all be the same, and our cooperation to achieve them would be complete. Society would be relatively simple in its structure, unless the complexity of its functioning as a unit were much greater than now is the case; and I believe that the human psyche, as well, would be a relatively simple phenomenon. Without conflicts of interest, it seems to me, the very concepts of ethical and unethical, moral and immoral, and
right and wrong would not exist. My reading of the literature in moral philosophy and the social sciences indicates that these assertions represent general agreement among those who have pondered the issues; I am aware of no contrary arguments, even though the conclusion of moral relativism that seems to follow is by no means universally accepted.

If ethical and moral problems arise out of conflicts of interests, then, to some extent, humans must be striving for the same things, and things which not everyone can possess, or possess equally, or to a degree that satisfies. To discover how to describe or model conflicts of interest in a quantitative fashion we must seek to understand the general nature of the goals of humans and the patterns of their striving. What do humans actually strive to achieve? What, after all, are their interests? How can they be classified and understood in everyday terms? Ultimately, how can we develop an appropriate set of subtheories from general evolutionary theory that will predict and account for variations in ethical and moral behavior?

By “conflict of interest” I do not refer to either (1) difficulties by individuals in making decisions—for example, because of inadequate information about costs and benefits of alternatives—or (2) the common situation that an individual cannot serve in a particular capacity because he has two sets of interests in relation to the two sets of interactants involved whose interests conflict. In the latter case we say that the individual involved—say, a judge or a mediator—has a “conflict of interest.” In fact there is no internal conflict within that individual. Rather, he has a potential conflict with one or both of the parties whose interests he is supposed to be serving, and one or both of them may legitimately fear that he will see his own interests as best served by settling the matter in favor of the other party.

If only the relatively mild point is acceptable that most of the time most people are doing things that could readily and justifiably be termed “pursuing their own interests,” then enormous significance is attached to the question of what people’s interests really are. To know this would be to know what is actually going on in the world. To the extent that, from generation to generation, people continue to pursue their own interests as individuals and groups, then those activities and their effects, taken collectively, must account for the institutions and concepts that we refer to as society, culture, laws, ethics, and morality, and for the changes in those institutions and concepts and their cumulative growth and development. As a result, we cannot even have a general behavioral theory until we have a reasonable answer to this question of what are people’s interests.
There are problems in seeking an answer. First, people often keep to themselves the nature of their own personal interests as they see them. They conceal their interests from others—at least they conceal some interests all of the time, and other interests part of the time. This fact is part of the evidence, I believe, that people do indeed follow their own interests and that the interests of different people conflict. There are many questions we do not wish to answer publicly or that we would regard as an invasion of our privacy. It is difficult to draw any conclusion other than that such concealment is part of following one's own interests when they conflict with those of others.

Second, there are reasons for believing that even though people are usually pursuing their interests, they do not themselves know precisely, in the general sense, what those interests are. By this I mean that such information is not a part of their conscious knowledge, and that if you asked people what they think their interests are they would usually give wrong answers, even though in many specific situations they would indeed know precisely which alternatives are in their own best interests. People are not generally aware of what their lifetimes have been evolved to accomplish, and, even if they are roughly aware of this, they do not easily accept that their everyday activities are in any sense means to that end.

All of this seems paradoxical. How can we possibly hope to examine conflicts and confluences of interest in the social interactions of people if those people do not themselves know what their interests are, and how can they be acting in their own interests if they do not know what their interests are? How can we tell what their interests are, moreover, if they are concealing them? And why should they accept the analyses of others if they did not wish anyone else to know about their interests in the first place? Is it really possible that people do not always know exactly what it is that they are keeping to themselves—concealing from others? Or even that they are concealing anything?

To think on these questions, consider nonhuman organisms for a moment. It is not so incongruous to imagine that they may be acting in their own interests without "knowing" it in the human sense of conscious understanding that can be communicated by language. The question, then, is whether or not we, as human observers, could find out what the interests of the individuals of other species are if we tried, and how we could do it. Of course that is precisely what the science of biology is all about: finding out about the interests of nonhuman organisms and their manners and extents of realization. Surely we can also secure at least partial answers to the question of what human
interests have evolved to be and the extents and manners of their realization.

**LIFE INTERESTS AS REPRODUCTIVE**

Lifetimes have evolved so as to promote survival of the individual's genetic materials, through individuals producing and aiding offspring and, in some species, aiding other descendants and some nondescendant relatives as well.

To regard a theory of interests as a theory of lifetimes is not necessarily a new idea, but it is firmly grounded in the new evolutionary theory. The idea was developed by a succession of authors, including Fisher [(1930) 1958] and Williams (1957–1966). For recent reviews see Stearns (1976, 1977).

It is part of the recent revolution in evolutionary theory that we know that natural selection is generally more powerful at lower levels in the hierarchy of organization of life, such as genes, chromosomes, and genomes (e.g., Fisher, 1958; Williams, 1966b; Lewontin, 1970; Dawkins, 1976, 1982; Alexander and Borgia, 1978; Alexander, 1979a; Leigh, 1977). We know this, first, because effectiveness of selection depends on the amount of difference between the involved entities, the heritability of differences, and generation time (Fisher, 1958; Lewontin, 1970). All of these features are more conducive to selection being potent at levels approaching the gene and less potent at group and population levels (Alexander, 1979a).

Second, the proponents of group (or population-level) selection (e.g., David Sloan Wilson, 1975, 1980; Michael Wade, 1976, 1978) have been forced to postulate populations with attributes much like those of individuals. They invoke groups that are founded by one or a few individuals (thus as near as possible to being single broods of offspring), and last about one generation (hence, have the same generation time as individuals). In the laboratory they create populations with minimal within-population genetic variance and maximal between-population genetic variance, and so forth.

Finally, many easily made observations on organisms indicate that selection is most effective below group levels. These include such things as evidence of conflicts among individuals within social groups, failure of semelparous organisms (one-time breeders) to forego reproduction when resources are scarce, and strong resistance to adopting nonrelatives by individuals evidently long evolved in social groups. None of
these observations is likely if the individual's interests are consistently the same as those of the group or if, to put it differently, allelic survival typically were most affected by selection at the group level (see also Alexander, 1979a).

If organisms are not evolved to use their lives explicitly to benefit their group as a whole, then what does all of their effort during life, their risk-taking, and their competing stand for? What is the evolutionary **raison d'être** of lifetimes and effort? In particular, why do individuals so often **seem** to be altruistic—to be striving to assist others?

One might at first assume that the goal of an organism's life is survival. Humans think and talk a great deal about survival, and obviously we all do things that increase our likelihood of survival. But we also do a very large number and variety of things that jeopardize survival. Most of this risk-taking has to do with status-seeking, resource control, and mate competition. If selection had always favored survival, risks should never be taken except in connection with acquiring basic resources, such as food, to enable continued survival.

Another powerful argument against survival as the function of lifetimes is that most lifetimes of organisms are extremely short; the vast majority are normally under one year. In a frequency distribution of the lifetimes of a wide variety of organisms (Figure 1.1), the skew is the opposite of what we should expect if natural selection had been maximizing the lengths of lifetimes. If natural selection had been maximizing life spans, we should all be more like bristlecone pines and redwoods, and there should be many species with life cycles longer than a few thousand years. After all, if natural selection can produce such wonderful things as giant squid, crickets, honey bees, naked mole rats, and people, it should have no trouble producing a few species with million-year life cycles.

The theory of lifetimes most widely accepted among biologists is that individuals have evolved to maximize the likelihood of survival of not themselves, but their genes, and that they do this by reproducing and tending in various ways offspring and other carriers of their own genes—descendant and nondescendant relatives. In this theory, survival of the individual—and its growth, development, and learning—are proximate mechanisms of reproductive success, which is a proximate mechanism of genic survival. Only the genes have evolved to survive. This theory is necessarily fairly new, since the gene concept is less than 100 years old. This means that if the theory is correct humans could not have **evolved** to know it, and to act directly and consciously in respect to it. We could have evolved to do a great many things that would make it **look** as though we know, and we might think that we know. But genes
remained outside of the range of our senses in all respects until the twentieth century—and they are still outside the knowledge of most people—so any effects of our conscious understanding of genes upon our conduct and our views of ourselves must be viewed as an evolutionary novelty.

Because of the novelty of knowledge of the genes, it is reasonable that individual humans might not be able to describe their life interests accurately in evolutionary terms. Nor is it surprising that it is difficult for us to accept that we could have evolved to enable the survival of our genes, and that our lifetimes may have been molded to serve that function, rather than what we might nowadays regard as our own, personal, selfish interests as individuals. Indeed, when we are told about genes, we tend to see them as alien manipulators, the very phenomena we are likely to be evolved to resist most intensively in our social behavior. It is perhaps understandable that we have a kind of xenophobia not only toward the genes, and ideas that such unchanging objects could somehow underlie our behavior, but also toward anyone who may argue that he has some special insight into our interests (implying, also, ability to manipulate or control them). There is also the possibility that pursuit of one’s own interests may be viewed so
negatively by others as to cause us to avoid any such suggestion and even to keep the possibility outside consciousness.

It will seem strange to many to use the term "interests" to refer to evolved tendencies whether or not these are conscious or deliberate. Nevertheless, there seems to be no reason (not even dictionary definitions of "interest") to demand that interests refer only to what people consciously believe are their interests or intentions. As I have already noted, biologists continually investigate the life interests of nonhuman organisms, while lacking knowledge on this point, and nonhuman organisms live out their lives serving their interests without knowing, in the human sense, what those interests are. Moreover, it is axiomatic that we are not consciously aware of all that motivates us, and that consciousness (including which parts of our knowledge and attitudes are conscious and which parts are not) could not have evolved if it did not serve reproductive interests.

To say that we are evolved to serve the interests of our genes in no way suggests that we are obliged to serve them. In today's novelty-filled environments, human activities may often be directed in ways that do not in fact lead to increased success in reproduction or the perpetuation of one's own genes. Moreover, people aware of their background in evolution may be able to use conscious reflection and deliberate decisions to live their lives contrary to, or irrespective of, whatever their evolutionary background has prepared them to do. Recognizing that interests are reproductive provides us with the means for understanding and quantifying their conflicts. This can only be true because of the particular manner in which we have evolved to acquire most of our knowledge (through learning, principally via social interactions or from others). Evolution is surely most deterministic for those still unaware of it. If this argument is correct, it may be the first to carry us from is to ought, i.e., if we desire to be the conscious masters of our own fates, and if conscious effort in that direction is the most likely vehicle of survival and happiness, then we ought to study evolution.

LIFETIMES AS EFFORT

Lifetimes can be regarded as composed of effort, and they can be divided into somatic and reproductive effort. Somatic effort increases residual reproductive value, reproductive effort reduces it.

A theory of interests is also a theory of effort (meaning expenditure of calories and taking of risks) in lifetimes. Organisms are commonly
FIGURE 1.2. A hypothetical human lifetime, showing a plausible distribution of different kinds of effort and changes in reproductive value. All early effort is somatic, which continues until death. Reproductive effort onsets before adulthood, here postulated in the form of extraparental nepotistic effort (e.g., help, or yielding of resources, to siblings). Senescence onsets shortly afterward, when the expense of reproductive effort becomes sufficient to reduce residual reproductive value. Mating and parental effort onset later, and each of the three forms of reproductive effort is postulated to maximize at a different time during adult life.

regarded by biologists as engaging in two general kinds of effort during their lifetimes; somatic and reproductive (Fig. 1.2). Somatic effort is, in general, that exerted in the prereproductive or juvenile stage and may be regarded as building the soma (phenotype, body, self) that will later be used in reproduction. It also maintains the soma of adults, when that soma still has some reproductive likelihood. In a sense somatic effort is personally or phenotypically selfish, while reproductive effort is self-sacrificing or phenotypically altruistic but genetically selfish. Somatic effort amasses resources, while reproductive effort redistributes them.
Somatic effort evolves to increase residual reproductive value by rendering subsequent reproductive effort more effective. Reproductive effort evolves to increase actual reproduction, thereby incidentally (via mortality and the fostering of the evolution of senescence—see below) reducing the residual reproductive value of the individual (Williams, 1966a; cf. Alexander and Borgia, 1978).

Perhaps the best examples to illustrate the existence of different kinds of effort across lifetimes are such extreme cases as certain butterflies. The juvenile is first a caterpillar, then a pupa. In most species the caterpillar does nothing but feed and protect itself from enemies. It is wholly involved with growth. It cannot produce offspring (although in some forms siblings move together in clusters and may show special forms of beneficence toward one another that would be regarded as reproductive effort). The pupa appears to be nothing more than a necessarily complex means of making the dramatic transformation from the caterpillar, highly specialized for somatic effort in one environment, into the remarkably different adult butterfly, just as highly specialized for the production of offspring in a different environment. The pupa, in other words, is wholly a developmental stage. Some adult butterflies are apparently wholly reproductive, not even giving much evidence that they protect themselves from predators. They do not feed at all, and have even lost their mouthparts and alimentary tracts; they do nothing but locate appropriate mates, copulate, and lay eggs in places where they are likely to hatch and grow up successfully. In most organisms somatic and reproductive effort are not so dramatically separated; but they exist, nevertheless, and together make up the raison d'être of the phenotype.

Reproduction and Senescence: Why Lifetimes Are Finite

Except when accidents intervene, senescence is the proximate reason for the finiteness of lifetimes, and for their general trajectories. Senescence evidently occurs throughout the entire adult human lifetime. Its effects are responsible for much of the trauma of human existence. In understanding lifetimes, therefore, senescence is a process and a concept just as important as those of somatic and reproductive effort, and ontogeny or development. It is curious that Williams' (1957) evolutionary theory of senescence, involving one of our most inexorable and disturbing characteristics, has not been adequately tested and has occupied very little research time and effort, despite its obvious explanatory potential and the expenditure of millions each year on gerontology.
Reproduction and Senescence

Rose and Charlesworth (1980, p. 141) define senescence as "the post-maturation decline in survivorship and fecundity that accompanies advancing age" (see also Charlesworth, 1980). In a sense this decline is more properly an effect of senescence. The changes that cause the decline are what actually represent senescence. Williams (1957, p. 402) hypothesizes that these changes result from "adaptively unfavorable morphogenetic changes that were brought in as side effects of otherwise favorable genes, and which have only been partly expurgated by further selection." One could also describe senescence as an increasing susceptibility to environmental insults, which seems to begin at about the usual age of first reproduction. It is a change that occurs across all of our adult lives. As the effect that ultimately causes lifetimes to be finite, it is a phenomenon that must be understood if we are to develop a general comprehension of human interests. Indeed, I believe that the existence and nature of senescence is the proof that the reproductive view of human interests is correct. One of the reasons I am going to treat senescence in detail is that my experience tells me that most people are still skeptical of this view of human interests.

Senescence is an odd concept, a bit intangible and difficult to grasp. This is partly because it is apparently not something that has evolved directly but rather something that natural selection has been unable to prevent; and, as William D. Hamilton has pointed out to me, partly because senescence evidently has not a single or a few causes, but a large number of contributing causes. The questions are: Why are we, and other organisms, mortal? Why do we and they deteriorate, become increasingly fragile, susceptible to disease, incapacitated, and eventually senile? Why, in the absence of accidents, do they and we fail to live forever? Why do life lengths of the individuals of different species vary from a few minutes, hours, or weeks to a few thousand years? Why are lifetimes in most species so brief compared to those in the longest-lived ones? Why has selection not favored the longest possible lifetimes? What general principles may be involved? These are the kinds of questions a theory of senescence—really, a theory of life lengths and life patterns—may be expected to resolve. The evolutionary theory of senescence discussed here seems to resolve such questions in such a way as to substantiate the view that lifetimes are vehicles of genic survival, and to justify utilizing this proposition to understand morality.

THE OLDER THEORIES OF SENESCENCE

Williams (1957), in what might be called the introduction to modern
evolutionary theories of senescence, reviewed earlier theories. Unfortunately, outside evolutionary biology, his careful discrediting of these early theories has had little effect; they persist and predominate in the medical and social literature, and in research on human senescence. I believe that, as with cancer research which largely ignores the evolutionary background of life, the short-sightedness of theoretically deficient senescence research imposes an unjustifiable burden upon taxpayers, and stirs unreasonable hopes in the minds of people. To illustrate the distance between the arguments presented here and those currently considered in gerontological research, one can read almost any semipopular treatment of senescence such as the article, "Are we programmed to die?" in the *Saturday Review* of 2 October 1976 (see also, Fries, 1980).

The outmoded arguments, largely based on a proximate causes approach without the guidance of evolutionary reductionism through generalization, are given below.

**Wearing-Out**

Machines wear out; so do some parts of organisms, such as teeth. Some people have supposed that living organisms also simply wear out. But machines are composed of static parts; organisms regenerate themselves continually. The wearing out of parts such as teeth, then, is not in itself senescence. What we are concerned with is loss of the ability to replace wornout teeth, loss of the ability to rebuild or regenerate the body's parts at least as rapidly as they deteriorate. As Williams (1957, p. 398) notes: "It is indeed remarkable that after a seemingly miraculous feat of morphogenesis [development from a single cell] a complex metazoan should be unable to perform the much simpler task of merely maintaining what is already formed." The wearing-out hypothesis thus explains nothing.

**Accumulation of Toxins**

Products of metabolism accumulate in some tissues, giving them the appearance of old or aging structures (Curtis, 1963). The theory that this explains senescence is also a proximate one: it gives us no explanation for the tendency of tissues to allow accumulations of deleterious products of metabolism, for differences between species, or for changes in such tendencies with age. Hence, it gives us no way to explain why senescence is generally restricted to individuals past the usual age of first
reproduction, regardless of the length of juvenile life, or (especially) why some organisms, such as fruit flies, mayflies, and annual plants, senesce rapidly while others, like turtles, elephants, parrots, and people, live thousands of times as long. Other theories of senescence share this shortcoming and are eliminated (as general theories or explanations) by the same reasoning; one such explanation is that somatic cells accumulate deleterious mutations (Curtis, 1963).

Death Mechanisms

Many theories of senescence implicitly or explicitly incorporate the idea of a death mechanism, supposing that organisms commonly senesce and die to make room for other younger ones. August Weismann (1891) included such a mechanism in his “wear-and-tear” theory, and Curtis (1963, p. 694) included one in his theory of accumulated mutations in the slowly dividing or nondividing somatic cells. “It is suggested that the mutation rates of somatic cells are very much higher than the rates for gametic cells, and that this circumstance insures the death of the individual and the survival of the species.”

The essential flaw in postulating general death mechanisms is that they call for a kind of altruism contrary to evolutionary principles except when relatives are assisted. No gene leading to death could spread on account of that effect unless other individuals carrying that gene were helped disproportionately as compared to individuals not carrying the gene. In a highly social organism, such as humans, tendencies to suicide in individuals who were causing an uncompensated drain upon the resources of their relatives could spread by natural (genic) selection (de Catanzaro, 1980, 1981; Chanley, ms.). But no general explanation of senescence appears derivable from this special case. For example, this theory has no way of explaining why rapid mortality occurs in semelparous organisms following reproduction, even when the eggs giving rise to the next generation will not hatch for weeks or months.

Selective Irrelevance

Comfort (1956) argued that senescence is not affected by selection because few wild organisms survive long enough to become senile. Thus, long life would be so infrequent that gene effects occurring late in life would always be trivial or irrelevant. But the processes leading eventually to senility begin early: mortality rates increase with advancing age, beginning remarkably early in the adult life of the organism.
This is what we are required to explain. Senescence and senility are not the same thing. Comfort's argument does not account for any relationship between mortality rates at different ages in the same species, and it does not explain the grossly different life patterns of different species, or of different forms within species, such as males and females or queens and workers in honeybees, ants, and termites (see pp. 60, 67). Moreover, the question of whether or not selection can be effective always involves not just how frequently it can act but how significant are its effects on reproduction when it does. If this were not true, for example, we might suppose that any genes acting only in adult codfish would be trivially significant because only one in a million or so codfish eggs survives to produce an adult.

WILLIAMS' PLEIOTROPIC THEORY OF SENESCENCE

As Williams (1957, p. 399) noted, "... other things being equal, a long-lived individual will leave more offspring than a short-lived one. If there is no specified death-mechanism, it is just as obvious that an individual that deteriorates slowly would be favored over one that deteriorates rapidly. Natural selection should ordinarily proceed toward lengthening life, not shortening it."

From this, Williams concluded that senescence is an unfavorable character, opposed by selection. To account for senescence, then, one is forced to postulate an opposing force of selection, with the existence and rate of senescence a compromise between the costs and benefits of the selective force incidentally resulting in senescence, and the costs and benefits of selection against senescence. This idea is immediately attractive, as it conforms to the general supposition that all attributes of all organisms represent compromises among opposing selective forces.

Williams' (1957) paper on senescence was the initial contribution to the refinements of evolutionary theory that created the current revolution in humanity's understanding of itself. It is therefore ironic that the principal criticism leveled at this revolution is that its practitioners are "adaptationists" in the sense that they insist on finding an adaptive function for every trait of every organism. Williams' argument, however, was that senescence is a maladaptive consequence of other adaptive traits. Moreover, he also argued, in his pivotal 1966 book, that adaptation is an onerous concept to be invoked only with great care and after considerable investigation. The primacy and prominence of these two arguments alone put the lie to the attack on evolutionary biologists as glib "adaptationists" who see evolved function in all effects of all traits. The only way this attack can be justified is by assuming that it is
reasonable to attack the worst arguments in a field as showing that everyone in the field is careless or misguided rather than to strip those worst arguments away from the good ones and use the latter to build a better argument. As I have suggested earlier, publicizing the worst arguments rather than building from the best does not seem to be the typical approach of scientists.

Williams (1957) noted that many previous workers had been aware of the decline in selective pressures with increasing age, and had suggested that senescence might result from processes or effects that were favorable early in life but deleterious later. Williams continued the development of this general proposition by noting that if genes have effects both early and late in life (multiple effects of genes, whether occurring at different times or not, are referred to as pleiotropy), those acting early are likely to be more important. This is so because genes acting earlier during the period of reproduction affect a greater proportion of the reproduction of their bearer (Figs. 1.3 and 1.4). Other things being equal, early-acting beneficial genes will thus spread more rapidly than late-acting beneficial genes (that is, early effects of genes will have greater consequence for the genes' spread and persistence than later
effects). Moreover, if early and late effects of genes should happen to be opposed, deleterious late effects will accumulate, because alleles will be saved as a result of their early effects and in spite of their later ones. This will lead to deteriorative effects that can be identified as the process of senescence.

Williams' pleiotropic theory (i.e., his theory of multiple effects of individual genes, here early beneficial ones and later deleterious ones), whether correct or not, unlike all others so far discussed, is an appropriate kind of biological theory. Medawar (1955, 1957) came closest to developing the same theory, but he did not take the step of distinguishing between linkage and pleiotropy to explain perpetuation of both beneficial and deleterious effects. In developing the theory, Williams pointed out that linkages can be broken, while pleiotropy would require substitution of alternative alleles. Simultaneously, Williams' theory provides a possible "ultimate" explanation, and a focus for identifying or analyzing genetic, physiological, or other proximate mechanisms. Williams' theory is a genetic theory in the sense that it
argues that organisms are programmed to senesce in particular fashions in the successions of environments in which they have evolved. It is a useful theory because it is both testable and provides a focus for all investigators of senescence, whatever the approaches, goals, or organisms. Until demonstrated to be erroneous, or replaced by a more convincing theory of similarly broad applicability and usefulness, it will be ignored by investigators only at the peril of having their results declared trivial and their efforts wasteful.

Now let us analyze the bases and the consequences of the theory and evaluate its apparent validity 30 years after its formulation.

THE NATURE AND EXTENT OF PLEIOTROPY

Heredity is particulate, but development is unitary. Everything in the organism is the result of the interactions of all genes, subject to the environment to which they are exposed.

Dobzhansky, 1961, p. 111

The above quote clearly implies that all genes are simultaneously pleiotropic (have multiple effects) and epistatic (affect one another’s effects). The more one reflects on this suggestion the more significant and the more convincing it seems. We usually think of individual genes in terms of obvious or dramatic single effects; but, as Dobzhansky points out, the unity of development makes multiple effects essentially certain. Different effects are also highly likely to be manifested at different times in the life of the organism.

It does not follow that such differently timed effects are likely to be known. Typically, biologists have examined gene effects individually without either the means or the curiosity to determine all of the effects of single allelic substitutions. As Williams remarked (1957, p. 400) “...we seldom know the total survival value of a gene in a wild population, let alone its values in different parts of the life cycle.” This is almost certainly the reason that the weakest part of the pleiotropic theory of senescence is the paucity of examples of appropriately acting genes.

Williams regarded it as being relatively unimportant to document the existence of appropriately pleiotropic genes, and one can scarcely disagree. To discredit the existence of the kind of selection relevant to his theory one would have to suppose (1) that most genes have single effects or (2) that the different effects of pleiotropic genes either (a) usually occur at the same time in the life cycle or (b) are equally
beneficial or harmful. I suspect that geneticists would be in general agreement that the evidence indicates that none of these things is true.

Different effects of the same gene, such as at different times of life, would be owing to differences in the soma, not in the gene itself. The soma may be viewed as an ever-changing environment of the genes. Different effects of single genes could occur at different places in the soma, at different times, or both. The greater the complexity of the life cycle or the greater the changes in the organism’s makeup, activities, or circumstances during its lifetime the greater the likelihood that there will be changes with time in a gene’s effects on the organism. Different effects of a single gene may have obvious connections to one another or be seemingly autonomous, although it is difficult to see how they could be completely independent. The same effect of a gene can be beneficial in one circumstance, or in one stage of life, and deleterious in another.

Hamilton (1966, p. 35) argued that “Williams may have been unnecessarily restricting the scope of his theory by making it depend upon genes which are pleiotropic in the ordinary sense of the word.” He pointed out that in a sense all age-specific genes are pleiotropic, simply because they yield effects at some ages and none at others; such genes are abundant (e.g., see Schneider, 1978, Charlesworth, 1980, and any of the journals of genetics). He explained this by describing the events resulting from appearance of age-specific genes with net positive or beneficial effects:

the mutant will spread, the spread will be accompanied by a rise in population, and this rise will in time be checked by density-dependent adverse factors of the environment which bear on the life schedules, raising mortalities or reducing fertilities in a pattern that has nothing to do with the particular pattern of the positive effect which initiated the sequence. When population has been made stationary again, the overall result will tend to be that fertility has been down-graded and mortality up-graded all along their length, so that the beneficial effect is itself slightly down-graded and all the null effects [absence of effects at other times in life] now appear as slight disadvantages. (pp. 35-36)

I believe that the idea, expressed earlier, that even the same effect of a gene is unlikely to be equally beneficial throughout a lifetime—especially a long-lived organism with its life patterned around complex sociality—represents a third reason (in addition to pleiotropy, *sensu strictu*, and age specificity) why Williams’ theory is reasonable.

Hamilton then developed a “picture of the evolution of the curve of force of mortality.” He saw it as

continually being “nibbled” from above, the nibbles representing the spreading of more or less age-specific advantageous mutations through the
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.......

population. They may be closely age specific or they may involve a lowering of the curve along a strip of considerable length. Following each nibble the whole curve, after more or less delay, makes a small ascent. The delay corresponds to the period of increasing population; the ascent to the coming into operation of the Malthusian [density-dependent] checks to increase. The nibbling takes place fastest at the left-hand end of the curve and towards the right-hand finally with infinite slowness at the age where reproduction ends. The greater the speed with which nibbles occur [with which mutations with advantageous effects spread] the sooner they can be succeeded by others. Thus the irregular downward movement is occurring fastest at the left-hand end, and the compensatory general upward movement results in a kind of dynamic equilibrium in which the curve trails upward indefinitely at the right. In the absence of complications due to parental care or other altruistic contributions due to post-reproductives, the curve should be roughly asymptotic to the age of the ending of reproduction. (p. 36)

Elsewhere in his paper, to test the probability of failure to senesce, Hamilton (1966) developed a model of a volvox-like organism with its cells undergoing synchronous division, every two divisions producing an independent daughter cell from each tetrad of cells. Even if (1) there is no mortality, (2) population expansion continues indefinitely, and (3) each individual expands its fecundity exponentially, he still found that "any mutation causing an improvement in early fecundity at the expense of an equal detriment later will . . . gradually come to numerical preponderance in the population; and if we allow any incipient incidence of mortality we likewise see that selection will favour resistance to it at early ages to a certain extent at the expense of greater vulnerability at later ages." (p. 25)

Hamilton then conceded that despite his argument that Williams had unnecessarily weakened his theory by restricting it to genes with beneficial early effects and detrimental late ones, his effort to model failure to senesce makes it "evident that Williams' [kind of] pleiotropic effects certainly do exist. . . ." Hamilton's findings with his immortal volvox-like model contradict Williams' arguments that asexual clones and protozoans should not show senescence (pp. 403-404) and, together with the above argument about pleiotropy, eliminate one of the four assumptions Williams regarded as essential to his theory (p. 400) and alter a second. The three remaining necessary assumptions are, then: (1) a soma essential to reproductive success but not passed on during reproduction, (2) natural selection of alternative alleles in a population, and (3) genes which either have opposite effects on fitness at different ages or are at least age-restricted in regard to beneficial effects. As Hamilton (1966, p. 26) concluded: "... for organisms that reproduce repeatedly, senescence is to be expected as an inevitable consequence of
the working of natural selection." Thus, either a gene with early beneficial effects and late deleterious effects, or one with beneficial effects early in life and none at any other time, would lead to senescence unless it could be replaced by an allele with equally beneficial effects at all times in life—which is highly unlikely because selection is not equally effective, and does not always operate similarly, across the whole life span.

THE GENERAL SHAPES OF MORTALITY CURVES

Figures 1.5 and 1.6 depict rates of mortality throughout the lifetimes of people in modern America (Alexander, 1979a) and Taiwanese in the late 19th century (Hamilton, 1966). The curves are similar (as are those from widely different societies all over the world; cf. Alexander, 1979a) raising interesting questions about the effects of technological and other environmental changes. One difference is noticeable: in 19th century Taiwan, juvenile females had a higher mortality rate than juvenile males, while in modern America, juvenile males, as with males at all ages, die more frequently than juvenile females. We can only speculate about this difference. It could represent a change in the activities of juvenile females, or it could reflect the fact that in some Asian societies male offspring tended to receive more parental attention, including better nutrition, causing female
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offspring to succumb to disease more frequently, especially during famines and epidemics. It is unlikely to reflect infanticide except at around the time of birth.

THE EFFECT OF MORTALITY RATES ON SENESCENCE

Williams (1957, p. 402) noted that:

Any previously established genes that cause senescence will increase the rate of decline in $p$ [reproductive probability] and make it easier for other such genes to become established. In this way senescence becomes a self-aggravating process. (p. 402)

He then added that senescence is nevertheless unfavorable and that:

The direct action of selection will always be opposed to it. The establishment of an important "senescence gene" in a population would cause the favorable selection of other genes that would reduce or delay the unfavorable effects. . . . As the suppression approached completion, however, the selection pressure for further suppression would diminish. Complete suppression would probably never be realized. Senescence might be regarded as a group of adaptively unfavorable morphogenetic changes that were brought in as side effects of otherwise favorable genes, and which have only been partly expurgated by further selection. There are, therefore, two opposing selective forces with respect to the evolution of senescence. One is an indirect selective force that acts to increase the rate of senescence by favoring vigor in youth at the price of vigor later on. The other is the
direct selection that acts to reduce or postpone the “price” and thereby
decrease the rate of senescence. The rate of senescence shown by any
species would depend on the balance between these opposing forces.
(p. 402)

Similarly, accelerated rates of mortality from high reproductive effort
increase the relative value of early reproductive effort. Although re­
tarded by direct selection, high mortality late in reproductive life will
evidently also produce a “self-aggravating” effect. On the other hand,
as Hirshfield and Tinkle (1975, pp. 2228–2229) pointed out, it does not
necessarily follow, as Williams argued (1957, p. 404), that “Low adult
death rates should be associated with low rates of senescence. . . .”
Regardless of adult death rates “Selection in (unchanging) environ­
ments could favor alleles that lead to high reproductive effort at the
earliest possible age because shortening the generation time would
increase the rate at which such alleles are incorporated into the gene
pool” (Hirshfield and Tinkle, 1975). This exact point was made by
Hamilton (1966) with his volvox-like model.

MALE AND FEMALE MORTALITY

Why is male mortality generally higher than female mortality at all
ages? For various reasons the net benefits of additional matings are
usually greater for males than for females (see Trivers, 1972; Williams,
1966b, 1975; Alexander, 1979a). When this is true males tend to invest
more in mating effort (partly because sex ratio selection is not altered by
differences in intensity of sexual selection, owing to the sex ratio, if
sexual selection occurs after termination of parental care; Fisher, 1958),
and only in species with such males should male mortality exceed
female mortality.

Not only do direct contests for mates involve high risks of injury that
may lead to death, but the phenotypic attributes that evolve in males as
a result of sexual selection often reduce viability even though increasing
mating success. As Williams (1975, pp. 138–139) stated:

In many species a typical adult female will enjoy something like the mean
reproductive success. A male, especially in polygynous species, may not
reproduce at all. Perhaps only the fittest 25% of the males will reproduce,
and the top 1% may enjoy many times the mean reproductive success. At
every moment in its game of life the masculine sex is playing for higher
stakes. Its possible winnings, either in immediate reproduction or in an
ultimate empire of wives and kin, are greater. So are its possibilities for
immediate bankruptcy (death) or permanent insolvency from involuntary
but unavoidable celibacy.

Greater variance in male fitness not only affects optimization of repro-
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Reproductive behavior, but all tributary aspects of adaptive organization. A male's developmental program must gamble against odds in an effort to attain the upper tail of the fitness distribution. A female's need merely canitalize against malfunctions. Female mortality will be found to exceed male, not in species with female heterogamety, but those with female masculinity.

In other words, because males typically gain more by increasing numbers of offspring via multiple matings, while females typically gain more by giving more parental care to fewer offspring, even the human male competes sexually a little more intensively. On average, he takes more risks than the female, and is more likely either to fail completely in reproduction or to outreproduce the average female. As a result, he has a higher rate of mortality and, correspondingly, has evolved to senesce sooner, a fact reflected in the relatively large number of widows around the world. The difference in senescence rate is not likely to be erased by an evolutionarily novel shift in women's activities, such as an increase in women taking over what have traditionally been men's jobs, or an increase in women's smoking, drinking, or assuming other risky activities formerly restricted to men. Equally risky activities by the two sexes may be expected to bring the mortality curves closer together, but they will only make the two curves coincident if there is no evolved difference between the sexes in senescence patterns. It is difficult to believe that there is not such an evolved male–female difference.

We can add that a female's reproductive success, especially in species with extended parental care, depends upon her ability to tend the offspring she has produced. A male's success, in species in which males invest more of their reproductive effort in mating, depends more upon activities that in many cases can be completed in a short period. A male highly successful during his first breeding season may lose little if he dies immediately afterward; a female in a parental species who dies shortly after mating may lose everything. Likewise, an old male may produce offspring that will be successful because of parental care from the mother; but an old female's youngest offspring may be unlikely to survive. One is tempted to speculate that this accounts for the evolution of menopause in human females and for sperm production and sexual potency in males that are much older than menopausing females (Williams, 1957; Alexander, 1974, 1979a; Dawkins, 1976).

Not all changes with age need be regarded as senescence. As an example, suppose that females sometimes favor older males largely because their greater age indicates a phenotypic success which may reflect a genotype superior in coping with the fluctuations in the species' environment (e.g., in maintaining resistance to rapidly evolving para-
sites and diseases). In the case of older males which are also obviously successful breeders, the relevant environment includes competing conspecific males. In such cases, attributes in males suggesting greater than actual age may be favored because they imply either resource control or power (as through ability to marshal assistance or assemble coalitions). Also, perhaps for all these reasons, they may enhance a male's attractiveness to females, as attributes in females suggesting youthfulness (hence, ability to bear and tend offspring well) may enhance their attractiveness to males. It would be inaccurate to regard such male attributes as simply evidence of maladaptive senescence, even if they started out as such. We may wonder, until someone figures out a way to test these ideas, if some tendencies toward gray hair or balding patterns in human males, or the "silver backs" of adult gorillas, might not represent effects of such selection.

Whenever different "morphs" within species maximize reproduction according to different routes, such as (1) male and female, (2) different kinds of males (e.g., large, flashy aggressive morphs versus small, drab, sometimes female-mimicking morphs in some birds, fish, beetles, and others), or (3) reproductives, workers, and soldiers (social insects), they may prove useful in analyzing the significance of different mortality schedules in relation to life functions and the history of selection upon factors leading to senescence. Unfortunately, not much advantage has yet been taken of the opportunity to compare such similar forms in these regards (although it is well known that queens in eusocial insects, living in the safe parts of nests and undertaking only relatively safe tasks, outlive by many times workers and soldiers who take on the riskiest tasks; for additional comparisons, see below, and Alexander and Noonan, in prep.).

SEMELPARITY, ITEROPARITY, AND SENESCENCE

Semelparous organisms, such as salmon and soybeans, reproduce but once in their lifetimes; iteroparous organisms, such as trees, fruit flies, humans, and most others, reproduce repeatedly. Semelparous organisms differ from iteroparous organisms in regard to effects of selection on senescence in at least two important ways:

1. Selection on the iteroparous organism will tend to result in a gradual senescence, beginning in each individual after it has achieved the usual reproductive age, whether or not actual reproduction is occurring (i.e., once the sum effect of its life activities is to reduce rather than increase the probability of future reproduction); contrarily, that of
the semelparous organism will tend to a greater degree to maintain its vigor, or prevent any senescence, until reproduction actually occurs. This is so because the iteroparous organism undergoes a gradual reduction in the proportion of its reproduction that still remains (residual reproductive value—Williams, 1966a), while the semelparous organism tends to retain more nearly its full reproductive probability (leaving aside the inevitable probability of mortality) until the act of reproduction, except when there is a history of gradual deterioration in the environment, and this deterioration sometimes begins before the organism is able to reproduce. In effect, if timing of its single act of reproduction is essential to the semelparous organism, the period before reproduction actually occurs, during which timing is possible, is more a part of juvenile life than is the case with an iteroparous organism; by timing its one act of reproduction carefully through delaying it, the semelparous organism is to a greater extent still increasing its reproductive probability. This argument predicts the common observation that both iteroparous and semelparous organisms prevented from reproduction will tend to live longer; but it also predicts that the effect will be less dramatic in iteroparous organisms, in which senescence is likely to be more significant after the usual age of onset of reproduction.

2. The last act of reproduction may be indefinite in the iteroparous organism, but will always be definite in the semelparous organism because it is also the first. Hence, iteroparous organisms will tend to deteriorate suddenly only in response to environmental insults that in the past have consistently terminated all further reproduction (such as, for insects, freezing temperatures in autumn).

On the other hand, the act of reproduction itself may in the semelparous organism lead to fatal chemical or other events which cannot be selected against. Unlike genes in the iteroparous organism, any one or all of the thousands of genes that may participate in the success of a semelparous organism’s reproduction may, without prejudice to the survival of its copies, incidentally produce effects leading to instant death, just after reproduction.

One therefore does not have to regard the semelparous organism as literally depleting all its phenotype in reproduction and dying afterward for that reason. Instead it can be thought of as converting all of the phenotype it can into offspring without prejudicing the phenotype’s ability to complete the act of producing the offspring and putting them into optimal circumstances and physical condition. The quick postreproductive death of the semelparous organism, then, is a consequence of the failure of selection after the point at which the act of
reproduction is completed. In a relevant experiment, Sokal (1970) found that when adult *Tribolium castaneum* (flour beetles) were killed just after first reproduction for 40 generations, they evolved a significantly shorter adult life; unfortunately, he did not verify if there had also been an increase in early fecundity. Rose and Charlesworth (1980), in a breeding experiment with *Drosophila*, claimed results that "provide evidence for (Williams') pleiotropy theory. . . ." They are correct, but their support of Williams' theory is weak because they did not perform the most useful test. Rather than breeding *Drosophila* for an early high rate of reproduction, and testing to see if senescence appeared early and more intensely as an incidental side effect, they bred for later high rates of reproduction and found that senescence was delayed. Several authors have recently obtained the same result but also failed to produce early rapid senescence (Rose, 1984; Luckinbill et al., 1984; Clare and Luckinbill, 1985; Luckinbill and Clare, 1985). It is strange that in the 30 years following its publication no one has been able to perform the most appropriate test of Williams' theory (see Bell, 1984, for an additional effort in this direction, comparing organisms that reproduce by budding with those that produce young via gametes). Possibly, it has proved difficult to select for early high reproductive effort in laboratory animals because they have already been selected in this direction for long periods. It is also possible that most species with rapid generation times (such as *Drosophila*) will have been similarly selected, so that to test the theory adequately will require results from species with long generation times, such as some domesticated mammals. If so, the time required for experimentation will be prohibitive, and the most convincing data may ultimately come from comparative study of unplanned long-term changes in directions of selection (e.g., in Holstein-Friesian dairy cattle, Alexander, ms.).

The remarkable difference between the patterns of senescence in semelparous (one-time breeding) and iteroparous (repeat-breeding) organisms is probably one of the best simple demonstrations of the central significance of reproduction in the individual's lifetime. How, otherwise, could we explain the fact that those who reproduce but once, like salmon and soybeans, tend to die suddenly right afterward, while those like ourselves who have residual reproductive possibilities after the initial reproductive act decline or senesce gradually? Both kinds of organisms, in other words, continue somatic effort until their possibilities of further reproduction have disappeared, even though they accomplish this in strikingly different fashions. Stated another way, once an organism has completed all possibilities of reproducing (through both offspring production and assistance, and helping other
relatives), then selection can no longer affect its survival: any physiological or other breakdown that destroys it may persist and even spread if it is genetically linked to a trait that is expressed earlier and is reproducively beneficial.

It is conceivable that within the same species one sex may be iteroparous, while the other is semelparous and their senescence patterns differ accordingly. For example, this may be the case in octopuses in which females lay only one clutch of eggs and tend it until the young more or less abruptly disperse, while males of the same species presumably mate with one female, and then seek others. We expect the females to die suddenly, normally at the time when their young disperse, and the males to senesce gradually (speaking comparatively). Wodinsky's (1977) results with females, and his mention of failure to obtain the same results with males, imply that this is the case, although further testing is obviously required.

PARENTAL CARE AND OFFSPRING REPLACEMENT

To demonstrate the changing effects of selection on alternative genetic units across a human lifetime, Hamilton (1966) compared four hypothetical genes (we can regard them as alternatives, thus competing alleles), each of which gives complete immunity against a lethal disease for 1 year of life in human females. The affected years are the 1st, 15th, 30th, and 45th. He assumed no parental care, and menopause before the 45th year (and, obviously, no ability afterward to help relatives), and then considered the relative selective advantages of the genes. The gene acting in the 45th year thus gives no advantage, and that acting in the 30th year gives less than the two acting earlier because women at 30 years have completed some reproductive years. It is less obvious that if reproduction never occurs by the 15th year, the genes acting at ages 1 and 15 will have equal likelihood of spreading. The reason is that, although the earlier-acting gene affects more individuals, the reproductive probabilities of those individuals are lower than those of individuals affected at age 15, and the amount by which their value is lower necessarily varies with the mortality rate between 1 and 15 precisely as to compensate the raised value of 15 year olds. Unless the immunity given by the gene is different at different ages or the disease affects different proportions of individuals at different ages, then, age-specific effects before the onset of reproduction are not more valuable if they occur earlier. This is the reason for Williams' statement that the usual time of reproductive maturation should mark the onset of senescence. Once the age of reproduction is achieved, the inevitable lowering of
residual reproductive value from that time on precludes compensatory increases in the value of individuals saved at later ages and causes earlier effects of genes to be more valuable.

One complication in applying this argument involves reproduction by juveniles via nepotism to nondescendant relatives. Diversion of calories or the taking of risks in such activities should cause senescence to begin during juvenile life, and consistent, large, successful expenditures of reproductive effort before adulthood may have caused a ballooning of such effects in special cases, like the termites, until individuals were eventually produced (termite workers) which have (by investigators unaware of this theory) been termed "permanent juveniles." These individuals live out their lives without producing offspring, without becoming sexually mature, and continuing to resemble juveniles rather than adults (see p. 67).

Trivers (1974) argued that juveniles evolve to take from their parents, as individuals, more than it is advantageous for the parent to give, but not enough to reduce the juvenile's inclusive fitness because of the consequent deprivation of its siblings. If this view of parent–offspring conflict is reasonably accurate—that is, if offspring really do refrain from taking resources from siblings—then senescence must begin as soon as the juvenile typically engages in such behavior to an extent that its likelihood of future reproduction is reduced. It would be interesting to look for evidence of senescence among juveniles in all of those species in which nepotistic acts occur regularly before adulthood. It is not idle to ask whether or not child labor—especially explicitly nepotistic forms like care of younger siblings—has occurred sufficiently long and intensively in any human societies to induce an earlier onset of senescence and a measurable modification of the life pattern. As suggested later, however (p. 82), it will be necessary to distinguish nepotism (as reproductive effort) from indirect somatic effort as social investment in reciprocity to determine this effect.

Hamilton’s (1966) description of the mortality curve has it reduced most powerfully early in life. Nevertheless, most organisms probably suffer greatest mortality early in life, whether or not there is parental care, because they are intrinsically more vulnerable. Parental care evolves because it is more valuable reproductively to reduce early mortality than to produce a larger number of offspring, each with less parental investment and, accordingly, a higher probability of mortality. Parental care is probably the most important “nibbler” at the left side of the mortality curve. High juvenile mortality relative to that later on does not mean that lowered early mortality is not valuable but that juvenile mortality is more difficult to reduce.
Extensive parental care may not merely lower the mortality of juveniles but may also change the shape of the juvenile mortality curve in iteroparous species because of the possibility of offspring replacement. Thus, if inferior offspring, or offspring produced during times when they cannot be satisfactorily reared, are terminated early, the parent will benefit from having invested less. This effect should lead to a steepening of the early part of the curve of juvenile mortality in relation to the later parts, even if parental care is simultaneously lowering juvenile mortality at all points.

Abandonment or cannibalism of offspring, infanticide, abortion, and miscarriage may all be mechanisms in some mammals by which offspring replacement or "culling" is effected at minimal expense. The evidence for widespread superovulation in mammals (ovulation of more eggs than can survive) appears also to be evidence of offspring replacement, although if selection of superior offspring is involved it is not clear whether in many cases the selection is occurring before or after fertilization.

Humans are unique in that parental care may sometimes continue until offspring have themselves terminated their reproductive lives, at least in terms of actual production of offspring. Nevertheless, more or less dramatic alteration of the kinds and amounts of parental care often occur at about the time of reproductive maturity. This effect is especially evident in societies in which female offspring are sold or preferentially passed to men of other groups—or other village or clans. If such females are passed to a group containing none of their relatives they may be relatively vulnerable until they have produced dependent offspring by a man with power or prestige.

At about the same age young men may frequently suffer high mortality, not only because of high-risk activities obviously associated with within-group sexual competition and the establishment of a suitable resource base for their reproductive lives, but also from activities less obviously significant in these contexts, especially participation in organized aggression such as wars.

**THE WONDERFUL ONE-HOSS SHAY EFFECT**

Finally, Williams pointed out that selection continually works against senescence, but is just never able to defeat it entirely. Perhaps the most important practical consequence of Williams' theory is that senescence leads to a generalized deterioration rather than one owing to a single effect or a few effects (Williams, 1957, pp. 406-407). In the course of working against senescence, selection will tend to remove, one by one,
the most frequent sources of mortality as a result of senescence. Whenever a single cause of mortality, such as a particular malfunction of any vital organ, becomes the predominant cause of mortality, then selection will more effectively reduce the significance of that particular defect (meaning those who lack it will outreproduce) until some other achieves greater relative significance. As soon as a source of mortality has been rendered barely second in importance, selection will be more effective in counteracting the new most important source of mortality. The new defect will also be selected toward insignificance, and the result will be that all organs and systems will tend to deteriorate together. Fries (1980), evidently unaware of evolutionary theories of senescence, presents data supporting the notion that when “acute” and accidental sources of human death are removed the consequence is a sharp compression of senescence without any great increase in maximum life lengths.

The point is that as we age, and as senescence proceeds, large numbers of potential sources of mortality tend to lurk ever more malevolently just “below the surface,” so that, unfortunately, the odds are very high against any dramatic lengthening of the maximum human lifetime through technology. This prediction is consistent with the finding of Fries (1980) that maximum life spans in the United States have increased little or none since 1900. This kind of selection also accounts for the fact that mortality curves for human populations in different times and places, and in different kinds of societies or cultures, are remarkably alike (compare Figs. 1.5 and 1.6 with Fig. 2, Alexander, 1979a). Similarly, the male and female curves tend to hold their relationships to one another cross-culturally.

Although this argument renders impractical research designed to locate the causes of senescence and thereby dramatically prolong human life, medical technology and bionics will undoubtedly continue to be directed at correcting deteriorations before they cause death (what Fries, 1980, called “progress in the elimination of premature death”). In consequence, small advances in average life length will continue to be achieved, and the significance of particular sources of mortality will be reduced. Others, in turn, will achieve new significance, and new crusades will be mounted against them. It is entirely possible, though, that gerontological research would lose a great deal of its support if it became quite apparent that no magic formula for dramatically lengthening life is likely to be discovered.

Supreme Court Justice Oliver Wendell Holmes may have presaged this part of Williams’ argument over 100 years ago. In the nineteenth century, when transportation was principally via horse-drawn vehicles (wagons,
buggies, shays), he wrote about the maddening tendency of all such vehicles to have one or another weak or short-lived component. According to his verse, "The Deacon's Masterpiece," one buggy was constructed so as to have no parts any weaker than all the others, with the consequence that it ran a hundred years then fell to pieces all at once.

**SUMMARY**

The reason, then, that natural selection has not been able to prevent senescence is that natural selection maximizes the likelihood of genetic survival, which is incompatible with eliminating senescence. The reason for this, in turn, is that genetic survival occurs through success in reproduction (presumably because throughout the history of life environments have been sufficiently unpredictable as to preclude indefinite avoidance of mortality), and such success is always relative. Senescence, and the finiteness of lifetimes, have evolved as incidental effects of the evolution of lifetimes as efforts to maximize success in genetic reproduction. Organisms compete for genetic survival and the winners (in evolutionary terms) are those who sacrifice their phenotypes (selves) earlier when this results in greater reproduction. The proximate vehicles of senescence are evidently multiple or pleiotropic effects of genes, with the different effects occurring at different times of life. Early effects are reproductively more important than later ones, with the evolutionary consequences that early beneficial effects will be saved even if they are absent later in life or actually replaced by deleterious effects of the same genes.

Senescence theory, together with sexual selection and parental investment theory, therefore predicts (or explains) a large number of differences between human males and females, including their relative body sizes, mortality and senescence rates, relative frequencies in the population (i.e., sex ratios), relative amounts of parental care, relative times to maturity, relative rates of lawbreaking, etc. (Trivers, 1972; Alexander *et al.*, 1979; Alexander, 1978, 1979a). Understanding these phenomena is a necessary part of understanding the nature of human lifetimes and which, in turn, is central to understanding conflicts of interest and thus the nature and roles of morality and ethics.

**Reproduction and Cooperation: Special Cases**

Interests of different organisms tend to coincide in three major kinds of circumstances:

1. When relatedness in genes identical by immediate descent is high.
2. When two or more unrelated individuals reproduce via the same third parties (e.g., in lifetime monogamy or eusocial insects that live in huge nuclear families).

3. When external threats can only (or best) be dissipated by cooperation.

GENETIC INDIVIDUALITY AND INDIVIDUALITY OF INTERESTS

If the life interests of organisms are in maximizing genetic reproduction (that is, if organisms have evolved by the repeated preservation of those genetic alternatives leading the individual to develop so as most effectively to promote the survival by reproduction of all its genetic materials), then it is out of this fact that a general theory about conflicts of interest must arise, namely: sexual reproduction causes individuals to be genetically unique. It creates genetic individuality because it consists primarily of random recombination in each generation of very large numbers of independently assorting genetic units (Williams, 1975; Maynard Smith, 1978; Parker, Baker, and Smith, 1972). A long history of genetic individuality means that individuals will evolve to behave as though their life interests are individually unique. Moreover, social organisms should be expected to be adept at judging partial overlaps of interest with other individuals through (1) proximate mechanisms that correlate with numbers and kinds of genealogical links and (2) opportunities to achieve goals or deflect threats by cooperative efforts with others. The longer the usual lives of individuals, and the longer individuals continue to interact significantly and repeatedly with one another, the greater will be their adeptness at assessing and acting appropriately with respect to partial confluences of interest, as well as conflicts of interest, and the more complex will be society. This, then, is the basic biological theory of conflicts of interest and therefore of moral systems. To understand our social and moral systems we have to unravel their fabric until we begin to see precisely how it has been created from the interlacing of the threads of individual reproductive striving.

Several facts support the hypothesis that conflicts of interests arise out of a history of genetic individuality. First there are evidently no reports of conflict among genetically identical individuals within clones among species that have for a long time reproduced asexually; and evidence of extraordinary cooperativeness in such cases abounds (cf. E. O. Wilson, 1975; Aoki et al., 1981; Alexander and Noonan, in prep.). Second, altruism appears generally to diminish with decreasing degrees of relatedness in sexual species whenever it is studied—in humans as well as nonhuman species (for reviews, see Sherman and Holmes, 1985;
Holmes and Sherman, 1983). Third, in cases in which identity or near-identity of genetic interests is achieved in sexual species (without genetic identity per se), cooperation is also dramatic. Examples are the two partners in lifetime monogamy and the members of the large social insect colonies that are actually nuclear families of enormous size (e.g., honeybees, ants, termites). In each case the cooperating parties (spouses; workers and queens) reproduce via the same third parties (offspring; siblings and offspring), to which they are more or less equally related genetically, and which are usually the closest (needy) relatives available to each of them (Hamilton, 1964; West Eberhard, 1975; Wilson, 1971; Noonan, 1981; J. E. Strassmann, 1981; Alexander and Noonan, in prep.). These various cases represent tests of the idea that lifetimes have evolved to maximize the likelihood of genic survival through reproduction.

This idea is likely to represent the greatest difficulty in acquiring support for the biological theory of morality developed in the following pages. Therefore it is important to review briefly some of these special cases.

THE PINNACLES OF ULTRASOCIALITY: HOW THEY EVOLVED

One kind of evidence that genetic reproduction is the raison d'être for the individual is the manner in which what E. O. Wilson (1971) calls the four "pinnacles" of complex sociality or "ultrasociality" (Campbell, 1975) have been achieved in clones, eusocial insects, nonhuman mammals, and humans. Here I will concentrate on the first two and the last—for nonhuman mammals, see Jarvis (1981) and Jarvis, Sherman, and Alexander (in prep.).

Complex sociality should be expected to arise only when confluences of interest produce benefits that override the costs of conflicting interests (see also Alexander, 1974, 1979a; Alexander and Noonan, in prep.), leading first to cooperative group living and later to complex sociality. It seems to me that there is one basic functional substrate for trends toward cooperative group living and that is active and cooperative defense against some common extrinsic threat or uncertainty (e.g., a predator or a powerful or elusive prey or food item). Three conditions promote cooperation as a means of overcoming such threats or hostile forces: (1) genetic similarity or identity (as in clones, e.g., of aphids; Aoki et al., 1981), (2) tendencies for close relatives to remain in close proximity (Hamilton's 1964 "population viscosity"), and (3) reproduction via the same third party (as with unrelated parents cooperating to produce and protect mutual offspring to which they are equally related).

One indicator of the degree to which conflicts of interests among social individuals have been minimized is the size of the group: only when
conflicts are minimal should very large group sizes be reached. The reason is that there are automatic costs to group living, mainly involving access to resources (Alexander, 1974, 1978; Hoogland and Sherman, 1976). These costs tend to increase as group sizes increase, so that net benefits tend to disappear above certain sizes (Alexander, 1979a).

Another indicator of minimal conflict is the level of cooperativeness, measurable partly by the complexity of tasks performed by individuals, especially considering groups like modern nations of hundreds of millions or even more than a billion (in China). Such human groups are necessarily highly cooperative, and this is especially true in wartime or when they are threatened externally. The tasks they have been able to accomplish by cooperative division of labor are without parallel among other sexually reproducing organisms.

Clones

Conflicts of interest are not expected when all group members are genetically identical. This is the case in clones of aphids, rotifers, or any other organisms in which reproduction occurs through parthenogenesis or fission without sexual recombination of the genetic materials—and has so occurred for a very long time. To my knowledge, no one has ever reported evidence of conflict or competition between individuals in such groups under natural or normal conditions, and I believe that any such reports would require careful scrutiny for the possibility of alternative explanations; mistakes would be easy when observers are accustomed to studying nonclonal forms. Parthenogenetic organisms, such as aphids, often remain together in clones of enormous size, and in some cases (Aoki et al., 1981) some individuals sacrifice their lives for the others, and are morphologically and physiologically specialized to do so. Of course, the cells of the bodies of metazoans such as ourselves are also clones of genetically identical units, and not only do they reach enormous numbers, but their cooperation is so complete that the result is unitary: a human being composed of hundred of millions of cells can think about a single goal and direct all of its attention to its realization. This astounding feat is so commonplace that we scarcely think about it.

In addition to the above examples, which are consistent with expectations from evolutionary theory, there are some unusual cases in which little is yet known of the interaction of the individuals involved but complete cooperation can be predicted. Thus, littermates of the North American nine-banded armadillo are monozygotic—products of a single egg and thus genetically identical. This has apparently been the case for thousands (perhaps millions) of generations. One predicts that if the argument being advanced here is correct, armadillo littermates should
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show signs of competitiveness or conflict only in circumstances when confusion with interlopers from other litters is likely (Alexander, 1974). So far no one has learned enough about armadillo social behavior to test this rather startling hypothesis. (Dawkins, 1982, seems to reject this line of reasoning because in parthenogenetic forms genotypes are “frozen”; but this only means that, depending on mutations for novelty, they would evolve more slowly.)

Eusocial Insects

Aside from clones and humans, the largest cooperative groups are those of certain social insects, reaching colony sizes of thousands and millions, the largest (certain ants and termites) estimated at more than 20 million individuals (Wilson, 1971). These colonies also accomplish astonishing feats, as a great deal of literature, scientific and popular, attests. Humans and social insects, unlike clones, are composed of genetically different individuals: their cooperativeness does not arise out of genetic identity. They have reduced their competitiveness within colonies or groups, moreover, in two entirely different fashions. The term “eusocial,” applied to ants, termites, and some wasps and bees by Wilson (1971), refers to forms in which the tendency has been to evolve colonies in which one or a few individuals produce all of the offspring, while the rest serve as helpers (workers, soldiers) in rearing them. In eusocial insects the reproductive individuals have become highly specialized during evolution to produce enormous numbers of eggs (e.g., one every few seconds for years, or possibly decades, in termites), and have sometimes become essentially helpless otherwise, being fed and cared for by their offspring. The millions of individuals in the largest social insect colonies are commonly the members of a single nuclear family comprising mother (and, in termites, father as well) and offspring. One interesting consequence of this arrangement is that the workers in a colony of modern eusocial insects, such as honeybees, have very little to disagree about, even though they are not genetically identical (Hamilton, 1964). The reason is that they all reproduce through the same individuals: those siblings, produced by their mother, who are destined to be males and queens in the next generation. This means, for example, that one should not expect to find conflicts or deception in the signals transmitted from worker to worker among social insects with respect to food, danger to the hive, or many other aspects of everyday life. This expectation, surprisingly, is unlike that for the vast majority of animal signals (Otte, 1974; Lloyd, 1977; Dawkins and Krebs, 1978; Dawkins, 1982; see also pp. 73 ff.). Further, when the members of a colony consistently have complex events about which they may profit from communicating, we should expect that their communication would
become extraordinarily effective. Of course this is precisely the case. Biological and social scientists have long marveled at the incredible communicative abilities of honeybees, with respect to rich food sites that may be distant from the hive in different directions and temporally restricted in their availability: they are able to tell one another the directions, distances, and nature of pollen or nectar sources miles away from the hive (von Frisch, 1954; Lindauer, 1961; Gould, Henerey, and MacLeod, 1970; Gould, 1976). I suggest that the two basic reasons for honeybees having evolved such potency in their communication are (1) they have something complicated and important to communicate about and (2) conflicts of interest have been dropped to near zero among workers. The objects of communication for honeybees are bonanza food sources—nectar and pollen—that last long enough, and are sufficiently difficult to locate, to make it pay for individuals in a sedentary or nesting species to be able to tell their nestmates how and when to exploit such bonanzas. Probably later in evolution, honeybees began to use the same signals to guide emigrant swarms to high-quality nest sites (Lindauer, 1961).

The reduction of conflicts in eusocial insect colonies is accomplished, then, not just by a high degree of relatedness (Hamilton, 1964), but by the workers in modern forms depending for their genetic success on exactly the same third parties—siblings produced by their mother. This fact, of course, does not tell us why the ancestors of modern eusocial insects initially were more successful in groups than alone (Hamilton, 1964; Wilson, 1971; Alexander, 1974; Charnov, 1978); because their social life originated millions of years ago this specific question may never be answered. Whenever stay-at-home helpers (helpers at the nest) produced more copies of their own genes by assisting with the rearing of siblings (or other relatives) rather than by having their own offspring (either at home or elsewhere), the route toward eusociality was begun. Close relatedness and some kind of group effect (predator defense, better provisioning of food, etc.) would both have been involved (this topic is discussed further by Alexander and Noonan, in prep.).

Humans: Ultrasociality Based on Reciprocity

Humans have taken a route to ultrasociality entirely different from that of the social insects. In the largest and evidently most unified or stable human groups (i.e., large, long-lasting nations) partial (rather than complete) restrictions on reproduction have the effect of leveling or equalizing opportunities to reproduce. Socially imposed monogamy and
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graduated-income taxes are examples of such reproductive opportunity leveling. The tendency in the development of the largest human groups, although not always consistent, seems to be toward equality of opportunity for every individual to reproduce via its own offspring, rather than toward specializing baby production in one or a few individuals and baby care in the others. However humans specialize and divide labor, they nearly always insist individually on the right to carry out all of the reproductive activities themselves. One consequence is that the human individual has evolved to be extraordinarily complex (and evidently to revere individuality), and another is that the complexity and variety of social interactions among human individuals is without parallel. Because human social groups are not enormous nuclear families, like social insect colonies, a third consequence is that competition and conflicts of interest are also diverse and complex to an unparalleled degree. Hence, I believe, derives our topic of moral systems. We can ask legitimately whether or not the trend toward greater leveling of reproductive opportunities in the largest, most stable human groups indicates that such groups (nations) are the most difficult to hold together without the promise or reality of equality of opportunity (see also Alexander, 1974, 1979a; Alexander and Noonan, 1979; Strate, 1982; Betzig, 1986).

OTHER SPECIAL CASES OF COOPERATION

Genes in Genomes

A corollary to reproductive opportunity leveling in humans may occur through mitosis and meiosis in sexual organisms. It has generally been overlooked that these very widely studied processes are so designed as usually to give each gene or other genetic subunit of the genome (= the genotype or set of genetic materials of the individual) the same opportunity as any other of appearing in the daughter cells. Alexander and Borgia (1978) and Williams (1979) have speculated that this equality of opportunity came about because only alleles with equal (or better) likelihoods of being present in daughter cells have survived; possibly, more generalized mechanisms have come to be involved in modern forms. It is not inappropriate to speculate that the leveling of reproductive opportunity for intragenomic components—regardless of its mechanism—is a prerequisite for the remarkable unity of genomes, some of them comprised of thousands or hundreds of thousands of recombining, potentially independent genes and other subunits (Leigh, 1983; Alexander and Borgia, 1978).
Monogamous Pairs

To the extent that males and females (of any species) commit themselves to lifetime monogamy, the interests of two individuals in a pair approach being identical. This point is often confused by biologists and social scientists alike (e.g., Dawkins, 1976, and Sahlins, 1976, both thought that unrelated spouses necessarily disagree more than relatives). The reason is the same as that causing identity of interests in the different individual workers in a eusocial insect colony: the two different individuals realize their reproduction through identical third parties which each of them gain by helping a great deal. In the case of worker insects the third parties are the reproductive brothers and sisters produced by the queen, their mother. If the queen dies and is replaced by one of the workers’ siblings, the situation may not be altered even though the workers are less closely related to a sister’s offspring than to their sisters, and less closely related to a sister’s offspring than is the sister herself. When a queen changeover occurs, unless workers retain some ability and likelihood of themselves becoming the queen (and in many modern species they have lost this ability), they can do no better than by cooperating fully with one another to produce reproductive nieces and nephews.

Given that the members of monogamous pairs are evolved to invest parentally, then, to the extent that (1) philandering is unlikely or too expensive to be profitable, and (2) the relatives of one or the other are not significantly more available for nepotistic diversions of resources, each member of the pair will profit from complete cooperation with the other to produce and rear their joint offspring. In humans this condition is most likely in (1) societies in which (a) families live and work separately and (b) husband and wife are in fairly close contact most of the time and (2) societies in which married couples are “neolocal,” living in some new location apart from both sets of relatives but close enough to be affected by the interests of their kin networks in sustaining the marriage. In such societies (which historically have probably been most often agricultural), I predict that the devotion of husband and wife will be measurably most complete.

Aside from clones, social insects and humans have developed the largest known societies, measured by numbers of complexly interacting individuals. They are also the most complexly communicating organisms. They have both accomplished this by expanding confluences of interest and reducing conflicts of interests, and it is at least possible that monogamy was involved in both cases, early in the evolution of social insects and late in the evolution of the largest human societies. What we
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have to understand, for both social insects and humans, is how the situations develop in which workership and monogamy, respectively, come to be the rule or norm. I believe I am correct in saying that in neither case are the answers yet available.

**MONOGAMY AND REPRODUCTIVE OPPORTUNITY LEVELING**

Our understanding of the manner in which monogamous pairs come to cooperate is not much better than our understanding of why social insect colonies sometimes become huge and sometimes do not. Because monogamy in large technological nations is imposed socially (meaning that the costs of its alternatives are imposed by the rest—or some part—of society), understanding its background becomes a part of the effort to understand moral systems. Alexander *et al.* (1979; see also Alexander, 1975) have argued that socially or legally imposed monogamy is a way of leveling the reproductive opportunities of men, thereby reducing their competitiveness and increasing their likelihood of cooperativeness. The imposition of monogamy by custom or law has the interesting effect of reducing both male–male and male–female conflicts to a minimum, especially when clans are discouraged (as in nation states: see Alexander, 1979a, pp. 256–259), and when married couples do not have differential access to their respective relatives (e.g., when they are "neolocal" or reside in a new locality rather than becoming a part of one or the other extended family of relatives). Moreover, the combination of socially or legally imposed monogamy, neolocality, and close association of the married couple in work not only leads to minimizing of philandering and conflict of interest between husband and wife, but also characterizes the largest (and perhaps the most unified—or durable—of all large) human societies. Young men at the age of maximal sexual competition are the most divisive and competitive class of individuals in human social groups; they are also the pool of warriors. It is not trivial that socially imposed monogamy (and the concomitant discouragement of clans as extended families that control members) correlates with (1) justice touted as equality of opportunity; (2) the concept of a single, impartial god for all people; and (3) large, cohesive, modern nations that wage wars and conduct defense with their pools of young men (Alexander, 1979a). To a large extent socially imposed monogamy has spread around the world by conquest. The social imposition of monogamy thus simultaneously (1) inhibits the generation of certain kinds of within-group power dynasties that might compete with government and lead to divisive within-group competition and (2) promotes those activities and attitudes that generate and maintain success in the wielding of reciprocity as the binding cement of social structure (honesty, sincerity, trust).
Humans almost certainly began to evolve their social tendencies and capabilities in small kin groups. If so, during that process they incidentally acquired the capability to maintain social organization in ever larger and more complex social groups through systems of reciprocity rather than nepotism per se. In such groups there is only one way to approach an equalization of reproductive opportunity, and that is by sets of rules or moral systems. In humans the laws and mores of larger and larger groups seem increasingly to (1) guarantee to every individual the right to produce and rear its own offspring and (2) restrict the amount and likelihood of variation in reproduction among families. China is currently an extreme in both size (over one billion) and regulation of reproduction (Keyfitz, 1984). Until 1981 or 1982, government assistance was given for a first child, but funds were withdrawn if a second was born. More recently it was reported (e.g., Ann Arbor, Michigan, News, 1982; Nova and 60 Minutes television programs, 1984) that enormous pressure for sterilization followed the birth of a single child. Not long ago, India briefly attempted to require sterilization after three children were born to any person; the government of India now pays individuals who submit to sterilization. More subtle, but also more widespread, are laws that reduce variance in access to resources, such as graduated income taxes, the vote, representative government, elected (not hereditarily succeeding) officials, and universal education.

MacDonald (1983) discusses the "leveling" effect of monogamy, although he seems to find it puzzling, in evolutionary terms, perhaps because he does not consider the significance of equality of opportunity as a basis for social unity in the face of extrinsic threats. Once this factor is weighed in, one sees that the real puzzle is not, as MacDonald supposes, to account for leveling processes, but to account for the maintenance of despotic societies, within which the greatest disparities in opportunities for individuals occur (e.g., Betzig, 1986); or, rather, to explain why some sizes and kinds of societies involved huge disparities in individual opportunity (those intermediate in size; Alexander, 1979a), while others (large and small) have leveled them to extreme degrees. I think the answer will come from comparing the histories of interaction between neighboring societies, effects of physical or physiographic barriers on their sizes, and separation of warriors (soldiers) from their families.

Despite their obvious and dramatic differences from one another, then, the most extremely ultrasocial systems of humans and other species are apparently all based on reproductive opportunity leveling. The essential difference is that in (some) clones and eusocial forms all individuals realize their reproduction through the same sets of
babies and have specialized baby production and baby care in different individuals, and humans have done neither of these things.

CONFLICTS OF INTEREST AND DECEPTION IN COMMUNICATION

A measure of the effects of the new precision in evolutionary theory on biology can be taken by considering that until a few years ago biologists had interpreted "communication" as little more than the honest, accurate transfer of information between and among individuals. Similarly, linguists have tended to regard the function of human language as to serve as a vehicle for transmitting accurate information. Now biologists realize that the conflicts of interests that exist because of histories of genetic difference imply instead that nearly all communicative signals, human or otherwise, should be expected to involve significant deceit (Otte, 1974; Lloyd, 1977, 1980; Dawkins and Krebs, 1978; Dawkins, 1982; Payne, 1983). Indeed, it is instructive to classify communicative signals according to the amounts of deception they may be expected, on evolutionary grounds, to involve, and the reasons for deception. I have already suggested that in rare circumstances, such as honeybee workers dancing about food sources or a pair of parents wholly committed to lifetime monogamy, signals may be totally honest. It is the rarity of this expectation from biological considerations that is most intriguing to us at this point. Conversely, signals involved in predator-prey relations, such as the mimicking of a poisonous prey species by a harmless one, may be expected to be totally deceptive. There is no overlap of interest between a predator and its prey, and no reason to expect any truth in their signals to one another. Neither will gain by doing anything at all that will help the other, and neither has any likelihood of evolving to tell the truth to the other. Anyone who has examined under a microscope a palatable butterfly that mimicks in its color pattern or otherwise an unpalatable or poisonous one will recognize that this prediction is upheld: at a distance the resemblance is remarkable, but up close the similarities are often so superficial that one is astonished that he could have been deceived.

Most communicative signals, such as nearly all that pass among humans, lie between the extremes of total deception and total honesty. I suggest two categories, which might be called restrained embellishment and unrestrained embellishment (Fig. 1.7). These two categories differ both in the proportion of deception involved in the signals and in the reason for the extent of the core of truthfulness within each of them. Restrained embellishment involves signals such as those passed between relatives or
Totally Honest, No Deception

The overlap of interests between signaler and signalee is complete

(e.g., honeybee worker’s dance indicating to sisters the direction and distance of sources of food to be fed to other sisters)

Totally Deceptive, No Truth

There is no overlap of interests between signaler and signalee, no reason for truth

(e.g., Batesian mimicry)

Restrained Embellishment

The core of truth is substantial

(e.g., signals between bonded mates or close relatives, as in parent-offspring or sibling-sibling interactions)

Unrestrained Embellishment

The core of truth is minimal

(e.g., signals between sexual or other intense competitors, especially when they are unrelated)

FIGURE 1.7. A classification of kinds of communicative signals, based on the amount of deception expected, and the reasons.

cooperative mates, in which the signaler would lose by too much deception because it shares so many of its interests with those of the individual to which it is signaling. The core of truth is large and the amount of embellishment rather small, because too much deceit is contrary to the interests of the signaler. Included are most signals between close relatives such as parents and offspring and siblings, and most signals between male and female in bonded pairs if either or both sexes invest parentally to any large degree (unless philandering or channeling of assistance to one’s own relatives, as opposed to those of the spouse, is possible, thus interfering with a likelihood of complete sharing of interests and honesty in signaling). Similarly, restrained embellishment should typify communication between long-term or
lifetime friends who may reasonably expect repeated and reciprocal interactions.

Unrestrained embellishment characterizes signals passed between sharply competitive individuals, such as brief interactants and nonrelatives, in which the degree of embellishment is determined, not by shared interests between signaler and signalee, but by how much the signaler can get away with—what Otte (1974) called “the limits of gullibility” in the responder. I can appear taller by wearing shoes that are slightly built up, but if the heels are too high everyone will laugh; I can wear small shoulder pads in my jackets but not too large or, again, the deception will be too apparent; and so forth. Unrestrained embellishment involves most signals between unrelated or distantly related competitors, and those between even close relatives when resources are severely restricted. Included would be individuals competing for the same mate or territory. Two sibling honeybee queens fighting for sole control of a hive, even though three-quarters alike genetically, may be an example; as may two sisters in our own species trying to divide the family heirlooms when their parents die without a will; or two brothers fighting over a single female or a single indivisible farm or kingdom. Unrestrained embellishment differs from total deception mainly because gullibility may be reduced among conspecific competitors.
References
In prep. Inadvertent selection for early senescence in dairy cattle .
Press.267
House.
Baker, J.R. 1938 The evolution of breeding seasons. In Evolution: Essays presented to E.S.
76:216-270.
Bell, A.P., and M.S. Weinberg 1978 A study of diversity among men and women. NY: Simon and
Schuster.
men and women. Bloomington, IN: Indiana Univ. Press.
Benshoof, L., and R. Thornhill. 1979 The evolution of monogamy and concealed ovulation in
Betzig, L.L. 1982 Despotism and differential reproduction: A cross-cultural correlation of conflict
Hawthorne, NY: Aldine.
Brandt, R.B. 1959 Ethical theory: The problems of normative and critical ethics. Englewood Cliffs,
NJ: Prentice-Hall.
Buss, D.M. 1987 Sex differences in human mate selection criteria: An evolutionary perspective. In
C. Crawford, M. Smith, and D. Krebs (Eds.), Sociobiology and psychology: Ideas, issues, and
applications. Hillsdale, NJ: Erlbaum.268
Psychol. 50:559-570.
NY: Plenum Press.
311.
Campbell, D.T. 1972 On the genetics of altruism and the counter-hedonic components in human
Campbell, D.T. 1975 Conflicts between biological and social evolution and between psychology
and moral tradition. Amer. Psychol. 30:1103-1126.
Campbell, D.T. 1979 Comments on the sociobiology of ethics and moralizing. Behav. Sci. 24:37-
45.
Campbell, D.T. 1983 Legal and primary group social controls. In M. Gru ter and P. Bohanan
(Eds.), Law, biology, and culture: The evolution of law, pp. 159-171. Santa Barbara, CA: Ross-
Erickson, Inc.
Caplan, A.L. (Ed.) 1978 The sociobiology debate: Readings on ethical and scientific issues. NY: 
Harper and Row.
Calif. Press], Ethol. Sociobiol. 4:237-238.
Chanley, J. In prep. Suicide: Evolutionary implications.


Luker, K. 1984b The war between the women. Family Planning Perspect. 16:105-110.


Meda war, P. 1957 The uniqueness of the individual. London: Methuen.


Powers, T. 1982 Choosing a strategy for World War III. Atlantic 250:82-110 (Nov.).


Sartorius, R. 1975 Individual conduct and social norms. Encino, CA: Dickenson.278


Schwartz, R.D., and J.C. Miller 1964 Legal evolution and societal complexity. Amer. J. Sociol. 70:159-169.


Simpson, G.G. 1964 This view of life, the world of an evolutionist. NY: Harcourt, Brace and World.


Turner, E.S. 1980 Dear old blighty. Michael Joseph Std.


West Eberhard, M.J. 1975 The evolution of social behavior by kin selection 50:1-33.280


California Press.
Williams, G.C. 1966b Natural selection, the costs of reproduction, and a refinement of Lack’s principle. Amer. Nat. 100:687-90.