

Evolution, Human Behavior, and Determinism

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Many of you know that there have been some dramatic theoretical changes in evolutionary biology during the past decade, and that sharp controversies have generated over whether or not, and how, they might be useful in our efforts to understand human behavior. It seems appropriate that these questions should be addressed at a meeting of philosophers of science.

Those of you who are aware of the controversies may agree that they have not always clarified the issues -- at least not to a degree commensurate with the intensity of the feelings aroused. The word sociobiology, for example, could have become simply a label for a new and broad interest in evolutionary approaches to social behavior. Instead, almost exactly like a predecessor, ethology, it has become associated with a concept of naive and intolerable determinism, and sometimes with only a few statements by one man about the genetic background of behavior.

On the other hand, two things have become painfully clear as a result of these controversies. The first is that it is very easy to be a non-evolutionist or an antievolutionist -- to deny, in one way or another, that organic evolution is the only useful explanation of life and its attributes. The second is that our understanding of the possible and probable relationships between gene action and behavior is woefully inadequate. I think I am forced to talk about these two problems, at least briefly.

When certain creationist groups became vocal and effective in an anti-evolutionary campaign, following the appearance of the first popular high school biology textbooks treating evolution as factual, Dick Lewontin wrote an editorial in Evolution titled "The Yahoos ride again." I suspect that his concern arose partly because he knows how ridiculously easy it is to get people to reject evolution. In fact, it seems easy

to get people to reject any explanation at all about human behavior that seems to have predictive value. This paradox, I believe, has always had a place in philosophy. It is unlikely that anyone would ever suggest that a theory about any other problem would be automatically less tolerable to the extent that it is predictive. Yet I suspect that everyone in this audience has some sympathy for that view of theories about human behavior. That is why, ultimately, we are in some fashion concerned here with the old paradox of free will.

Antievolutionary implications can be very subtle things. Thus, some speakers and writers have emphasized recently that if one finds phenotypic variations without measurable heritability -- for example, behavioral differences that do not depend upon gene differences -- then natural selection by definition cannot act on those variations -- cannot cause genetic change as a result of them. Others have asserted that if one finds phenotypic variations that are heritable this implies that selection has not been acting on them -- otherwise, it is suggested, the genetic variations would have disappeared. If we accept both kinds of logic, we might not be blamed for supposing that we are left with but a single alternative: Since all phenotypic variations are either heritable or nonheritable, and since all phenotypes are by definition variable, then selection must not have acted, and selection must not be able to act, and evolution, therefore, may be dismissed as irrelevant. It's easy to be an antievolutionist.

It's easy to forget that the only real test of heritability is continual and unrelenting selection. Natural selection is differential reproduction of phenotypic variants, and it does not pause when heritability is absent; it is just not effective then. Heritable variation may be totally absent at any particular time in many traits which have undergone enormous evolutionary change in the past, and which will undergo significant evolutionary change in the future. Only on such a basis could we understand, for example, why females in polygynous species, and in which males do not invest parentally, use calories and time, and take risks, to select mates whose differences from other males are not easily shown to be heritable (e.g., the sage grouse -- [10]).

It's also easy to forget that selection is never exactly the same in different environments, and that even copies of the same allele are never in the same genetic, physiological, ecological, and social environments. So, in fact, some heritable variations may not disappear under even the most relentless selection because selection is not spatially or temporally uniform.

Finally, it is easy to forget that some nonheritable phenotypic variations are failures of developmental canalization -- hence, failures of evolutionary adaptation (for example, because of environmental change), while other nonheritable phenotypic variations are products of canalization -- hence, products of natural selection. Abilities to learn, ranges of abilities to learn, and relative eases of learning different things -- all of which lead to particular ranges of nonheritable phenotypic variations -- are, in reasonable facsimiles of natural environ-

ments, more plausibly products of natural selection than failures of it.

The curious thing is that, while a zoologist may say things like these about organisms in general and arouse no particular suspicions or animosities, for anyone thinking primarily about human behavior, and especially about social and educational programs, the questions that go racing through the mind are: "Is he implying that learning differences among humans are always genetic? Is he advocating social Darwinism? Is he justifying some kind of racism?"

I have to admit that when I first started writing and thinking about evolution and human behavior it did not occur to me that people would make such interpretations. I think that is because I saw myself as talking primarily about natural history -- about interpreting the past -- while some people evidently see all evolutionists who deal in human behavior as automatically attempting subtly and deliberately to design the future in particular, self-serving, and unpleasant ways.

One time I debated a creationist on a small town television show. And I looked into the little black tube that held the lens of the camera and I thought, "Good grief! All of those people out there have gone to Sunday School all of their lives! And many of them pronounce evolution 'eevilution'!" I have had a similar feeling, justifiably or not, when lecturing to university audiences of nonbiologists whom I knew very well had spent much of their professional lives excluding biology and genetics, as they see them, from their considerations of human behavior and culture, for reasons that they believed to be excellent.

It is all too easy to be one kind or another of antievolutionist. It is all too easy to declare that culture is not related to biology without bothering to consider seriously what that means, and what are the alternatives. I cannot resist pointing out that philosophy, in some fashion that I have never been able to understand, has managed always to remain essentially nonevolutionary in its perspective.

And so we have evolutionary biologists, justifiably fearful that the basic significance of evolution will lose rather than gain as a part of human understanding, and we have social scientists, humanists, and others, justifiably fearful that naive determinism deriving from evolutionary approaches will lead to pernicious social programs.

This brings me to the second fact that has become painfully clear as a result of the recent controversies -- namely, that most peoples' views of the possible and probable relationships between genes and behavior -- especially between genes and human behavior -- are appallingly rudimentary and inadequate. The alarming consequence is that even a very good theory about the relationship of natural selection to culture is unlikely to be appropriately interpreted on a wide basis.

Perhaps I can illustrate. Not long ago, an article published in a magazine called Science News was titled "War" [9], and under the title was printed this supposedly explanatory statement: "Anthropologists and

sociologists ask whether warfare and aggression are inherited or learned." That ridiculously oversimplified statement could have been asking: (1) Are we all genetically programmed so that war, is, in essentially any human environment, inevitable? (2) Do variations in the amount of intensity of aggression in different parts of the world reflect genetic differences among people? (3) Do we all carry genes that have contributed to our tendencies to engage in the intergroup aggression under certain circumstances? (4) Have genes contributing to aggression accumulated during the long human history?

These are all different questions. I would hypothesize no answers to the first two and yes answers to the last two. Thus, there is much evidence that aggression can be avoided and is not inevitable; and there is much evidence that differences in aggressiveness among extant humans can be taught or acquired, and essentially none that any of these differences in aggressive behavior is heritable. Even if differences in aggressiveness could be shown to be heritable, it does not necessarily follow that we could not, even quite inexpensively, create environmental differences that would erase them. On the other hand, I regard it as silly to suppose that we have no genes at least enabling us to be aggressive and to conduct wars in the usual environments of history, or to suppose that the evidence of aggression across our history says nothing about selective genetic change. We have evolved a capacity for culture, and it seems to me parsimonious to suppose that a part of that evolved capacity is a capacity for the expression of aggressiveness in particular circumstances.

I regard it as naive to suppose that if modern variations in culture are not genetically heritable then genetic change and culture have not been related during the long human history. I regard it as naive to suppose that the capacity for culture appeared suddenly and full-blown, at some time in history, and that all subsequent cultural change was independent of changes in the capacity for culture via natural selection. I regard it as naive to assume that how the evolving capacity for culture has been used during its evolution has not influenced the survival and reproduction of those evolving the capacity.

I hypothesize that the vast bulk of cultural variations among peoples alive today will eventually be shown to have virtually nothing to do with their genetic differences. I also hypothesize that changes in capacity for culture have nevertheless occurred throughout essentially all of human history, as a result of genetic evolution, and now involve very significant proportions of the human genotype. These two hypotheses are not incompatible. One reason is that scarcely any heritability needs to be associated with cultural variations at any given time for cultural variations to have guided genetic evolution of cultural capacity all through human history, and the other reason is that at any given time there may be as much or more heritability of differences within any culture as between any two.

I also hypothesize that much of our social behavior today -- and more than ever before in our history -- represents not evolved canalizations but breakdowns in evolved canalization because of massive novelty in

our technological and social environments. And I suggest that there is no reason to be unhappy about such an interpretation and much reason to be happy about it, for it is evidence of our ability to escape our history. The more we understand our history, the better, I would suppose, that we will be able to escape whatever aspects of it we do not like. Humans are alone among organisms in being able to cancel -- literally to cancel -- any behavioral traits identified to them as typically or uniquely human, which they then decide that they do not like.

1. Inclusive Fitness: The Concept

Now let us turn directly to the particular refinement of evolutionary theory that is responsible for this symposium. It is William D. Hamilton's [5] hypothesis that, in the environments of their selective pasts, individual organisms behave so as to maximize their inclusive genetic fitnesses. The question I will address is whether or not, and how, we can use this idea to further our understanding of ourselves.

Inclusive fitness is a simple idea. It can be explained by reference to a diagram of genetic relatives (Figure 1, p.8) and the nomenclature commonly applied to them within our own society. As humans, we are sexual and social organisms. As sexual organisms we are able to reproduce only by helping others; we do not fission and produce potentially immortal daughter cells. As social organisms we tend to lead our lives imbedded in networks of near and distant kin. The concept of inclusive fitness simply tells us that not merely our offspring but any genetic relative socially available to us is a potential avenue of genetic reproduction.

The figure shows the genetic relationships between Ego and his or her various relatives. Arrows indicate my view of likely net flows of nepotistic benefits. Half the genes of parent and offspring are identical by immediate descent. Other relationships are averages. Dashed lines indicate closest relatives other than Ego, thus the most likely source of nepotistic benefits. Widths of arrows indicate my predictions about the relative flows of benefits to or from Ego, assuming these to be based on the combination of genetic relatedness and ability of recipients to use benefits in reproduction.

Inclusive fitness, then, implies that sexual, social organisms evolve to be altruists, but altruists of a very special sort, whose benefit-giving is, in the environments of their selective pasts, directly or indirectly aimed at genetic relatives. According to this theory, we should have evolved to be exceedingly clever nepotists, and we should have evolved to be nothing else at all.

This means that to test the idea that the maximizing of genetic fitness by individuals has been a central theme in the history of human behavior, we have to consider not only parent-offspring interactions, but how we tend or have tended to distribute social benefits among all the various genetic relatives whom we identify and interact with.

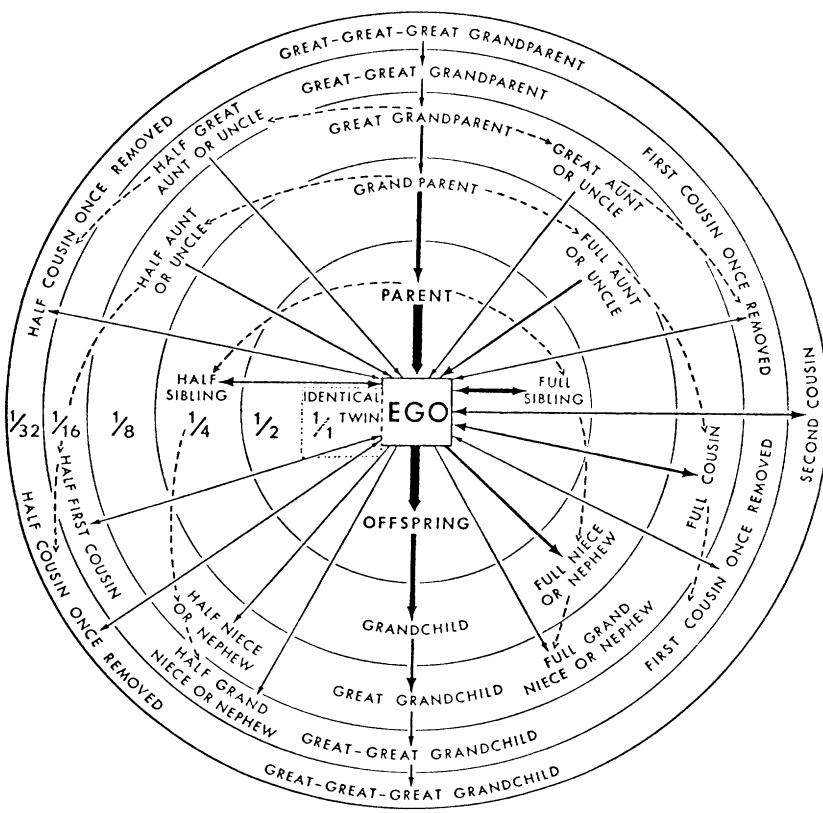


Figure 1

Whether or not human social behavior fits an inclusive fitness model is our first real question, and the only one I have seriously considered up to now in my own thinking on this whole topic. In other words, I have proceeded in my considerations of human behavior just as any evolutionary biologist would in starting to analyze any nonhuman species. In general, evolutionary biologists proceed as follows: They first identify phenotypic traits in organisms and then study the adaptive or reproductive significance of those traits, almost as if the traits had no ontogenies -- as if there were no proximate physiological or developmental mechanisms on which they depend. Evolutionists postpone the analysis of ontogenies because their initial interest is only in how the trait is expressed in the usual environment of the species, which is what determines its evolutionary adaptiveness.

The justification for this approach is that it parallels the way in which natural selection works. It does not matter, in selection, how a trait comes to be expressed -- only that it is expressed in the optimal way and at the optimal time and place. The reasons ontogenies vary for different organisms and different traits are simply that, first, different kinds of ontogenies deliver particular phenotypic responses more or less reliably, and, second, natural selection always begins with last year's model, and the previous lines of specialization may have caused different routes of further specialization to be more or less likely.

The evolutionary approach of deferring the scrutiny of ontogenies is perfectly all right for nonhuman organisms. Suppose that I make a few predictions from an inclusive fitness model about how a group of frogs will behave in a pond. And I test the predictions and discover, sure enough, that the frogs' interactions meet them. The people I tell about this analysis may accept my arguments, reject them, or draw no conclusions. All of those people, however, will probably work up some kind of mental image of what my arguments about the frogs' behavior mean with regard to the ontogenetic background of the behavior. The chances are very good that, whether they accept my arguments or not, their views of how the frogs' genes influence their behavior will be oversimplified.

After all, the idea that behavior is determined by the genes is simpler than the idea that behavior is determined by the environment, or by the genes and the environment. To say that behavior is determined by the environment, or by the genes and the environment, doesn't say much of anything, because the next question is: How? To say that behavior is determined by the genes seems to settle everything.

So what if everyone oversimplifies the ontogenetic basis of frog behavior? It matters, but it's not crucial. After all, no one thinks up social and educational programs for frogs.

But they do for humans. And what they think up depends upon what they think about the genetic, ontogenetic, and physiological backgrounds of human behavior.

I am embarrassed to say that this was a startling revelation to this evolutionary biologist, and it came only on the heels of what I saw as repeated misinterpretations of my discussions of human behavior in an evolutionary context. Again, I had always regarded Darwinism as essentially a way of interpreting history, rather than as a basis for ideology. But if everyone misinterprets its application to human affairs, then it unavoidably becomes ideological in its effect even if not in the purpose of its practitioners. If one sees himself as an anti-determinist, then it is very easy to be an unreasonable anti-evolutionist; if one sees himself as an evolutionist then it is very easy to be an unreasonable determinist.

Some individuals seem to be telling us that the proper way out of the dilemma is to stop analyzing human behavior in evolutionary terms until we have solved the ontogenetic problems. I emphatically disagree, for at least two reasons: First, everything we know about evolution we have learned without fully understanding the ontogenetic basis of any behavior in any organism; and, second, the ways to analyze ontogenies fruitfully all too often become clear only as a result of evolutionary approaches. Ontogenies, after all, are also products of natural selection.

The alternative solution is to devise hypotheses about ontogenetic mechanisms which, even if incomplete and imperfect, will be testable starting points, and will demonstrate, if possible, that to apply Darwinian models to human behavior does not automatically require an intolerable determinism.

So the second big question is: What are the necessary and sufficient proximate mechanisms, or immediate causes, that could account for human behavior conforming to an inclusive fitness model? What is the simplest, most parsimonious kind of gene action that could account for individual humans behaving socially in such fashions as to maximize their inclusive fitnesses?

I'm going to consider this question first because I have found that unless people have an ontogenetic or physiological mechanism in their minds that is satisfactory to them personally they will reject out of hand whatever is being said about the structure of culture or the behavior of individuals. And, when you think about it, why shouldn't they? I can find no justifiable reason why any of us ought to accept a degree of determinism in human behavior which does not make sense when applied to our own behavior. I have never thought that a distasteful determinism is a necessary or even likely concomitant of a Darwinist theory about human behavior. If the actual behaviors of people seem to evolutionary biologists to fall into place when viewed in an evolutionary context, so that evolutionists are inclined to say "Of course!" so ought the actual mechanisms of those behaviors be familiar when considered by, say, learning psychologists, so that they too, when we have finally gotten together, should be saying, "Of course!"

2. Inclusive Fitness: Proximate Mechanisms

Accordingly, I will try to describe some very rudimentary aspects of a set of hypothetical proximate mechanisms of human sociality which neither is inconsistent with inclusive fitness theory nor, I hope, will offend the anti-deterministic sensibilities of most. I do not feel particularly competent at this task, but I have concluded that if we are to get on with things, it must be undertaken now. It's exactly the same feeling that I have about evolutionary approaches to human behavior in the late 1960's when I realized that all we had then were Konrad Lorenz, Robert Ardrey, and Desmond Morris, and that people were thinking that their views reflect those of the evolutionary biologists.

I begin by asking you to consider the investments parents make in their offspring. Parental investment is universal among sexual organisms, and parental behavior or parental care, as a form of parental investment, is either universal or nearly so among organisms that are social in any usual sense of the word.

Few will disagree with my assumption that in most social organisms the altruism that is called parental care is adjusted and refined by natural selection so as to maximize the genetic fitness of the individual parents involved through their offspring. This idea dates from Darwin, who noted that to increase its rate of offspring production, a parent would have to reduce the amount invested in each individual offspring. This view has never, to my knowledge, been seriously challenged, and I believe that a number of recent tests of either sex ratio theory or reproductive effort alone could be applied generally so as to demonstrate its reasonableness.

The argument goes like this: Fisher [4] suggested, and others have since shown, that a parent maximizing its inclusive fitness via offspring would invest equally in the two sexes when siblings do not devalue themselves by competing for mates. Hamilton [6] showed that parents would increase their investment in females when sons compete for matings. The widespread existence of approximately 1:1 sex ratios, together with female-biased investments in cases where siblings are known or suspected to compete for mates [6], is strong confirmation that selection leads to individual, not group, reproductive maximization, and that this effect is achieved through parental investment patterns. Some recent unpublished work (David Cowan, personal communication) indicates that females in some cases adjust their investments in the two sexes to meet both situations; and I regard these studies collectively as tending to confirm all of the hypotheses involved here.

Here I ask only that you accept this view of parental investment as that of an evolutionist so that we can see how much and what kind of developmental determinism it requires.

According to an inclusive fitness model, the selective refinement of parental altruism should operate as if in response to three hypothetical cost-benefit questions:

1. What is the genetic relationship of the putative offspring to its parents (Is this juvenile really my own offspring?)?
2. What is the need of the offspring (More properly, what is its ability to translate parental assistance into reproduction?)?
3. What alternative uses of its altruistic assistance are available to the parent?

These are the same questions that apply to the analysis of all nepotism. The one that is initially crucial is that of genetic relatedness. We need to ask, then, how genetic relatedness might be accurately assessed among organisms in general.

First, except for one of the two parents -- usually but not always the mother -- evidence of genetic relationship is always circumstantial. Some female mammals can observe their babies being born and keep them in direct contact until unmistakable recognition has been established. Male seahorses which take unfertilized eggs more or less directly from the female, place them in a brood pouch, and fertilize them there, are in a similar position. But all other assessments of genetic relationship, and thus all behavior appropriate to them, are necessarily based on circumstantial evidence. In other words, particular social interactions predict particular genealogical relationships. I may, with some accuracy, assume as my siblings those individuals who are cared for by the same adult female and male; a caterpillar may assume as its siblings whoever hatches next to it at about the same time. I assume as my offspring those juveniles accepted as such by the woman with whom I live. Error is obviously possible in all of these cases.

I emphasize that it is not necessary, in inclusive-fitness-maximizing, to know who one's kin are, only to behave as though one knows.

One might suppose that kin selection could be, or even has to be, based on the appearance of mutant genes which enable their bearers to recognize their own effects in other individuals. Such a gene would have to, first, have an effect on the phenotype; second, cause its bearer to be able to recognize the effect in others; and, third, also cause its bearer to take the appropriate social action. Not only are these requirements of gene action unreasonably complex, but any such mutant would act on the basis of its own presence in the genome of the potential recipient of its bearer's altruism, independent of the probability of the presence of other genes in its genome which also contribute to its bearer's altruism. Thus, it would necessarily act against the interests of all the other genes in its own genome; and the extraordinary organization of the genome, which, for example, is responsible for the ability of some phenotypes to carry out the peculiar activity called philosophizing, could not be sustained if such genes became prevalent. Any gene mutating so as to suppress such an "outlaw" effect would thereby help itself, and in any large genome the mutational probabilities of suppression, as opposed to the probability of sustaining outlawry, would be enormously high [3].

Heritable variation in phenotypic traits may be used in some species to assess the likelihood that a particular individual is or is not a particular relative. On occasion they are so used in our own species. I once had a neighbor who rejected his wife's offspring as his own because of its striking resemblance to his hired man, and he was able eventually to secure acknowledgment from the other parties involved.

Parents, in ordinary sexual species, are truly 50% like their actual offspring, if we ignore the slight asymmetries caused by the sex chromosomes. But, as I noted earlier, the genetic similarities among other relatives, because of the uncertainties introduced by meiosis, are only averages. Full siblings only average 50% alike, and any particular pair of full siblings is likely actually to share either more or fewer than half their genes.

One might suppose, therefore, that the same kind of phenotypic judgments used to assess whether or not an individual is one's own offspring could also be used to judge the actual proportion of overlap with individual relatives such as full siblings. Not so. Any gene which contributed to a tendency to assess the actual amount of genetic overlap between its bearer and a full sibling would extinguish itself unless it used only its own expressions to make the assessment. Genes with such ability, however, would again not only be extraordinarily complex in their action, but would tend to break up the genome, putting the lie to Dick Lewontin's [8] assertion that "The primary focus of evolution by natural selection is the individual," which I believe is correct.

I have been making what must seem to you a very parochial and genetic argument. It is a necessary argument, however, if we expect to test human behavior against an inclusive fitness or kin selection model without oversimplifying its ontogenetic basis and without, as a result, assuming an unlikely and therefore unwarranted genetic determinism.

If nepotism depends upon circumstantial evidence of relatedness, then inclusive fitness becomes a meaningful concept in evolution only to the extent that social interactions permit accurate assessment of genetic relationships. The interesting consequence is that the essential ontogenetic basis of appropriate patterns of nepotism in any species need be no more complex or deterministic than learning through ordinary positive and negative reinforcement schedules. In other words, I am pointing out that whatever it is that enables us to construct a diagram of this sort, whatever it is that makes the labels on Figure 1 (p.8) familiar to all of us, whatever it is that enables you and me to put ourselves in the role of Ego and then fill in the diagram with actual names of actual people -- whatever that learning process has been in each of us -- it is entirely adequate to account for any ability by you and me, or anyone else, to behave so as to maximize our inclusive genetic fitnesses. Indeed, it is the only proximate, genetic, physiological, ontogenetic series of events that is even an appropriate candidate. That is why I am so confident that there is no intolerable determinism in an inclusive-fitness-maximizing model of human behavior.

All that remains to complete a set of assumptions about proximate mechanisms that will allow the predictions of our evolutionary model to be met is to establish that the usual context of distinguishing relatives is favoritism, based on relatedness, need, and alternatives. If it turns out that we have indeed tended to treat our closer relatives better, and to help our dependent relatives more, than a Darwinian model, an inclusive fitness model, a kin selection model -- in other words, a blatantly evolutionary model -- for the history of human sociality is an appropriate one.

Should our social history conform to Darwinian predictions, then, nothing more deterministic is required than regular and predictable differences in our learning experiences with different relatives, which lead to regular and predictable differences in our treatment of them. What would have evolved, then, would be our tendencies to behave exactly as learning psychologists already know we do under what they call negative and positive reinforcement schedules -- or, more precisely, our tendencies to react as we do to the particular learning schedules which are then labelled as positive and negative because of our reactions to them.

The least demanding kind of relationship between gene effects and social behavior that I have been able to imagine, which might lead to the regularity this hypothesis requires, is the accumulation of genes causing us to be positively reinforced according to the number and intensity of physiologically or socially "pleasant" interactions with any particular individual. In small clans of genetic relatives that effect alone could cause us to favor closer relatives; and no anthropologist would dispute that humans have, during nearly all of their history, lived in small clans of genetic relatives. The effects I am suggesting would have to be modified and qualified by many other kinds of learning in different circumstances to explain a great deal of sociality. For instance, an utterly and continuously dependent juvenile might gain by being positively reinforced by almost any kind of repeated interactions with an adult -- even unpleasant, traumatic ones -- and I believe there is good evidence that juveniles are so reinforced. On the other hand, some degree of generality is implied. For example, parental teaching about who our relatives are becomes a subset of this hypothesis.

When I initially had this rather simple idea about learning to be appropriately nepotistic, I immediately tried to think of exceptions: When do we treat with extreme altruism individuals with whom we have not had long histories of positive social interaction? It seemed to me that such events should be unusually dramatic if genes with the effects I have described have accumulated, for in such cases the postulated gene effects would in some sense have to be overridden. I thought of several cases, such as newborn babies, and strangers tossed together in disasters and wholly dependent upon one another for survival; each of these deserves analysis. But the example that stuck in my mind is the event that we call "falling in love." Humans, apparently everywhere, tend to select as mates individuals with whom they have had relatively few social interactions, or, in some cases who are even poorly known, and

at least in our own society we draw them rapidly from strangeness to ultimate intimacy and make them long-term or life-term partners, usually in what might be referred to as the dearest of all biological enterprises. There is much evidence in music, art, and literature that few events are more dramatic in human sociality than falling in love -- falling, it seems to me, across the chasm from social strangeness to social intimacy. I regard this phenomenon as at least potentially supportive of the existence and importance of the kinds of gene effects I have postulated.

Patterns of nepotism dependent upon learned associations in the manner I have just described are fragile things in a changing society. Mixing relatives and nonrelatives can, on a wide scale, create confusingly diverse kinds of friendships between nonrelatives which historically would represent nepotistic interactions. Appropriately nepotistic patterns would be most fragile of all in a society of individuals with a general awareness of the historical and proximate backgrounds of social altruism. Thus, contrary to the view of both determinists and anti-determinists, a history of evolved nepotism does not restrict a modern human being from choosing his own friends and his own charities -- in other words, from behaving socially as he or she personally sees fit. And the reason is that inclusive fitness can only be maximized in human social groups through learning experiences that in our sophisticated world are easily redirected.

3. Inclusive Fitness: Do Humans Maximize It?

Now let us turn to the question whether individual humans really do behave so as to maximize their individual inclusive fitnesses. I have found it difficult to think how to test this question. One approach is to make as many predictions as possible and then test them one by one. This is not very satisfying, since the so-called predictions often turn out to be already established facts. Thus, one might "predict" that relatives by marriage will reveal interests quite different from those of their spouses, in regard to how well the spouse should treat its relatives or be treated by them: The spouse will be interested in the welfare of its relatives, and thus somewhat less selfish and greedy. But we already have too many jokes about free-loading in-laws for this kind of reasoning to be very powerful. Only a very large number of such "predictions," with a very high rate of success, would be very meaningful.

It is also difficult to measure nepotism, except perhaps in last wills and testaments. One wishes to deal principally, at least at first, with preindustrial societies, in which the social environment is likely closer to those typical of most of human history. I found myself turning to the formal analyses by anthropologists of so-called "kinship" systems (which are really systems of social reciprocity and marriage as well as patterns of interaction between genetic relatives [2]). The nomenclature of these systems gives at least a glimpse of social pattern; the analyses already carried out are inevitably nonevolutionary or even antievolutionary, removing one source of bias; and their formality tends to give

the possibility of clearcut comparisons.

If we return to the network-of-kin diagram and consider nomenclature for a moment, it is evident that not every possible distinction among kin has been made there. Thus, maternal and paternal aunts and uncles are not distinguished (although in this society we do sometimes make such distinctions). Nor are the various kinds of cousins: For example, mother's brother's daughter is not distinguished from mother's sister's daughter, father's sister's daughter, or father's brother's daughter. In many cases the sexes are not distinguished by the terms given here. This aspect of kinship systems is commonly referred to as "classificatory" because relatives derived through obviously different routes are classified together, and such "classification" has been used to deny a biological significance for kinship systems. Some classificatory aspects of kinship systems, however, clearly do not conflict with predictions from inclusive fitness. The diagram indicates, for example, that there are tendencies to lump together relatives of the same degree, the same dependency relationships, and the same sex, and to distinguish those that differ in these regards.

Some rather formal classificatory aspects of kinship systems, on the other hand, clearly do not seem to accord with Darwinian predictions. Several years ago I deliberately chose what seemed to me to be the two outstanding apparent exceptions, those which had most frequently been used to deny the biological significance of kinship systems. I decided that unless I could explain these two cases I could not proceed. These two phenomena were, first, the one called "mother's brother" and, second, the distinctive treatment of parallel and cross cousins, especially in regard to marriageability. I have discussed these two phenomena elsewhere, at different stages in their analysis [1,2]. Here I want to quickly summarize my conclusions about them and then relate the results, if possible, to my hypothesis about proximate mechanisms of inclusive-fitness-maximizing.

First, mother's brother: In many societies, paternal benefits are dispensed, and paternal responsibilities are assumed, not so much by one's putative father, mother's spouse, as by a particular uncle, the mother's brother; or mother's brother is at least an important dispenser of such benefits. This relationship is often a general feature of society. It has always puzzled students of culture although various explanations have been offered. A close examination of the situation reveals a curious fact: Lowered confidence of paternity leads to asymmetry in the genetic relatedness of putative nephews and nieces.

The offspring of a man's full sister are $1/4$ like him in genes identical by descent; those of his half sister are $1/8$ like him. Only by a remote accident of meiosis or an almost equally remote mistake in maternity can the offspring of a man's sister be totally unlike him. His spouse's offspring, on the other hand, are either one-half like him or totally unlike him. As a man's confidence of paternity diminishes, therefore, his sister's offspring become more important to his reproduction compared to his spouse's offspring. Similarly, the brother of a

woman whose husband has a low confidence of paternity becomes a more appropriate candidate for paternal benefits to her offspring which may otherwise suffer from a lack of paternal assistance.

If low confidence of paternity is general throughout a society, a man's sister's offspring, because of her high confidence of maternity, can become his closest relative in the next generation. Thus, if paternity is on average correctly ascertained only 1/4 of the time, then a man's spouse's offspring will average 1/8 like him (and 3 of 4 will be totally unlike him), while his sister's offspring will average 5/32 like him, and all will approach this degree of overlap. Moreover, if men accept certain of their spouse's offspring and reject others, mother's brother can become important when confidence of paternity is much higher.

The effects of society-wide lowering of confidence of paternity are different for a man's brother's offspring for his brother will suffer equally from lowered confidence of paternity, and for a woman's siblings' offspring, since women will retain high confidence of maternity and will always be more closely related to their own offspring.

To summarize, whenever general living conditions or other society-wide circumstances lead to a general lowering of confidence of paternity a man's sister's offspring, alone among all possible nephews and nieces, can become his closest relatives in the next generation. In consequence, so long as adult brothers and sisters tend to remain in sufficient social proximity that men are capable of assisting their sister's offspring, a general society-wide lowering of confidence of paternity is predicted on grounds of kin selection to lead to a society-wide prominence, or institutionalization, of mother's brother as an appropriate male dispenser of parental benefits.

This appears to be exactly what happens. The evidence indicates that lowered confidence of paternity, fragility of marriage bonds, matrilineality, and shifts toward a prominence of mother's brother go together, in a pattern almost dramatically consistent with a Darwinian model of human sociality [2].

Now let us consider the asymmetrical treatment of cousins.

Cousins are the offspring of siblings. Offspring of full siblings, which share both parents, share on average 1/8 of their genes; offspring of half-siblings share 1/16 of their genes.

Cousins are sometimes divided into two kinds, offspring of siblings of the same sex, called parallel-cousins, and offspring of siblings of different sexes, called cross-cousins. In technological societies derived from Europe (such as our own) -- in other words, those which have a socially-imposed monogamy -- cousins are usually not subdivided in this fashion; so, in such societies, these terms are novel for most persons other than anthropologists. But cousins are so divided in many other societies, and in many different parts of the world.

In general, close relatives are not only predicted (from kin selection) to be more likely objects of nepotism, but they are in fact less likely to be objects of sexual behavior than are more distant relatives. In the case of cousins there is a general correlation between the distinguishing of cross- and parallel-cousins, the assigning of asymmetrical nomenclature, and their differential treatment, at least in regard to marriage. In many societies which distinguish cross- and parallel-cousins, parallel-cousins are termed siblings rather than cousins, and marriages between them, but not between cross-cousins, are either forbidden or discouraged. Although nepotistic behavior has not been as easy to quantify as marriage behavior, the nomenclatural asymmetry also implies that parallel-cousins may favor one another in nepotism over cross-cousins.

Since the genetic relatedness between cousins is 1/8 whether they are parallel- or cross-cousins, why should they be treated differently?

As was first pointed out by the anthropologist Marvin Harris [7], the symmetry of relationships of putative cross- and parallel-cousins holds true only when assessment of relationships has a symmetrical likelihood of error. Such symmetry evidently prevails in monogamous societies in which families tend to live apart, but in polygynous societies both kinds of putative parallel-cousins may have a significant likelihood of being half-siblings instead. Thus, polygynous men often marry women who are sisters to one another. Also, because sex ratio selection is not influenced by the breeding system, male sexual competition is enhanced under polygyny. When the sex ratio is 1:1, if some men have harems, others have no wives. One correlate is that powerful men sometimes secure extra wives and pass them to younger less powerful men still unable to obtain and hold wives on their own. Both situations would lead to putative parallel-cousins being more likely to be half-siblings than putative cross-cousins. In polygynous societies, then, what seem to be parallel-cousins may actually be half-siblings, and in many societies they are called "siblings."

I have shown [2] that asymmetrical treatment of cousins is very strongly concentrated in precisely the kinds of polygynous societies in which it is predicted to occur from an inclusive fitness model, and least frequent in the kind of monogamous society where that is expected.

When I analyzed mother's brother and asymmetrical treatment of cousins I was behaving like a true evolutionary zoologist and merely testing to see if these behaviors could reasonably be interpreted as adaptive, in an evolutionary sense, rather than the opposite, as had been argued up to that time.

After I had struggled reluctantly with my speculations about proximate mechanisms, I realized that if they had any validity I should be able to go back and easily explain cultural variations like those involving mother's brother and asymmetrical treatment of cousins.

Frankly, I did not expect any light to be shed by this procedure, and

I was ready to console myself with the realization that I never had wanted to speculate about proximate mechanisms anyway.

To my surprise, I was not as badly off as I at first expected to be. In regard to mother's brother, there is little doubt that fathers in the relevant societies have fewer and less satisfactory social interactions with both their wives and their wives' offspring than in other societies where mother's brother is not prominent. Men are thus in a position to learn not only to behave toward spouse's offspring as if they are unlikely to be their own true offspring, but also to behave as though realizing, even if not actually realizing, that sister's offspring not only represent a reasonable alternative investment, but also are in need because of their mother's spouse's failure to care for them. The simple kind of learning I had postulated thus could work very well in the case of mother's brother. In other words, the cultural change represented by mother's brother becoming prominent in some societies could have resulted from the changes in learning situations provided in the two societies, leading to different circumstances that in each case result in individual-fitness-maximizing by the parties involved in the changes.

Cousin treatment is equally interesting in this regard. For the reasons I have already given, intimate social interactions between an individual and spouse's same-sex sibling or same-sex sibling's spouse are more likely in polygynous than in monogamous societies. Even within polygynous societies they are more likely in certain kinds of living arrangements than in others, a realization I have not yet been able to follow up. Asymmetrical social interactions and greater likelihood of philandering or shifting of spouses between same-sex siblings are both more likely in the societies in which cousin treatment is most asymmetrical, and the social asymmetry is in the appropriate direction relative to the asymmetrical treatment of cousins. The philandering would lead to asymmetry in genetic relationships, and the social intimacy correlated with it would lead, through the kinds of learning differences I postulated earlier, to a corresponding asymmetry in nepotistic favoritism and its well-established corollary in avoidance in marriage.

These circumstances follow almost too beautifully from the simple kinds of reinforcement or learning schedules that I have here postulated to lie behind the operation of inclusive-fitness-maximizing. I think we can be certain that the actual relationships are much more complicated. Nevertheless, this line of reasoning may open the way to understanding how cultural change can occur without genetic change, while nonetheless maintaining a structure consistent with the maximizing of their inclusive fitnesses by the individuals comprising the societies. This may be the first time a proximate mechanism with this effect, other than genetic change, has been postulated. The possibility of this kind of mechanism dilutes the contention that evolutionary approaches to human behavior are vulnerable because they cannot specify how reproductive maximization can be approached through cultural change. It removes any necessity of an intolerable determinism. It relieves the necessity of supposing that the evolution of culture and the evolution of genes must somehow be examined independently. The nature of the mechanism, moreover, blunts the criti-

cism that the evolution of merely a capacity for culture makes the relationship between natural selection and the structure and variations of culture a triviality.

To summarize: All that I have said today is that tests of a Darwinian model of human sociality are feasible; they are being attempted with increasing frequency; they have some reasonable likelihood of appropriateness; they require neither an unreasonable determinism nor pernicious plans for the future; and proximate mechanisms to account for them are not beyond reason. I think there is ample excuse to continue with the kind of approach I have described, and no reason for emotional efforts to block such studies, or to regard them as evil or ill-conceived.

Everyone knows that once in a while the baby is thrown out with the bath water. In the controversies about evolution and human behavior the bath water is the label Sociobiology. The bath water is erroneous, careless, ignorant, or asinine remarks by determinists or anti-determinists. Everything that I have said today may turn out to be bath water when we know better what we are about.

The baby is the real relationship of organic evolution to human social behavior -- the real relationship between genes and culture. There is a baby. We have managed to throw it out before. Maybe, one of these times, we will recognize it well enough to save it and bring it up properly.

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