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## *Genes, Consciousness, and Behavior Theory\**

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During the past two decades, a theoretical revolution has occurred in evolutionary biology. It is a revolution that concerns the generation-to-generation operation of microevolution, and therefore the interpretation of long-term cumulative changes in macroevolution. It has focused our attention on what I believe to be the most profound paradox of human existence, and on phenomena important to everyone concerned with understanding the complexity of human behavior and of the human psyche.

I will approach this topic by considering, first, some of my own personal reflections on disagreements between biologists and psychologists which have fascinated and bothered me since I took my last formal course as a doctoral student over twenty-five years ago. That was a seminar in physiological and comparative psychology taught by Donald R. Meyer at The Ohio State University. I happened to take it shortly after the appearance of Lehrman's (1953) critique of Lorenz (1950), and in a year when the mission of the seminar was to tear to shreds the arguments advanced by Niko Tinbergen (1951) in his then fairly new book *The Study of*

\*I appreciate the efforts of those who involved me in the symposium associated with this volume and of Professor Koch in urging me to submit the manuscript. I note that several passages in this paper have been taken with minor changes from my 1979 and 1981 papers and my 1979 book, all published since the APA symposium.

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*Instinct.* In the middle of that same term I had the privilege of hosting T. C. Schneirla while he talked to the entomologists about the behavior of army ants and to the psychologists about the ontogeny of emotions in higher mammals. So I received a sudden and powerful dose of the controversy and excitement in the hybrid arena between biology and psychology during the heyday of what is sometimes called “European ethology.” I was made aware that the central questions in this controversy have always involved the ontogeny of behavior. My presentation here is developed with this fact in mind. Let me now describe some thoughts I have had since then about the history of disagreements between our two disciplines.

#### Differences between Psychology and Biology

First, it seems to me that only the most general discoveries in biology, especially in regard to theory, are likely to attract much attention within psychology. But general biological theory is always evolutionary, and evolutionary theory is about genetic changes. For this reason, it is always easy for social scientists to believe that any new theory about behavior from biology is just another effort to reintroduce genes, probably in an unsupportable way or for ideological reasons rather than scientific ones, or to revive the tired old dichotomies of inherited and acquired, innate (or instinctive) and learned, genetic and environmental. These practices usually have a negative effect on psychologists who, unlike biologists, concentrate on the effects of the environment on ontogenies, not on the effects of genes. Moreover, most psychological theory is about the effects of changes or variations in the environment, while evolutionists most often generalize the environment rather than particularize it and therefore talk about its stable components. Evolutionists may talk about whether environments are certain or uncertain, predictable or unpredictable—things that general—and they often are satisfied to discuss the environments of whole species. Psychologists are interested in environmental variations, not merely in the lives of different individuals within a species but variations occurring within an individual’s lifetime as well. These are just differences between the two sciences. They are not good or bad, but they sometimes reduce our ability to communicate.

Precisely unlike psychologists, evolutionists also tend to put ontogenies aside, and they do so for two reasons. First, evolutionists generalize most about the adaptive (reproductive) significance of phenotypes, while the ontogenies underlying adaptive phenotypes (traits) tend to be particular, not general, and may even be unique to the individual. Second, evolutionists presumably always know that there is an ontogeny behind any behavior, and they assume that all ontogenies have been appropriately shaped by natural selection. In studying adaptations, therefore, they feel justified in delaying attention to ontogenies. Psychologists, on the other hand, who focus on ontogenies and on their variations because the question of human individuality lies at the heart of their science must feel that this is putting aside all that is interesting,

and their suspicions that we biologists are all genetic determinists are further reinforced.

Evolutionists may make a prediction about sex ratios in broods of offspring or about altruism to relatives. Then they check to see if sex ratios or altruism come out that way. They don't worry—at first—about what developmental experiences or physiological events underlie the attribute that interests them. And they only use ontogenies to put limits on their arguments when it seems that no proximate mechanism could reasonably exist that would explain a postulated trait or function. For example, while serving on a doctoral committee recently, I learned that silver maple trees often behave as females for a few years when very young and then later turn entirely to being males. When I first heard this I suggested that perhaps they reverse their sex if males are scarce, and therefore reproductively valuable, in their particular vicinity. Immediately a botanist responded: how could a tree possibly measure the sex ratio in its vicinity? Somehow I had the gumption to suggest that it might do so by being a female for a while and reacting to the proportion of its ova that are fertilized year after year. The important point, however, is not that I happened to come up with an hypothesis that satisfied the botanist temporarily, but that I was acting like an evolutionary biologist while the botanist was acting more like a social scientist. I wanted to hypothesize a particular evolutionary or adaptive function; he was demanding that I describe a reasonable proximate mechanism before continuing.<sup>1</sup>

A final note on sources of disagreements between us: I think that biologists often use terms like “innate” intending only to emphasize that they are temporarily bypassing the question of ontogeny, or they use it for behaviors with cryptic ontogenies. But it sounds as though they mean the behavior has no ontogeny. When such biologists are challenged by psychologists either to defend concepts like innate or to explain what their theories mean for particular ontogenetic questions, a curious thing happens: many biologists actually seem to become genetic determinists in the course of defending themselves against social scientists' criticisms of their ignoring of ontogenies. To say that maybe a certain percentage of human behavior is genetic, that incest avoidance is an instinct based on genes, or that a birdsong may

<sup>1</sup>It is important that I have used the word *hypothesis* here. Those who criticize the approach of evolutionary biologists or all those who look for the adaptive significance of traits sometimes refer to such predictive statements as “stories,” “just-so stories,” or “conclusions.” To view them as conclusions on the basis of the anecdotal, nonsystematically gathered, or even unconsciously acquired knowledge that led to their formulation is obviously circular, unscientific, and inadmissible. On the other hand, it would be surprising if some proponents of the evolutionary approach did not make this mistake. What is more surprising, however, is that reputable scientists attempt to discredit an entire discipline by parading such mistakes as typical and using them to play upon the sympathies of those for whom the evolutionary approach, especially to human behavior, is still alien and difficult, rather than by using the best examples from evolutionary biology to show how that discipline can help advance our knowledge of ourselves.

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be completely inherited with no learning involved are all examples from the recent literature (see discussion by Alexander, 1979b).

#### Survival of the Fittest What?

With these remarks I will turn to another area of communicative failure between biologists and social scientists. Hamilton (1970) noted that we had still not discovered what it is that organic evolution by natural selection maximizes. Darwin never explicitly addressed this question. If we could resurrect him long enough to ask about it, we might put the question to him as simply: survival of the fittest *what*? For anyone who accepts organic evolution as the underlying process responsible for life and its traits, this is a central question. I think, however, that unless Darwin had somehow acquired knowledge since he died he could not answer it, and for a reason that is completely understandable. Let me explain by considering briefly the possible answers.

First, we talk and think a great deal about our own personal survival as individuals. We like to think it is (or we wish it were) our own survival that is at stake in the great race of life, and our view of the medical profession and our support of it implies that this is indeed our view of life. If that is what evolution is all about, however, it has been a colossal failure, for of all the units in the hierarchy of organization of life, the individual is just about the shortest lived; moreover, individuals in most species are very short-lived compared to the longest-lived in a few species. Scarcely anyone is challenging redwoods and bristlecone pines for life length. The skew is in the wrong direction. Whatever individuals may have evolved to do—and I happen to believe that there are few questions more worth asking—they have not evolved to survive.

Families, social groups, populations, and species all last longer than individuals do. But neither can they be described as having evolved to survive, even though biologists were fooled for a long time on this point. For one thing, all of these units change continually: they don't reproduce themselves accurately or precisely, and that's one way of failing to survive. More importantly, there is a continually growing body of evidence backed by solid theory indicating that at least in general the attributes of living things simply are not there because they perpetuate the species or the group, or even because they perpetuate the family per se, even if they do so incidentally. In other words, the mechanisms of evolution clearly do not favor the survival of species or populations as such. I realize that not all readers will be familiar with the evidence behind this conclusion against what has been called group selection, but it has been around for more than a decade now, beginning with Williams (1966), and it has been widely discussed. I have reviewed the evidence elsewhere (Alexander, 1979a; Alexander & Borgia, 1978). Recent works arguing that group selection does occur (e.g., Wilson, 1980; Wade, 1976) only support its lack of generality by revealing the narrow conditions under which it can be effec-

tive. Here I wish to discuss the meaning for psychologists of the conclusion in biology that group selection is not a general explanation for the existence and nature of traits. What effect of selection is such a general explanation?

Because individuals do not survive, and groups do not now appear as appropriate targets for “survival of the fittest,” Darwin only had one other unit in the hierarchical organization of life to which he could turn to answer the question we would put to him, and that is traits. In some sense he knew this. For example, consider how he explained the trait of sterility in social insects. First he noted that traits may be carried by individuals that never express them, and if the expression of those traits, when it does occur, contributes to the reproduction of family members who are not expressing the traits but nevertheless carrying them, then the traits themselves, he said, can spread, or as he put it, be “advanced by natural selection.” In 1859 Darwin explained it this way: “A breed of cattle always yielding oxen [castrates] with extraordinarily long horns, could be slowly formed by carefully watching which individual bulls and cows, when matched, produced oxen with the longest horns; and yet no one ox could ever have propagated its kind.” Similarly, he noted that tasty vegetables could be produced by saving seeds from relatives of the vegetables tasted or eaten, therefore unable themselves to produce seeds, and that cattle with “the flesh and fat . . . well marbled together” could be bred although “the animal has been slaughtered” if “the breeder goes . . . to the same family.”

This analysis was almost unbelievably prescient, clearly anticipating the refinements of evolutionary theory that we modern biologists are only belatedly beginning to understand and use.

But we still haven’t answered the original question. It cannot be traits as such that have evolved to survive either, and we can use Darwin’s own argument to prove it. In his argument, sterility in the social insects would have been facultative from the start, and it remains so today; so it was the potential to be sterile or not that spread and survived. Perhaps it is always, in some sense, the ability or potential to have one or another of two or more alternative traits that tends to survive longer and longer. Such abilities or potentials necessarily derive from the possession of genes. Indeed, that is almost a definition of gene: a heritable potential to produce certain traits in certain environments. So the answer to our rude question to Darwin is that what selection maximizes is the survival of the fittest genes, and the reason he could never know the answer is that for reasons we cannot reconstruct he didn’t get around to understanding Gregor Mendel’s contemporary studies of sweet peas. Apparently Darwin never knew a thing about genes, although he came very close to describing them in his argument about the evolution of sterility in the social insects.

Genes that survive for long periods—and there are probably many that have been around for billions of years—do so by reproducing or copying themselves exactly, and they yield not traits but potentials for different traits. They reproduce themselves exactly inside localized buffering environments that continually adjust to the rest of the environment (that remains) outside them. Some of these local environ-

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ments of genes have developed the ability to generalize about all such local environments, and, communicating among themselves, they have agreed on the label “phenotype” to describe such local environments, including themselves. These intelligent, reflective, analytical, local gene environments are called by themselves “humans.”

The genes that survive the longest must be the ones whose potential as expressed in traits can match the environment for the longest periods—in other words, those that can best generalize the environment. One way of “generalizing” the environment is to use predictive contingencies or signs within it to modify yourself to meet its variations. Of course we call that “learning.” And the potential for traits—even for the trait of learning—resides in the genes of the evolutionist.

Like a good evolutionary biologist, I have reintroduced genes. But, I have introduced them to account for learning. And I mean it just that way—that at one level the existence of certain genes is the only way to explain the existence of learning. It is unfortunate that the kinds of genes I am talking about—those postulated to account for learning—are simultaneously the kind most likely to underlie behavior, as opposed to morphology or physiology (because they are concerned with plasticity), and those most concealed from our analytical efforts. They are the genes least likely to be exposed to our view, again because the variations in the phenotypes they produce are triggered by environmental differences. Sometimes it is not easy to realize that genes are saved because they yield particular phenotypes in two or more particular and recurring environments; but I will venture that this is the rule and that the other kinds of cases, more obvious and better known to us, will turn out to be the exceptions that require special explanations. It is from these circumstances that the unbelievably complex and protracted arguments over heritability derive (e.g., Feldman & Lewontin, 1975); we ought not to allow them to obscure the real issues.

Before this decade no philosopher, no social or biological scientist—not Darwin or Freud or Marx or any of the rest—could have known that we people are, in terms of history, just complicated local gene environments—or genetic replicator vehicles, as Dawkins (1977) has put it. In my view it is the most profound paradox of human existence that throughout the entire evolutionary elaboration of the traits that now enable us to talk or think about genes (consciousness and self-awareness), the tiny objects that underlie it all remained totally outside the range of our senses. This has to mean that, without formal biological training, we could not know what we are really doing in our day-to-day activities and endeavors or what they represent. Whatever we have thought we were doing is either some substitute, as close as possible to being an accurate reflection of “maximizing the likelihood of survival of our genes,” or else a matter of self-deception.

For the first time—because we do now know about genes and know their mission (a missing link, so to speak, in our self-understanding)—we are in a position to ask intelligently whether or not it is possible to generalize about what people are doing

minute by minute, hour by hour, lifetime by lifetime in their everyday existences. For the first time we have a way to proceed in analyzing conflicts of interest at every level of human social organization, and we know that to be accurate and useful these analyses must be driven right down to the level of the gene. For the first time we can understand that human beings seem to be group-altruists partly because throughout history their associates have carried some of their genes (and partly because the group was otherwise useful to their own reproductive success) and individually selfish because throughout history individuals have carried individualized, unique sets of genes. For the first time we may be able to do more than guess or flounder about with respect to things like the significance of free will, self-awareness, self-deception, introspection, dreams, conscience, the subconscious, and morality.

### **Inclusive-Fitness-Maximizing**

Now let me turn more explicitly to the question: what are human beings really doing? There is just one way to replicate genes that are invariably carried in phenotypes and that is to produce and help other replicators (phenotypes) who carry the same genes. We knew that all the time. There is a twist to it, however, that we never understood from the arguments of Darwin (1859/1967, 1871), Fisher (1930/1958), and Haldane (1932/1966) until William D. Hamilton (1964) explained and applied it: we can help both descendant and nondescendant relatives. For a species in which individuals never interact with anyone but mates and offspring, this frill is irrelevant. For an organism like a human being, in which throughout history individuals tend to interact consistently with a horde of different relatives, scarcely any fact could be a more important clue to understanding its sociality and the development of each individual's social tendencies.

Hamilton called helping all genetic relatives in the way that maximizes survival of one's genes "inclusive-fitness-maximizing." I will use that term from now on.

The theoretical and philosophical significance of the facts that I have just reviewed seems to me as profound as that of Darwin's original development of the theory of evolution, and the most important advance in human knowledge of the twentieth century. Anyone who cannot accept that must somehow deny or trivialize the proposition that what people are doing from hour to hour, day to day, lifetime to lifetime is carrying out activities that, not necessarily in current environments but in terms of our long-term history, represent inclusive-fitness-maximizing. We are doing those things that, if we had not rapidly and radically modified our environment, would actually be enabling and promoting the survival of our genes. To me that notion represents a monumental shortcut—one of unparalleled potential—for all students of human behavior.

Our history of ignorance about genes must be one of the reasons for feeling that

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we must deny that we have evolved to be vehicles of genic reproduction. But I think there is another fascinating reason for such denials. To introduce a person to genes as the objects that underlie his or her whole behavior is to make genes into the very phenomena that I suspect we are most powerfully evolved to resist in our social behavior: foreign entities who, precisely for the reason that we think of them as foreign, will not be expected to even know about, let alone share, our interests. Entities of that sort usually represent hostile forces. We are in effect xenophobic toward our own genes because and to the extent that they are anthropomorphized (one is tempted to speak of genophobia!). We can be sure that the whole phenomenon of evolutionary self-analysis is a trait wholly unanticipated during the evolutionary organization of genomes. Self-analysis is, in effect, an environment of development created accidentally by the genes, and not necessarily conducive to their long-term survival, but with enormous potential for determining what humans may become.

In some sense this aspect of self-awareness may be the biggest change in an environment of a living thing since life began, for that is what knowledge of the mission of our genes really is: a change in our environment of behavioral development and expression. In part it represents a giant step toward closing the feedback loop between need (or desire) and novelty in evolutionary change, a causal connection which organic evolution has never otherwise managed. Unlike cultural innovations, genetic novelties do not appear because the organism needs them, or in the form needed. But humans are now well on the road to accomplishing this connection for genetic as well as cultural change.

Biologists view the lifetimes of organisms as "effort" (expenditure of energy and taking of risks), and they divide this effort into two general categories: somatic effort and reproductive effort. Somatic effort is that used to build the soma toward later or better possibilities of reproduction. Reproductive effort can be divided into two categories: mating effort and nepotistic effort. Mating effort amounts to beneficence toward one's gametes. Nepotistic effort can in turn be divided into parental effort, or beneficence toward one's offspring, and extraparental nepotistic effort or beneficence toward one's nondescendant relatives (Low, 1978; Alexander & Borgia, 1978).

In terms of sociality the part of effort that concerns us is parental and extraparental nepotistic effort. Elsewhere I have divided nepotism (beneficence toward relatives) into two general kinds: discriminative and nondiscriminative (Alexander, 1977, 1979a). Nondiscriminative nepotism refers to beneficence offered indiscriminately to one's associates or contacts. In my view it is an unlikely kind of behavior in an organism capable of distinguishing relatives of differing degrees and differing needs except when powerful external threats tend to synonymize individual interests. Therefore I assume that discriminative nepotism, including parental behavior—or its surrogates in changed environments—represents the basic or essential element in human sociality. (One can also speak of direct and indirect nepotism—

the latter being sometimes termed reciprocity [Trivers, 1971]—and of discriminative and nondiscriminative reciprocity.)

I assume that identifying the immediate or proximate mechanisms by which discriminative nepotism develops in the individual constitutes a major or central problem of psychology. To say it another way, I assume that it will be useful to psychologists to view the world of human sociality as an enormously complex system of discriminative nepotism and to view the ontogeny of social behavior as patterned toward achievement of maximal reproduction via nepotism, at least in terms of the environments of history. In other words, I am predicting that theories of social learning will someday be explicit efforts to understand discriminative altruism of both nepotistic and reciprocal sorts.

To maximize the effectiveness of discriminative nepotism, the individual requires three kinds of information about potential recipients of its nepotism: the degree of relatedness, the need of the individual (more properly its ability to turn beneficence into reproductive success), and the available alternative uses of any resources that it might invest.

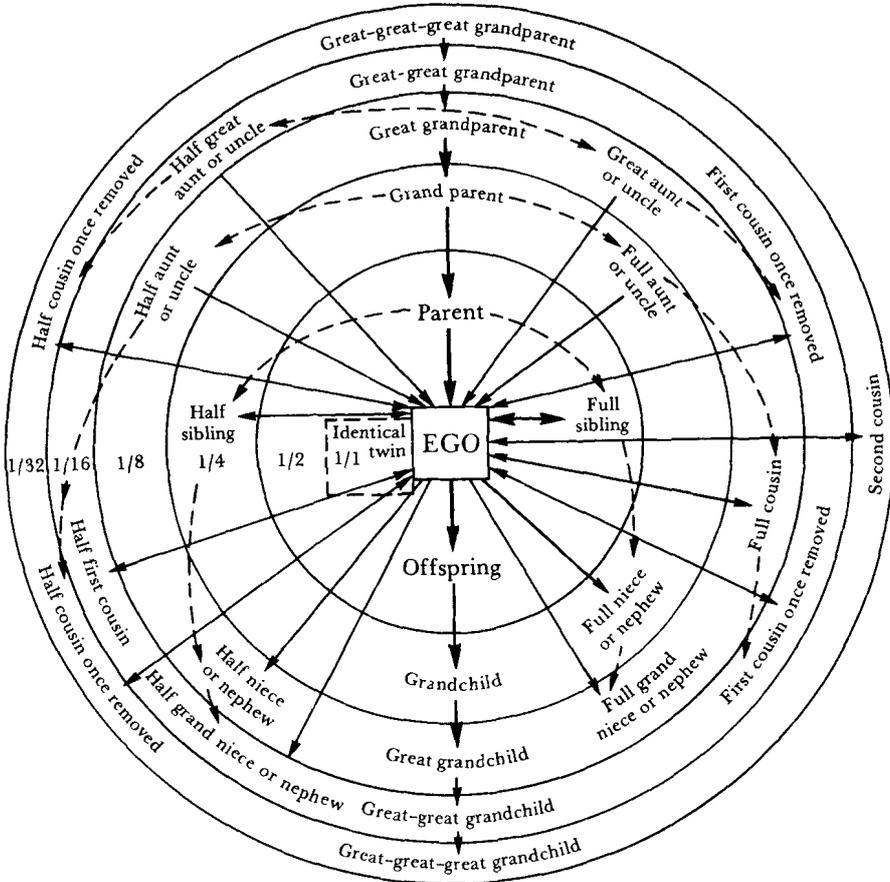
Figure 33.1 is a diagram of the set of genetic relatives potentially associated with a given human individual. Mates are not included, nor are in-laws and other relatives by marriage, although it is possible to quantify one's expected relationship or reactions to them.

### **Mechanisms of Kin Regulation**

Given an ability to evaluate the relative needs of different individuals, this diagram amounts to a blueprint for inclusive-fitness-maximizing. If one does know all of these relatives and is keenly aware of their needs, then he or she is in a position to maximize the effectiveness of reproductive effort via nepotism (in its general sense of beneficence to relatives). It is indisputable that we know who our relatives are: anthropology has proved that for every society it has studied. With regard to ontogenies, we may ask how it is, in fact, that we do know who our actual relatives are. Anyone can fill in actual names of relatives on a diagram of the sort in Figure 33.1, usually out to first cousins or beyond (e.g., Schneider & Cottrell, 1975) unless one's family is extremely large or unusual, or unless, in this modern mobile technological society, one has been geographically divorced from them—a situation quite unlike that in which humans have lived throughout history. I am particularly interested in the problem of modeling the ontogeny of nepotism because it seems to me that this is the only way to bring our two disciplines into accord on the important topics of how to understand the life activities and motivations of humans and how to interpret social learning.

I think it is obvious to all of us that we know who the different relatives are in our various families as a consequence of learning experiences that are often entirely conscious. We know that our parents told us who some of these relatives are. We

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**Figure 33.1** Genetic relatives potentially available to an individual, Ego, for reproductively self-serving nepotism. Arrows indicate likely net flows of benefits. Half the genes of parent and offspring are identical by immediate descent. Other relationships are averages. Dotted lines indicate closer relatives other than Ego, of Ego's relatives, thus the most likely alternative sources of nepotistic benefits. Widths of lines indicate likely relative flows of benefits to or from Ego based on the combination of genetic relatedness and ability of recipients to use the benefits in reproduction. Extreme lateral relatives are less likely to be encountered or identified because of social or geographic distance, extreme vertical relatives because of temporal nonoverlap. Double-headed arrows indicate relatives whose statuses in regard to need of benefits or ability to use them to reproduce and ability to give benefits are doubtful owing to the uncertainty of age relationships of the individuals involved. (Thus one's second cousin may be much younger, much older, or about the same age; one's sibling, on the other hand, is much more likely to be of comparable age.) Relatives on the right side of the diagram are those resulting from monogamous marriages; polygyny results in relatives indicated on the left. I argue here that natural selection would save genetic materials leading to behavioral

know that our understanding of the identity of siblings and parents and some close relatives has built up through extensive and intimate association across years and decades. On the other hand, some of the learning experiences involved are not conscious—or do not remain so—even if the individuals responsible for causing them do indeed remember them: a parent may recall introducing his child to particular relatives even if the child itself has forgotten.

To use an aside briefly, it has been shown—conclusively, I think—that not only in human but in nonhuman mammals as well, avoidance of sexual relations with close relatives is also a consequence of learning, of intimate social interactions or associations that occur when one or both individuals are prereproductive. In humans this aspect of the association is not necessarily conscious. How many individuals know why they are not interested sexually in their siblings? How many know the laws in detail with regard to incest? How many have even a faint notion of the actual disadvantages of sexual interactions with very close relatives? Yet we avoid those relationships rather consistently, and we know now that we do it as a result of learning experiences—learning experiences that are not for the most part conscious, or not remembered (or even well enough understood to be reliably reconstructed).

I think that much of the informational background of nepotism is much more conscious than is that of incest avoidance. It seems to me that genealogical connections—their length and directness—constitute the principal means by which individuals are apprised of and remember their obligations to relatives. These genealogical relationships are learned. Their significance is learned. Humans do not have a history of knowing what their actual genetic relatedness is, but they do have a keen understanding of closer versus more distant relatives, and in the end that amounts to the same thing. In this connection it is interesting that to count genealogical links and halve the relationship with each additional link—which is precisely what courts of law and churches do in assessing matters like inheritance—is an accurate method of determining fractional relationships in order to put numbers in Hamilton's original formula for maximizing inclusive fitness.

I believe that when social learning is approached as essentially a problem in

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tendencies (such as learning biases) that in usual social situations promote the assisting of closer relatives over more distant ones, and of more needy relatives among those able to convert assistance into reproduction. Recognition of relatives (except a mother's recognition of her offspring born while she is conscious and observing) most often (at least) occurs as a result of social learning and circumstantial evidence. Numbers and kinds of social interactions (and not some kind of innate kin-recognition mechanism) are likely to be the sources of the cues for behaving socially in reproductively appropriate fashions. How such cues are used in households of different structures in different societies and how social learning is structured as an evolved mechanism of adaptive nepotism are problems that remain to be elucidated. (From Alexander, 1977.)

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understanding inclusive-fitness-maximizing through nepotism, evolved in certain kinds of environments that have been variously modified, sometimes with extreme rapidity, many clarifications will occur, with respect to not only patterns of human social behavior but learning itself as a general phenomenon.

Social learning may seem like an adequate mechanism for much of nepotism—much of human sociality—but the question remains whether or not other mechanisms also exist. The biologists who have become excited about the central significance of nepotism in recent years have all been through periods of wondering whether or not mechanisms other than social learning might be involved. I do not believe so, and I would like to present the reasons very briefly (see also Alexander, 1977, 1979a).

First, one might suppose that individual genes would be able to cause their phenotypes to search the phenotypes of other individuals for evidence of their presence or absence in the other genome and then cause the phenotype to act appropriately (Hamilton, 1964). This is a lot of activity for one gene to cause. Leaving that aside, I regard such a mechanism as extremely unlikely on other grounds. Any such gene would continually be serving its own presence in potential recipients of nepotism, and any mutant that suppressed its effect would help itself and everyone else in the genome by that action and would spread on that account. I am saying that “outlaw” genes that help only themselves in nepotism cannot persist (Alexander & Borgia, 1978; Alexander, 1979a). Instead, one expects that the genes in a group as cooperative as a modern genome has to be to produce a successful phenotype will surely be served approximately equally by the actions of the individual genes comprising them, and the only way this can be accomplished is for the genome to act as a whole, through the phenotype, on the basis of each gene’s probability of being in a genome that is available for assistance. The way this can be accomplished is through considering whether the relative falls into one or another class of relatives—each class having a certain amount of genetic overlap with the potential altruist—a certain probability of carrying any individual gene. Even if we do use individual traits that are themselves closely tied to the presence of certain alleles—eye color, hair color, ear shape, or the presence of distinctive “family-wide” birthmarks or other features—to place individuals into or out of certain categories of relationship, we do so as a result of learning what the mark, feature, or trait means by seeing it in relatives already known by other means. That is merely a variant of the social-learning model I mentioned first.

Since I originally predicted (Alexander, 1977) that organisms must somehow learn who their relatives are, a number of studies have been conducted which deserve review here. Greenberg (1979) demonstrated that sweat bees learn who their sisters are during their association as young adults in the natal burrow. For several reasons, Greenberg’s results have been widely misinterpreted (e.g., May & Robertson, 1980). First, Greenberg used the phrase “innate recognition mechanism” in his title, although he was actually referring to genetically determined differences

(presumably in chemicals) used by the bees to recognize one another. Second, Greenberg's note that he reared the bees in individual isolation has been mistaken by some biologists to mean that there was no learning opportunity; but sweat bees always develop isolated in their own earthen cells and learn as young adults whom to accept while guarding the burrow entrance. Third, Greenberg showed that sisters can be recognized as such even though they have never previously been encountered, apparently by comparisons of their chemicals with those of sisters encountered. Finally, it is my feeling that for some biologists the whole notion of "kin selection" loses its flavor if there are no "innate mechanisms" of kin recognition and they see such mechanisms wherever they look.

May and Robertson (1980) reported, apparently with inadvertent correctness, that a mechanism "exactly analogous" to that shown by Greenberg in sweat bees "was reported by K. E. Linsenmaier . . . in a desert-dwelling social isopod." They did not give the reference, but probably referred to a 1972 study in which juvenile woodlice also learn to recognize their parents, and parents their offspring, by association, perhaps using specific chemicals which vary with genetic variation. May and Robertson then asserted that in a third study "Waldman's and Adler's [1979] evidence for kin recognition in frogs [it actually involved toads in the genus *Bufo*] . . . does not distinguish between innate and environmental mechanisms. . . ." This is correct, but they fail to remark that the tadpoles associated in sibling groups before they were mixed and shown to re-aggregate as siblings. It is clear, then, that appropriate learning situations were available. Waldman (1981) has now shown that isolated tadpoles also recognize maternal half-siblings but not paternal half-siblings, indicating that some stimulus provided by the mother, perhaps in the jelly-like milieu of the egg mass, is the critical learning vehicle. Buckle and Greenberg (1981) have shown that sweat bees use other individuals with whom they associate, but not themselves, to learn the attributes of relatives.

The only recent publication with data implying that appropriate situations for learning to recognize relatives are not available seems to be that of Wu et al. (1980) dealing with recognition of paternal half-siblings by infant macaques. These babies were removed from their anesthetized mothers within five minutes after birth, kept in individual wire cages in a room (7.6 m × 11.0 m) housing fifty other macaques, "such that they had no opportunity for visual, physical or olfactory interactions with relatives or any other animals used in the experiments," and allowed play time each day only with four to six nonrelatives. Auditory cues and learning from their own personal attributes were not excluded as possibilities, and no proximate mechanism for the apparent recognition was postulated. Such studies are vulnerable, on the question of innate (versus learned) recognition of relatives, because, like all isolation studies, they depend upon the exclusion of all relevant aspects of the environment rather than the positive demonstration of a particular mechanism, as is possible with studies showing that learning occurs. Merely to identify a possible relevant variable not explicitly eliminated requires that the study be repeated to be useful.

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Such studies are also problematical because no likely innate mechanism for differentially recognizing relatives, or relatives of different degree, seems ever to have been proposed. The mechanisms suggested so far can be criticized because they involve either unprecedentedly complex activities by single genes or the likelihood of conflict within the genome that could thwart their evolution (see Alexander, 1979a, pp. 103ff).

May and Robertson were probably misled by the demonstration by Greenberg that genetic differences among sweat bees cause the differences (probably in chemicals) that are learned by other bees, enabling differential treatment. But the mechanism Greenberg demonstrated is by no means new: human beings use it all the time. They learn what individuals of their own or other families look like, and then they use those features to remember old individuals and place new ones into the right groups. Every time humans use a heritable physical difference to guess at relationships between humans, they are doing precisely what the sweat bees do (e.g., "Judging by the shape of your nose, I would say you are a Durante"; "That family is from Japan"; "The baby looks just like his father"). That May and Robertson were indeed confused is shown by their remark, "It is not yet known whether vertebrates have similar innate abilities."

It is possible to argue about the definition of innateness. Wilson (1975) defined it so as to include learning (for a comment, see Alexander, 1979b), and another biologist with whom I discussed this problem remarked that he would regard a learning event as "more innate" if it occurred earlier in life. Perhaps, in some sense, this would make it more "inborn." But the more common usage is to oppose innateness and learning, as May and Robertson clearly did. If such opposition of the two concepts eliminates the possibility of proximate mechanisms of particular forms of social behavior alternative to learning, then so be it. It is unfortunate that so many biologists and nonbiologists alike continue to suppose that there must be such alternatives to learning without carefully exploring what would be involved. Until a reasonable model is proposed, or, even better, a mechanism actually demonstrated, it is appropriate to be skeptical about the entire concept of innate recognition of kin. If animals like bees, sowbugs, and tadpoles learn who their kin are, it seems likely that those who argue that various kinds of social learning will prove to be the only vehicle of kin recognition are correct. I predict that the results of Greenberg and Buckle will prove to be general, and that other studies will be planned to test for the same possibilities. Particularly interesting are the questions (1) whether one's own attributes are used in assessing classes to which putative relatives may belong, (2) whether individual relatives not previously encountered are accepted, (3) what kinds of stimuli used in kin recognition, (4) what sex differences in kin recognition correlate with social difference, and (5) how many classes of different relatives are regularly distinguished by the different possible means. In this connection, a particularly interesting—and surprising—finding is that of Sherman (personal communi-

cation) that females (but not males) of Belding's ground squirrels seem able to distinguish maternal full- and half-siblings within their own litter.<sup>2</sup>

Learning studies demonstrate mechanisms; studies of innateness typically seek to demonstrate absence of mechanisms (learning). In view of the apparent difficulties in postulating mechanisms not involving learning, and the results with arthropods and lower vertebrates, it seems appropriate to be skeptical about the entire concept of innate recognition of kin. Indeed, Greenberg (personal communication) has pointed out that the word *innate* is inappropriately used to modify *recognition* unless recognition is used not in the usual sense of "previously known" but according to secondary meanings like "to acknowledge, or take notice of."<sup>3</sup>

I conclude that terms like *instinctive* and *innate* and *genetic* might as well be abandoned in considering why and how patterns of discriminative nepotistic assistance arise in social groups of humans. The only thing that is inherited or innate or instinctive is the genes themselves, not the behavior or any other aspect of the phenotype that develops in one or another environment. Moreover, the ontogenetic mechanisms of nepotism are, at least in some large part, ordinary learning phenomena. I believe that a thorough exploration of all this will represent an investigative aid to psychologists of immeasurable importance. I do not deny that one can get along without it, but I would hate to try to ignore all of these things and have to compete with other investigators who understand them well and are continually taking into account how they could assist in their investigations. I would not suppose that any other point need be stressed in this regard.

## Past and Future

It should be obvious that several differences exist between the approach of modern evolutionary biologists and that of the ethologists of two or three decades ago: (1) recognition of the importance of understanding the levels at which selection is generally effective, causing an avoidance of the concept of altruism in the context of group selection (as with, for example, Lorenz's notion of forbearance in contests between conspecifics in the interest of preserving the species); (2) an avoidance of

<sup>2</sup>For an excellent update of known mechanisms of kin recognition, see Holmes and Sherman, 1983.

<sup>3</sup>Unless one uses a peculiar and rationalizing definition of *innate*, progress toward a demonstration of innateness amounts to a demonstration of the absence of ontogenetic influences, or of an ontogeny. To demonstrate learning, on the other hand, is to show that particular stimuli influence ontogeny. Because of this difference, the usual dichotomy with respect to observed behaviors is not between learned and innate but between behaviors for which some ontogenetic stimuli are known and others for which none is known. To some extent this always means that the ontogeny of the behavior that is termed *innate* is to some extent (or may be) cryptic or hidden. Since it is premature to call all such behaviors innate, I suggest that a new term is needed for behaviors with cryptic ontogenies, and I suggest *cryptonate*, meaning that the origin, its birth, or development of the behavior is difficult to trace.

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the dichotomy of innate and acquired (except for some writing of a few sociobiologists; see discussion by Alexander, 1979b); and (3) a keener analytical capability in respect to altruism, egoism, behavioral development, and the functions of learning.

What is likely to happen in the near future in respect to the hybrid discipline lying between the social sciences and evolutionary biology? I have already suggested that efforts will continue in the analysis of the ontogenetic mechanisms of nepotism and of culture in terms of a history of inclusive-fitness-maximizing. I think that increasing attention will be paid to the problem of understanding why social life sometimes, but not always, evolves toward ever greater complexity, and specifically to elucidating the forces that guided the evolution of human traits and human sociality. I believe that great strides will be made in developing the study of communication, and that the entire branch of philosophy concerned with social issues like morality and ethics will be literally transformed—much of it into a science—by incorporation of the principles now evident from evolutionary biology.

#### Free Will and Individual Interests

Finally, I shall comment briefly on one of the topics I mentioned earlier: free will—a concept that many feel is antithetical to any biological theory of human behavior. Because of my impression that this kind of feeling underlies much of the resistance to biological-evolutionary interpretations of human tendencies, and because I regard it as an unwarranted pessimism, I think it is useful to show that reasonable and testable hypotheses can be generated about the biological nature and function of what we call “free will.” There is not much new in what I am about to say, and it is in no way a comprehensive treatment of the subject; but I do not think we have to rely any more on our intuitions alone to decide whether we like our arguments, as I believe has been necessary for such arguments in the past.

An integral aspect of consciousness is the phenomenon of self-awareness, and self-awareness, in turn, at least partly involves what Robert Burns called seeing ourselves as others see us. To a biologist—probably to almost anyone at all—this aspect of self-awareness is easily seen as crucial to success in social matters; in turn, biological reproductive success—the focus of the evolutionary biologists’ interest—depends upon social success.

In some large part our conscious awareness of ourselves and our social circumstances is taken up with what might be called social “scenario-building.” Almost continually we play out in our minds the possible and probable moves in the game of social living, which of course is not a game at all but the real thing. How can I write this paper (deliver this lecture, study for this examination, approach this policeman or judge or merchant or bully or friend) so as to achieve this or that personal goal? What will he or she do if I do this or that? What action by me will

most likely cause my desired ends to be achieved? If I do this, and he does that, and then I do something else, then what? And so on and so forth.

In such scenario-building we seem to see before us alternatives. We actually perceive beforehand—through a marshaling of all the information available to us from the past and present—possible choices that we can make. We assume that we can make any one of those choices that we wish to. We evaluate them, and we apparently make whichever one we decide is best (or preferred or whatever). We cherish the right to make the decision ourselves, on our own bases, and the additional right to keep the reasons private, and not even to review them consciously if we do not wish to.

This projecting and weighing of possibilities, it seems to me, has the obvious correlate that the most unpredictable aspect of our environment is the sets of other social individuals and collectives with which we must interact. They too are building scenarios.

I suggest that free will amounts to the right to build our own scenarios and act on them for our own reasons without having to justify them—in other words, that free will involves nothing in particular about the causes of our behavior except our right to determine them, to weigh costs and benefits in our own terms.

To the extent that this is correct, the problem of understanding free will resolves to that of understanding the bases on which we make our judgments of possible alternatives and why we cherish the right to be personal, private, and individual about such judgments.

The only background I can imagine for a compulsive adherence to such a privilege by every different individual—and at the same time a compelling one in biological terms—is that, throughout evolutionary history, reproductive individuals have been genetically unique.

This means that, in biological terms, the right to make our own personal decisions about our own futures is the ultimately precious possession of individual humans. Even if societal rules and obligations actually place enormous restrictions on this privilege, we strive for the right to apply and interpret these restrictions, as they affect us, by and for ourselves.

I offer the hypothesis that decisions of free will—judged in terms of the environments of history—will tend to be those which maximize our inclusive fitnesses, that we have evolved to be exceptionally good at such decisions, and that this is the precise reason for the existence and nature of consciousness and self-awareness.

I would like to finish by drawing my wild speculation about social scenario-building, or individual social planning, out to its limits—or perhaps well beyond its limits—by suggesting a possible connection between science and the humanities. A sort of no-man's land has always existed between these two arenas of human endeavor, with each proudly disdaining the other in selected regards. As a columnist in the *Ann Arbor News* put it recently, harking back to her college days with respect

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to her fellow students who went into science, "It just seemed as though they went their way and we went ours."

Scientific studies seek generalizations—kinds of understanding that immediately have the same kind of applicability to large numbers of people. A scientist's discoveries, and therefore fame and fortune, are predicted on the generality of his or her conclusions. In some sense the same is true of a novel or a play or a poem: Shakespeare, after all, lasts because we know deep down in our souls that he understood us—which means that he understood general human nature in a very special way. But there is a difference, and I have wondered if the difference is not in part that we tend to a much greater extent to use those experiences and discoveries that come from the humanities as theater—or, if you will, as condensed scenarios—in terms of our own personal social existences. We use them as experiences that we as individuals can turn to our own advantage by applying their lessons to our own unique existences in our own unique fashions. To some extent this is true of science, but not nearly so much so. Perhaps we are talking here about the romanticism that is widely acknowledged in some realms, and absent—for most—in some others. Science may be romantic for the scientist whose existence—and success or failure—is wrapped up in it, but it is much less so for the ordinary person than is a poem or a deeply moving drama.

Perhaps I can complete this thought appropriately by quoting the social anthropologist Anthony F. C. Wallace (1961) in a statement that seems to me to be entirely consistent with the new evolutionary view of human nature and human activities. It is appropriate that I should be quoting an anthropologist, since anthropology is a discipline that now and then undergoes some formal strife in its annual meeting over whether it wishes to call itself a science or an aspect of the humanities. Wallace wrote as follows:

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

As an evolutionary biologist, all I feel like saying in response to that statement is *yes*. With our individualized sets of genes, and our history of individualized interests, we humans write poetry, philosophize, pursue truth, seek adoption by surrogate kin groups, sometimes commit suicide, and travel on through history trying to decide where we should go from here, given what we seem to have found out about

where we have been. A part of that finding out is the new knowledge of the extent and nature of our conflicts of interest during history, measurable only by carrying our analyses of these conflicts right down to the level of the gene.

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