

NATURAL SELECTION AND THE ANALYSIS OF HUMAN SOCIALITY

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INTRODUCTION

“In most primitive societies the social relations of individuals are very largely regulated on the basis of kinship. This is brought about by the formation of fixed and more or less definite patterns of behaviour for each of the recognized kinds of relationship. There is a special pattern of behaviour, for example, for a son towards his father, and another for a younger brother towards his elder brother. The particular patterns vary from one society to another; but there are certain fundamental principles or tendencies which appear in all societies, or in all those of certain type. It is these general tendencies that it is the special task of social anthropology to discover and explain.” (A. R. Radcliffe-Brown, 1924).

“No worse affront can be hurled in the teeth of a Kurnai Australian than to call him an orphan; and the same is true of the Crow Indian in Montana. That so harmless a term should be resented as the most offensive imprecation seems strange, but there is an explanation for it. Among the ruder peoples [sic] influence is often directly dependent upon the greater or lesser number of faithful relatives. The kinless orphan is consequently damned to social impotence and considering aboriginal vanity [sic] it is natural that the vocabulary of vituperation should contain no more degrading epithet. It is therefore not only certain that neither the Kurnai borrowed from the Crow nor vice versa, but the reason for the observed parallel is clear from known facts of primitive [sic] life.” (Robert Lowie, 1920).¹

“Around every person there is a circle or group of kindred of which such person is the centre, the Ego, from whom the degree of the relationship is reckoned, and to whom the relationship itself returns. Above him are his father and his mother and their as-

¹ The term “bastard,” which only orphans us on the father’s side of the family, has parallel implications in our own not-so-primitive society.

endants, below him are his children and their descendants; while upon either side are his brothers and sisters and their descendants, and the brothers and sisters of his father and of his mother and their descendants as well as a much greater number of collateral relatives descended from common ancestors still more remote. To him they are nearer in degree than other individuals of the nation at large. A formal arrangement of the more immediate blood kindred into lines of descent, with the adoption of some method to distinguish one relative from another, and to express the value of the relationship, would be one of the earliest acts of human intelligence." (Lewis Henry Morgan, 1870).

To a modern evolutionary biologist these statements might suggest that 50 or 100 years ago the young science of anthropology was on the verge of adopting the principle of kin selection to explain at least part of human sociality. Instead, almost the opposite happened. Thus, only fifteen years ago, the social anthropologist, David Schneider, wrote, ". . . my conviction is that biological relatedness, used as an analytic category in terms of which kinship systems may be compared and analyzed, has been as much of an impediment as a useful tool in understanding kinship in general." (Schneider and Gough, 1974, p. 2.) Perhaps Schneider's statement is not entirely typical, but anyone interested in this general topic has heard over and over some version of the declaration that human kinship systems (or patterns of culture, or of human sociality) are not to be explained by reference to biological phenomena or backgrounds.

Schneider's statement and the declarations to which I refer above are similar for another reason. They are essentially negative, telling us a way in which human sociality is not to be explained. The current spate of arguments against an evolutionary approach to human behavior, from both scientific and political directions, is similarly for the most part negative, telling us much more forcefully what we cannot do than what we can. Even the suggestion that culture is independent of biology is essentially negative, in terms of analysis.

What is indicated, I suggest, is the perplexity and even, perhaps, despair of the successions of scientists who have sought simplifying principles or generalizations by which to understand human sociality. At no time was this essential despair more evident to me than when an anthropologist recently remarked, without additional comment, that "The effort to explain culture in utilitarian terms was abandoned long ago."

Whenever the concept of "utility" undergoes a significant alteration, as it has during the past decade owing to refinements of our views of Darwinian selection, then it seems to me that we are obliged to try again to identify functions in culture. This is particularly true in the absence of alternative generalizations, and I submit that one can search in vain throughout the literature of the social sciences for theories that, individually or collectively, are satisfyingly general or potentially all-encompassing. The two possibilities that stand out are learning theory in psychology and a rather diffuse implication of group benefit in cultural anthropology. But learning theory, as presently constituted, is concerned with physiological and ontogenetic mechanisms and sequences, and carries no probability of accounting for the presence and nature of such mechanisms, or even for different mechanisms in different kinds of organisms; hence, the tendency, perhaps, of learning theory to revert to singularity and, paradoxically, to seem more general than it is. On the other hand, the unresolved notion of group benefit in culture is in large degree directly contrary to the Darwinian model of behavior that has been developing recently.

It seems to follow from these apparent theoretical inadequacies in the study of human sociality and history that we are required to take seriously all reasonable propositions for filling the gap. Darwinian selection is at the moment the most promising and well-defined model. Indeed, it may be the only such model.

It may not be unfair to suggest that a point has been reached from which almost any simplifying generalization or theory about human sociality is likely to be viewed, automatically, as an oversimplification. There is little reason to be surprised if this is true. For no more complex task can be imagined than that of an organism, complex enough to analyze itself, undertaking the analysis by means of the very attributes to be analyzed, when one of those attributes is a resistance to all such analyses. The task becomes an endless succession of ever more frustrating introversions, except as one restricts his attention to the history of sociality among humans largely unaware of the systems of analysis and interpretation now being employed. There are other reasons for such restriction, since attempts to deal simultaneously with the past, present, and future lead us into problems of ethics, morality, and justice, a step which can quickly lead to pernicious and self-serving interpretations based on incomplete information and deliberate or unconscious distortions. One of the most difficult and confusing aspects of efforts to analyze human sociality is that the analysts, and all those who must

evaluate and use the analyses, are prejudiced and interested participants in the system.

Perhaps if evolutionary biology had been primed and ready to offer to the anthropologists the conceptual tools it has available today, when their science was still young and receptive, the history of the social sciences would have been somewhat different. The sad fact is that biology was not ready to provide the tools needed when the students of human behavior formally began their task. One consequence is that now the evolutionary biologist who believes he has found a useful analytical tool must be a much more effective salesman. None of the social sciences is any longer a receptive infant or adolescent. The modern evolutionary biologist who wishes to communicate with his social science colleagues must be prepared not only to explain the logic of his approach but to defend his motivations, and to explain why the rejection of some form of his approach decades ago was inadequate; and he must be prepared to justify his approach by explaining how to prevent it from being misused.

Evolutionary biology does have some apparently new conceptual tools. They have not yet been applied on any large scale to analyses of human social history; their nature is still so sketchily understood as to lead to bitter controversies; and they are different enough, as a set, from any used previously to require a whole new test of their value. I will review the history and nature of these conceptual tools briefly, and then try to apply them, tentatively and rudimentarily, to the problems described and suggested by the anthropologists quoted above.

I describe the conceptual tools of modern evolutionary biology as only "apparently" new, because each traces quite clearly either to Darwin, contemporary with Morgan, or to R. A. Fisher, whose critical book, *The Genetical Theory of Natural Selection*, was first published five years after Radcliffe-Brown's descriptions of the task of social anthropology. What has happened in evolutionary biology during the past decade is, to some large extent, a rediscovery of Fisher and an updating of Darwinism. I believe that the extent and nature of this updating deserves a brief review here.

THE STRUCTURE OF EVOLUTIONARY THEORY

Darwinian theory is simple to state, difficult to apply, and astonishing to contemplate. The evolutionary process from which it stems derives from the interaction of five basic phenomena:

1. *Inheritance*: All living organisms (phenotypes) are products of the interaction of their genetic materials (genotypes) with their develop-

mental (ontogenetic) environments; these genetic materials can be passed from generation to generation unchanged.

2. *Mutation*: The genetic materials do change occasionally, and these changes are in turn heritable.

3. *Selection*: All genetic lines do not reproduce equally, and the causes of this variation may be consistent for long periods.

4. *Drift*: Genetic materials are sometimes lost through accidents, which are random or non-repetitive in their effects on populations.

5. *Isolation*: Not all genetic lines are able, for various intrinsic and extrinsic reasons, to interbreed freely, and thus to continually re-amalgamate their differences.

These five phenomena have all been demonstrated repeatedly, and they can be demonstrated at will, as can various of their interactions. No living things have been demonstrated to lack any of them, or are suspected to lack any of them. Hence, they may be described as the factual basis of evolution.

The theory of evolution is the proposition that the interactions of these five phenomena, in the successions of environments in which organisms have lived, account for the traits and history of all forms of life. The difficult problem we face here is how to translate this simple proposition so as to apply it, if possible, toward a better understanding of human sociality.

Of the five main components of the evolutionary process, natural selection, or the differential reproduction of genetic variants, is almost universally accepted as the principal guiding force. The reasons for this assumption are: first, that altering directions of selection apparently always alters directions of change in organisms; second, that the causes of mutation and the causes of selection appear to be independent; and, third, that only the causes of selection remain consistently directional for long periods.

Mutations are caused, at least chiefly in the past, by atmospheric radiation. Selection is caused by what Darwin termed the "Hostile Forces of Nature": climate, weather, food shortages, predators, parasites, and diseases. This list implies competition for resources, such as food, and shelter or protection from the other hostile forces; accordingly, for all sexual species, we must include as a selective factor competition for mates, and for the best mates.

Because directions of mutation evidently remain random in regard to directions of selection, mutational changes as such are independent of adaptation, or the fine tuning that organisms exhibit in response to their physical and biotic environments. The same is true of genetic

drift, for its causes are by definition without cumulative directional effects on the genetic materials. This means that as evolution proceeds mutations must increasingly tend to become deleterious, and their rates have likely been severely selected downward. It also means that directional evolutionary change has to be caused by directional selection. The only exception that I can imagine is the concept of selection suddenly becoming absent in the environment of a complex organism, with mutational changes then leading to steady reductions in complexity. Although this effect has sometimes been postulated when some particular selective pressure has evidently disappeared (e.g., reductions in size and complexity of human teeth with the advent of cooked food, or disappearance of eyes in cave animals), such cases are more appropriately explained as changes in directions of selection. In no way do they support an argument that selection itself somehow mysteriously disappeared from the organism's environment. When one direction or force of selection is removed from the environment of a species, the effect is to cause other previously opposing forces to become more intense or powerful.

These are the reasons, then, for the common tendency to refer to the theory of evolution as the theory of natural selection. They lead us to the conclusion that to apply evolutionary theory to human problems we must focus our attention on the causes and effects of differential reproduction.

DARWIN'S CLAIM OF UNIVERSALITY

Theories are supported by their ability to explain observations, and to explain them better than alternative theories. They are discarded when they do not match verifiable observations. In consequence it is possible to prove that a theory is incorrect, but impossible to prove in a precisely parallel fashion that another theory is the correct one. To prove a theory correct it would be necessary to test all possible predictions. Since this is impractical, if not impossible, the correctness of a theory can be supported but not proved.

This logical problem has sensitized scientists and philosophers to the significance of locating, for any theory, observations or predictions that if true would falsify it. The theory in question will be supported if such predictions repeatedly prove false, or if such observations are impossible because the falsifying conditions do not exist. Theories are not regarded as useful unless means exist by which they can be falsified, whether in the form of alternative theories or contrary predictions.

The supposed universality of Darwinian selection has caused a succession of writers to describe it as a non-falsifiable theory — a useless

theory which explains nothing because it explains everything. We can dismiss this contention and introduce a compelling and provocative aspect of evolutionary theory by considering again the bold challenge issued by Darwin (1859, p. 201):

“If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection.”

Darwin thus provided, in 1859, a means by which his theory could be falsified, and he so identified it. He said, in effect, that his theory if correct, should explain everything *observable* but not everything *imaginable*. Moreover, he did not say that an exception to his view of adaptation would weaken or diminish his theory, rather that it would annihilate his theory. Darwinian theory thus demands that the traits of organisms take their forms largely because of their selective backgrounds, and simultaneously rejects the possibility of certain kinds of altruism being adaptive or reproductively advantageous. Although Darwin spoke only of “structure” we are obviously forced to expand the challenge to include all traits, whether morphological, physiological, or behavioral. Although he spoke only of altruism between species we cannot avoid the fact that all forms of genetic or reproductive altruism within species are also contrary to evolutionary theory, and should exist only as a result of accidents, or sudden environmental changes rendering an organism temporarily maladapted or incompletely adapted; whenever present, such altruism should be tending to disappear. Obviously, in considering evolutionary theory, one passes quickly from the mundane to the startling.

UPDATING DARWINIAN THEORY

In addition to Darwin’s challenging explanation of the means of falsifying the universality of selection, six generalizations may be extracted from the history of evolutionary biology to give focus to a modern application of Darwinism to the behavior of humans or the traits of any and all organisms. Nearly all of these insights were actually generated by either Darwin (1859, 1871) himself or Fisher (1929, 1958). Each was brought to the attention of biologists, however, only by later investigations, spanning the years 1964-1975.

INDIVIDUAL SELECTION

When conflicts in function exist at group and individual levels, those at the individual level are expected to prevail. In the 1958 revision of

his book, Fisher added an admonishment that his fundamental theorem and its associated considerations, contrary to their use by many or most population biologists since the publication of the earlier edition, refer strictly to "the progressive modification of structure or function only in so far as variations in these are of advantage to the individual . . . [and afford] no corresponding explanation for any properties of animals and plants . . . supposed to be of service to the species to which they belong."

This statement was largely overlooked until after George C. Williams had made its substance the theme of his 1966 book *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. The generality of the issue caused it to be perhaps the most prominently discussed problem in evolutionary biology during the following decade. Although much remains to be learned on this subject, it is fair to say that the above italicized statement now represents a rather strong consensus among evolutionary biologists. The important point is that, at least outside humans, populations evidently do not regulate their numbers so as to utilize the habitat most efficiently or to most effectively avoid extinction. Organisms apparently do not evolve to be the kinds of altruists who predictably and consistently behave so as to save their populations or species at their own individual expense. The arguments have been detailed elsewhere (Williams, 1966-75; Lewontin, 1970; Hamilton, 1964-75; West-Eberhard, 1975; Maynard Smith 1964-1976; Alexander, 1971-1976, in press).

The consequences, if these same arguments apply to humans, are clearly enormous. They must affect our views of almost every aspect of human behavior. As one example they raise a question we have almost entirely overlooked in the history of biology: What kinds of benefits can cause group-living to be profitable to individuals, and what are the consequences for individual behavior if group-living is mandatory; what if, indeed, living in a particular group already having a particular structure and a particular set of social rules is mandatory, as it is for most of us today?

Elsewhere (Alexander, 1974, 1975b) I have argued that there may be but three general classes of benefits in group-living overcoming the automatic expenses of more intense competition and the greater likelihood of spread of diseases and parasites: protection from predation; group- or pack-hunting; and extreme localizations of resources such as food or shelter, which literally force individuals together. I have also argued that none of these benefits remains for humans except that of predation, if we assume that the aggressive competition of human groups against one another can be included in this category. We no longer

live in groups to avoid sabre-toothed tigers, or to bring down large game. Moreover, our groups have grown and grown since these possible benefits disappeared. Perhaps there are reasons for this growth other than balances of power among the groups involved, but if so they have not been brought forth.

I have also noted (Alexander, 1975a) that our uniqueness as an intergroup aggressive or warring species is complemented by our uniqueness as a species in which groups compete with one another in play; human groups do this very intensively and extensively. We ought not to ignore the apparent fact that more of both war and group-competitive play is carried out by males than by females.

Here I insert a caution: The kinds of things I am saying may be right or wrong as interpretations of human history. In any case they are not appropriately regarded as deterministic for the future. On the contrary, I suppose that the individuals and groups least bound by history are those who best understand it. Hence, the question is only whether or not the view of history suggested here is correct. I reject any notion that what I am saying leads to an acceptance or promotion of a social Darwinist future, or is involved with or contrary to any other particular ideological trend. Those who would reject my arguments about history on such grounds are much more deterministic in their view of human behavior than I am.

Now let us return to another of Darwin's hypotheses.

REPRODUCTIVE EFFORT

The reproductive effort of any individual is finite, and reproductive effort evolves so as to be fully expended during the organism's lifetime.

In 1871, in *The Descent of Man and Selection in Relation to Sex*, Charles Darwin wrote as follows:

"The only check to a continued augmentation of fertility in each organism seems to be either the expenditure of power and the greater risks run by parents that produce a more numerous progeny, or the contingency of very numerous eggs and young being produced of smaller size or less vigorous, or subsequently not so well nurtured."

Darwin was saying that in the race of natural selection individuals are kept from evolving to produce more and more offspring by (1) forces preventing increases in size, and (2) the necessity either of (a) giving fewer parental benefits to each offspring, because of selective forces nullifying the benefits, of, for example, growing larger so as to have more benefits to give, or (b) taking greater risks in the interests of giv-

ing more benefits. Darwin's statement embodies the principle that reproductive effort is finite, and that it evolves continually to be fully and most effectively expended. The clear implication is that every lifetime of every organism is to be viewed, in evolutionary terms, as no more and no less than a strategy of reproduction by a group of genes (the genotype). Darwin's implication regarding the caloric costs and risks of acts was further developed in Fisher's (1929) use of cost-benefit analysis to explain sex ratios as an individual rather than a population adaptation. The topic of reproductive effort has been widely discussed since (e.g., see Hirshfield and Tinkle, 1976).

Again, the implication is clear that all functions of the organism are reproductive, and maximally so. Darwin's and Fisher's arguments lead us to the hypothesis that, in evolutionary terms, every individual's lifetime is a series of unwitting cost-benefit decisions, leading, in the organism adapted to its environment, to a maximization of reproduction. The extent to which this is true of humans depends partly on the aspect of our environment which involves ability to reflect consciously about personal motivations, and to ask questions about our backgrounds and seek answers to them.

The ramifications of this rather simple statement are astonishing: It seems ludicrous to suggest that all activities of humans tend to be reproductive to the individual, or more properly, its genes, except activities that because of environmental changes are temporarily maladaptive (that is, in the biological sense of not maximally reproductive).² Unless there are flaws in the argument presented to this point, however, we are at least forced to examine this hypothesis.

Senescence, and the finiteness of individual existence, can be used to support the arguments I have developed so far. The only viable general theory of senescence seems to be that of Williams (1957) (see also Hamilton 1966). Its basic argument is that pleiotropic genes with beneficial effects on reproduction early in life have been saved in spite of deleterious effects they cause later in life. The reason for this selection is the higher reproductive value of younger individuals, thus their greater ability to transmit genes. Human mortality curves are astonishingly similar for widely different times and places, and the mortality curves of the two sexes tend to keep their relationship. I can think of no valid

² This use of the concept of evolutionary adaptation is essentially universal in modern evolutionary biology. In regard to human behavior, maladaptive, in this sense, carries no connotations of pathological, unfeasible, or unhealthy. Whether or not maximal reproduction is deemed a desirable or appropriate personal goal is another question entirely.

reason except that embodied in the principles just considered, namely, the maximizing of reproduction.

Thus, not personal satisfaction — not even “long term” personal satisfaction — is appropriately described as the individual’s “goal in life” throughout history: Instead, cost-benefit analyses must be in terms of genetic reproduction. Such an argument predicts, for example, that an individual may be quite willing to die if in the process it saves a number of its offspring.

To my knowledge “functionalism” in cultural anthropology has never been identified in this fashion. Cultural functionalism instead dates to Bronislaw Malinowski (e.g., 1944) who interpreted “biological needs” in terms of the proximate physiological satisfaction of the individual organism. A prominent anthropologist has noted that for Malinowski’s kind of functionalism culture was a “gigantic metaphorical extension of the physiological processes of digestion.” Malinowski might have been embarrassed by this simplification of his approach. But if the word reproduction is substituted for digestion in the above statement (or for “survival” in another common version of functionalism), then the Darwinian model of culture is appropriately described; and if the word “culture” is also replaced by “the phenotype,” then the basic theory on which all biology operates is correctly stated. I believe that this insight also removes the criticism of functionalism in theory from other branches of the social sciences (e.g., Homans, 1961) by providing simultaneously a historical dimension and a reasonably testable proposition: that humans behavior tends to develop as it does because in past environments such behavior led to a maximizing of reproduction.

NEPOTISM

Altruism to nondescendant genetic relatives is like the altruism of parenthood.

In 1929 Fisher took up a problem of almost unbelievably broad significance when he tried to explain how distastefulness could evolve in caterpillars. If Fisher had accepted that traits may evolve because they help the group, even if they diminish the reproduction of the genes of their individual bearer, he would not have been troubled by this phenomenon. He noted that most other means of defense, such as stings or disagreeable secretions and odors, can be explained by their beneficial effects on individuals in which they are best developed. Because a tasted caterpillar is likely to die, however, it is difficult to understand how tendencies to be more distasteful than average could spread and cause an overall increase in distastefulness.

Fisher next noted that distasteful larvae tend to travel in tightly knit sibling groups. If there is a positive correlation between the degree of distastefulness and the likelihood of avoidance of that group or kind of caterpillars by a bird that had tasted one of them, then a highly distasteful caterpillar, even if it died as a result of being tasted, might enable more of its brothers and sisters to survive and reproduce than a less distasteful caterpillar. Since brothers and sisters of very distasteful caterpillars have a higher than average likelihood of themselves carrying the genes leading to greater distastefulness, such genes could spread. Fisher even quantified this phenomenon, later to be called "kin selection" (Maynard Smith, 1964) by noting that "The selective potency of the avoidance of brothers will of course be only half as great as if the individual itself were protected; against this is to be set the fact that it applies to the whole of a possibly numerous brood." In other words, full siblings on average have 50% of their genes in common, or identical by descent (*ibd*). This means that each protected full sibling is 50% likely to be carrying an allele causing greater distastefulness in a tasted sibling. This kind of selection leads to nepotism, or the dispensing of benefits to relatives other than offspring or other direct descendants. In 1957 George and Doris Williams used a similar explanation to account for the appearance of sterile castes in the social termites, ants, bees, and wasps. In 1964, William D. Hamilton developed and further quantified the theoretical basis of nepotism, concluding that "*The social behaviour of a species evolves in such a way that in each distinct behaviour-evoking situation the individual will seem to value his neighbour's fitness against his own according to the coefficients of [genetic] relationship peculiar to that situation.*" This is clearly a prediction of enormous consequence for the analysis of social structure in any species in which genetic relationships correlate with stable social relationships, allowing the evolution of patterns of nepotism.

As Hamilton (1964) noted, the parent-offspring relationship is not fundamentally different from that between other kinds of relatives. Hence, we can generalize that: *In sexually reproducing organisms reproductive effort is evolved to be expended entirely as nepotism, including parenthood and the effort involved in placing one's gametes in the best possible environment.* This is a particularly important statement for the understanding of sociality since it says, in effect, that sexually reproducing organisms literally evolve to be altruists, but altruists of a very special sort whose altruism, whatever form it takes, is ultimately channeled to genetic relatives. Such altruism, which uses

the phenotype to reproduce the genes, may be described as phenotypically (or self-) sacrificing but genotypically selfish (Alexander, 1974).

It is worth emphasizing that, despite a recent prominence accorded the view that kin selection is a kind of group selection (Brown, 1966, 1974, 1975; E. O. Wilson, 1973a, 1975; D. S. Wilson, 1975a, 1975b), this view is misleading if not erroneous (see also West-Eberhard, 1976; Maynard Smith, 1976). Group selection thwarts the reproductive interests of individuals when they differ from those of the group; kin selection is a way in which individuals further their genetic interests via other individuals. Kin selection not only may include the favoring of more closely over less closely related individuals within the group, but, even when such discrimination is precluded, it is synonymous with group selection only in circumstances in which the reproductive interests of the group and the individuals are identical.

SOCIAL RECIPROCITY

An organism can gain by dispensing benefits to nonrelatives if over-compensating benefits are reciprocated to itself or to its genetic relatives.

In 1859, Darwin spoke of the "lowly motive" of helping another individual in the expectation of receiving even more assistance back, and in writing of human heroism Fisher (1958) noted that it is possible for heroic qualities to be selected "beyond the limits set by prudence, by a method analogous to that used . . . to explain the evolution of distasteful qualities in insect larvae. The mere fact that the prosperity of the group is at stake makes the sacrifice of individual lives occasionally advantageous, though this, I believe, is a minor consideration compared with the enormous advantage conferred by the prestige of the hero upon all his kinsmen."

Fisher again stubbornly seeks explanations which do not invoke the unlikely phenomenon of group selection. He acknowledges that nepotism may explain heroism, then adds another factor — the effect of the prestige of the hero upon his kinsmen. Such prestige, and its accompanying benefits, are necessarily conferred by nonkinsmen. In other words, Fisher is suggesting that heroism has been elaborated and maintained at least partly because of an implicit promise or guarantee within human society that anyone displaying unusual heroism in protecting or saving nonrelatives may expect his relatives to benefit even if he is killed in the effort. Laws which prohibit certain acts also represent societal guarantees or promises. The principle of reciprocity, which has been very widely considered by social scientists, was first discussed in detail

in an evolutionary context by Robert L. Trivers (1971). (For anthropological discussions, mainly of nontechnological or "primitive" societies, see Malinowski, 1926; Durkheim, 1933, 1938; Mauss, 1954; Sahlins, 1965. For sociological and psychological discussions, mainly of modern, urban, or technological societies, see Homans, 1961; Blau, 1965; Emerson, 1969; Simpson, 1972; Berkowitz and Walster, 1976).

Rewards from society at large, or from other than the actual recipient of beneficence, may be termed indirect reciprocity. Direct reciprocal transactions, which we engage in more or less continuously, are illustrated by many kinds of cooperation, the buying and selling of goods, and all forms of trading or barter. A buyer always supposes that his purchase is worth more to him than its cost, and the seller supposes the purchase price to be greater than the value of the item to him. Both can be correct, because of asymmetry in their abilities to obtain the bartered objects or in the intensity of their respective needs to obtain them. Some reciprocal transactions may involve long delays, and because of the significance of having risks covered may never require actual reciprocation beyond a promise or guarantee; an insurance policy is an example.

In nepotistic interactions the reward to the altruist is genetic; in reciprocal systems it is measured in terms of altruism returned to one's self or one's genetic relatives. In consequence, the net cost or benefit of a given nepotistic act depends upon three variables: (1) the genetic relatedness of altruist and beneficiary, (2) the ability of the recipient to translate the benefits into reproduction, and (3) the cost of the act to the altruist. For reciprocity, only (3) and the likelihood of an over-compensating return are involved.

Systems of reciprocity thus differ from nepotistic interactions in that any participant can gain by cheating so long as the cheating is not detected or there is no strong likelihood of retaliation. Thus, the way is opened for the elaboration of abilities to recognize cheating as well as to cheat successfully, and even tendencies to cheat by falsely accusing others of cheating (Trivers, 1971). In nepotistic interactions a potential recipient of benefits can cheat by deception about the extent of his need or by causing himself to be accepted as a closer relative than is actually the case; this is true whenever, and to the extent that, the benefit-giver maximizes his own reproduction by distributing his benefits among two or more genetic relatives in a fashion differing from the interests of the potential recipient. A potential benefit-giver, on the other hand, simply cheats genetically when he short-changes a genetic relative.

Two more concepts will complete the updating of Darwinian theory.

Neither can be traced to the writings of any particular individual, and they are properly described as less well understood or somewhat more controversial than the preceding four items. Like nepotism and reciprocity each has special applicability to human affairs.

ONTOGENIES

The ontogenies of organisms should evolve such that organisms tend to learn, or develop abilities, to reproduce maximally in their particular environments and not to develop any other abilities.

All traits are products of the interaction of the genetic materials with the environment. Darwinism says nothing about the directness, indirectness, or complexity of the routes between gene action and behavior. It only suggests that whatever routes exist must be those most appropriate to the changeability and predictability of the succession of environments in which the trait has been expressed throughout human history. On the other hand, if Darwinism is a reasonable theory about history, it must encompass all learning and all theories of learning. Moreover, although it has not been widely considered in this context, a Darwinist approach should lead to more useful predictions about learning than any other kind of theory.

Appropriate ontogenies, in selective terms, are those leading to maximal reproduction. This does not imply, however, that every act of every human is to be interpreted as maximizing its reproduction, but that evolutionary change, in the history of environments in which humans have lived, has tended to be in the direction of maximizing reproduction. Not merely physical and general biotic stimuli but knowledge of human history in general, and of one's own personal history, tendencies, motivations, and the probable rewards and punishments for given acts, are all parts of the environment in which human behavioral traits are expressed. Whatever the extent or nature of biologically-based constraints on the modifiability of human behavior, therefore, such constraints seem most likely to be bypassed effectively or superseded by humans who individually and collectively are aware of them and understand them well. Behavioral constraints and plasticities are each to be understood only in terms of the particular environments in which they apply, and these environments are probably best identified from a thorough understanding of both proximate and ultimate backgrounds of behavior. Indeed, the most significant change possible in one's environment may be the improvement of one's ability to reflect on his own tendencies and motivations, and those of his fellows. Hence,

we may expect that merely reading these words could represent a significant alteration of the adaptive environment of some readers.

For example, should I suggest to an acquaintance that he is compelled to do in any situation what will be for him most reproductive, he might scoff and invite me to identify such courses of action so that he could prove me wrong by repeatedly doing the opposite. If the opposite were a very expensive or detrimental act he might prefer to bet me that he would do the unexpected. Upon doing so he would triumphantly take ownership of whatever I had lost in the bet. He might not even consider the significance of the use to which he would eventually put his winnings, or exactly how he arrived at the size of the incentive necessary to make him take the particular course of action that would cause him to win the bet. Moreover, it would be easy for him to neglect considering what it means that the intensity of our argument, or the number and significance of the persons observing our disagreement, might also influence his decision about which course of action to take.

Human reproduction is realized through devious, complex routes, and its currencies are numerous, variable, and sometimes unrecognized as such. The important point is that my statements to the person in this example, as well as all of the circumstances created by our actual disagreement, would be a part of the environment in which he made his cost-benefit decision about which course of action to take. A history of differential genetic reproduction is thus most deterministic for the human still unaware of it.

DARWINISM'S NON-IDEOLOGICAL NATURE

Darwinism is not a social, political, or economic ideology.

Darwinist natural selection is evidently the core item in analyzing the causal history of the traits of living organisms. On the other hand, it does not follow, in any sense whatever, that Darwinism provides a basis for the formulation of desirable political, economic, social, moral, or ethical systems of human sociality to be employed now or in the future. Regardless of its relationship to human history, Darwinism has no direct role in determining the nature of deliberately modified systems of human interactions. Its usefulness in these regards remains strictly in the realm of providing information which may assist humans in the most efficient realization of whatever systems they may elect to strive for.

Because natural selection tells us nothing about the directness of connections between genes and behavior, it also says nothing about the exclusion of any particular kinds of social systems as impossibilities; and it does not imply that there are either natural laws that must be fol-

lowed or instincts that cannot be thwarted. Efforts to derive rules of human conduct from Darwinian explanations of history are properly labelled "social Darwinism." Like Marxism, capitalism, feudalism, democracy, or totalitarianism, social Darwinism is an ideology — a system of behavior or government to be considered for its applicability now and in the future. Darwinism, on the other hand, is a system of historical explanation; as such it does not appropriately compete with or support any particular or any conceivable ideology, although it has unfortunately been so used in the past.

OBJECTIONS RAISED AGAINST A DARWINIAN APPROACH TO HUMAN BEHAVIOR

THE ASSUMPTION OF DETERMINISM

The last item discussed above embodies one of three major objections to applying Darwinian theory to human history: that it leads to an intolerable assumption of determinism. The discussion above is intended to show that the necessary assumptions about ontogeny may not after all be intolerable.

APPARENT LACK OF CONCORDANCE BETWEEN CULTURAL PATTERNS AND BIOLOGICAL PREDICTIONS

A second objection is that cultural patterns simply do not accord with biological explanations: Kinship conventions, marriage rules, incest taboos, and patterns of cooperation and competition in human societies, it is argued, do not match predictions from a nepotistic model. In light of recent changes in our view of what constitute satisfactory applications of Darwinism to human sociality, however, previous failures are cast into doubt. I believe that we are compelled to try again.

THE ONTOGENETIC PROBLEM

A third objection is that traditionally transmitted culture is by definition too remotely and too indirectly tied to gene action, and thus to inheritance through genes, for evolutionary theory to predict anything significant about the structure of culture or the directions of its change. From this stance it might even be argued that, should Darwinian predictions prove accurate for cultural patterns, the correlation is necessarily fortuitous.

Objections to Darwinism from ontogenetic considerations are more complex than may at first be supposed. Ontogenies are the most difficult and perplexing phenomena that evolutionary theory must account for, and behavior is the most perplexing of all phenotypic attributes, in

ontogenetic terms, for it is less directly related to gene action than its underlying morphological and physiological correlates. Especially difficult to understand is the evolutionary background of learning, as is illustrated by the fact that nearly all theories of learning are either physiological or ontogenetic theories, scarcely any of them adaptive theories.

The essence of learning is adaptation to immediate contingencies. Learning, and especially deliberate planning, represent establishment of the feedback between need and novelty that has evidently never been established at the level of gene mutations. A paradox, in exploring learning as an evolutionary adaptation, is that the more prominently an organism's phenotype becomes tuned to immediate contingencies the less obvious is its connection to genetic or evolutionary history. It becomes easy to forget that whenever responses to immediate contingencies fail to maximize reproduction the flexibility leading to them will be counterselected. Moreover, phenotypic flexibility does not mean that there is no genetic command as to which responses will result from which environmental contingencies. Nor does an absence of heritability in phenotypic variance because selection has been inexorably directional imply that there is no genetic contribution to the expression of the phenotype. The commands given by genes are for the production of given phenotypic responses in given environments. So far, at least, we have always countermanded by changing environments.

To some extent the ontogenetic or experiential backgrounds of human behavior may actually seem liberated from the ontogenetic inscrutability typical of other traits, or of much of the behavior of other species. The essential stimuli for altering human behavior, after all, are frequently apparent. Nevertheless, given stimulus sequences lead predictably to particular behavioral responses, indicating that all possible responses are not equally probable. Before evolutionary explanations can be eliminated one must know the relationships between ontogenetic stimuli, behavioral responses, and the routes to reproductive maximization in the relevant environment.

Most difficult of all ontogenetic problems is that of discovering the connections between genetic change and change in the traditionally transmitted learning of humans which assumes the structural forms that we call culture. This problem is so central and immense that a description of the process of organic evolution such as I have given here may seem, to those who deal every day with human behavior, as if it were totally irrelevant to their problems and discoveries. It is my theme, however, that many more connections can be drawn now than ever

before, and that drawing as many connections as we can at each stage in the growth of our knowledge about ourselves will always be a useful enterprise.

Our general ignorance of ontogenies, despite concentration on learning and other developmental theories in the social sciences and among a significant proportion of zoological behaviorists, indicates that arguments from ontogeny about the probable failure of Darwinian theory are likely to be vulnerable. After all, if patterns of culture can be shown to match predictions from Darwinian theory to a much more significant degree than has been found in the past (and I believe they can be), then objections from ontogenetic arguments must at least be re-examined. Moreover, ontogenies in general, of whatever kind of trait, are essentially inscrutable; yet scarcely anyone invokes the complexities or supposed indirectness of ontogenies to support a general rejection of an evolutionary background for morphological and physiological traits.

A DARWINIAN ANALYSIS OF HUMAN SOCIALITY

The selectionist view of social behavior causes us to focus on the altruism of parenthood, the altruism of other kinds of nepotism, the seeming or temporary altruism of reciprocal transactions, the argument that selection is focused at and below the individual level, and the notion that lifetimes, and thus ontogenies, are series of cost-benefit decisions with their historical significance solely in maximizing reproduction. These are the concepts which represent the modern tools for applying Darwinism to understanding the history of human behavior. As such, they have all been widely available for only a few years. Our problem now is to develop their consequences and test their ability to explain observed patterns of human sociality, and if they fall short to determine whether we must seek additional principles modifying or clarifying the application of Darwinism to human affairs, or an explanation outside or beyond Darwinism. If Darwinism is to be effective in analyzing human sociality, it will have to explain the existence and history of nepotism, beginning with parenthood, family life, incest taboos, and marriage rules, and also lead us to a better understanding of the most complex systems of social, economic, and political cooperation, reciprocity, exchange, and barter. It will have to form the basis for explaining the causes and effects of group living, from its simplest forms or beginnings right up to the largest, most complex technological nations. It will have to provide the best insight into a variety of biological phenomena underlying and influencing sociality such as sex ratios, sex-

ual competition and selection, senescence, parental investment, marriage systems, and sexual dimorphism.

The important questions faced at this juncture are: (1) How can the composite hypothesis about social behavior that derives from a Darwinian approach be tested, in such fashion as to provide critics of Darwinian interpretations of human history with obvious procedures for falsifying it if they can (partly so that rejections based on less appropriate grounds, such as political motivations, emotionality, or attempted ridicule, will no longer be accepted); and (2) how can the hypothesis be developed, and related to human motivations and desires, so as to allow its use, if appropriate, in developing whatever kinds of social, economic, or political systems may be arrived at through open-minded, collective, and optimistic rationality, while simultaneously thwarting its use as a vehicle for promoting systems favored by narrow special-interest groups?

I have already attempted to begin answering these questions about human behavior with preliminary discussions of the fit of a model of reproductive maximization to infanticide and the related phenomena of abortion, coital taboos, and postpartum inhibition of ovulation; the evolution of menopause; the ecological distribution of polyandry; the phenomena of asymmetrical cousin marriages and mother's brother (Alexander, 1974: 367-374); and the relationship between nepotism and reciprocity (Alexander, 1975, pp. 91-95). Irons (in press) employs an inclusive fitness model in discussing the relationship between residence location and reproductive success of Turkmen. Chagnon's (1975, 1976) data on Yanomamö Indian village sizes at fissioning, and the genetic relatedness of inhabitants, accords with Darwinian predictions. Dickeman (in press) has tested and confirmed Darwinian predictions about sex-preferential infanticide in polygynous caste systems (Alexander, 1974, p. 369). Hartung (1976, in press) has used Darwinian models to discuss patrilineal inheritance and intrafamilial conflicts of interest. Several authors have recently considered the significance of intergroup aggression in human history in Darwinian terms (Alexander, 1967-1975; Alexander and Tinkle, 1968; Bigelow, 1969; E. O. Wilson, 1973b, 1975).

Here I shall attempt to further the testing of human cultural patterns against the Darwinian model by concentrating on several phenomena relating to nepotism and genetic outbreeding. I choose these two categories of behavior because I believe they are singularly well suited for settling the question of whether or not, or to what extent, patterns of human culture have been influenced by their effects on the reproduction of human genes.

Many cultural variations will be difficult to assess in terms of genetic reproduction, or the history of genetic reproduction. They may be more or less neutral, such as the difference between eating one or another equally nutritious kind of food. Their effects may oscillate confusingly, such as the optimal family size for maximizing reproduction under different economic, social, or other circumstances. They may be exceedingly varied and complex, such as the optimal ways to respond to particular social situations or particular individuals. Or they may be novel, or without a historical basis, such as whether or not to fasten seat belts or submit to yearly chest x-rays.

The relationship between nepotism and outbreeding to the reproduction of genes is by contrast simple and direct. A Darwinian model predicts that, in the absence of other variables, in nepotism humans should favor closer relatives over more distant ones, and in outbreeding they should favor more distant relatives over closer ones.

The initial reaction of social anthropologists — indeed, of almost any thoughtful person — to these predictions is likely to be that they are far too simple to account for the incredibly varied and complex patterns of behavior exhibited toward kin among the hundreds of different human societies in the world. Humans do not always favor their closest kin, and they do not always avoid sexual relations or marriage with all but nonkin or the most distant possible kin. In each case, however, we will need to know if there are circumstances which cause the expressed behavior actually to meet Darwinian predictions. The important point is that to favor in nepotism a more distant kin, when there are no compensating variables, is to act contrary to the interests of one's genes; and provided that humans benefit from maximizing genetic outbreeding, the same is true whenever genetic relatedness is not minimized between sexual or marriage partners.

Scarcely anyone would deny that humans at least tend to behave nepotistically in some circumstances. On the other hand scarcely any social scientist would assume that they tend to maximize genetic outbreeding, even though the phenomenon of incest avoidance is usually deemed one of the most universal of all attributes of culture. Social scientists would probably agree, however, that a stringent requirement of maximization of genetic outbreeding would make it more difficult, rather than less, for a Darwinian model of human behavior to be supported. I employ this restriction because, during several years of investigation in the literature of human behavior, I have been unable to locate any reason for assuming that incest avoidance (and here I restrict my usage of this term to refer to taboos, inhibitions, and proscriptions

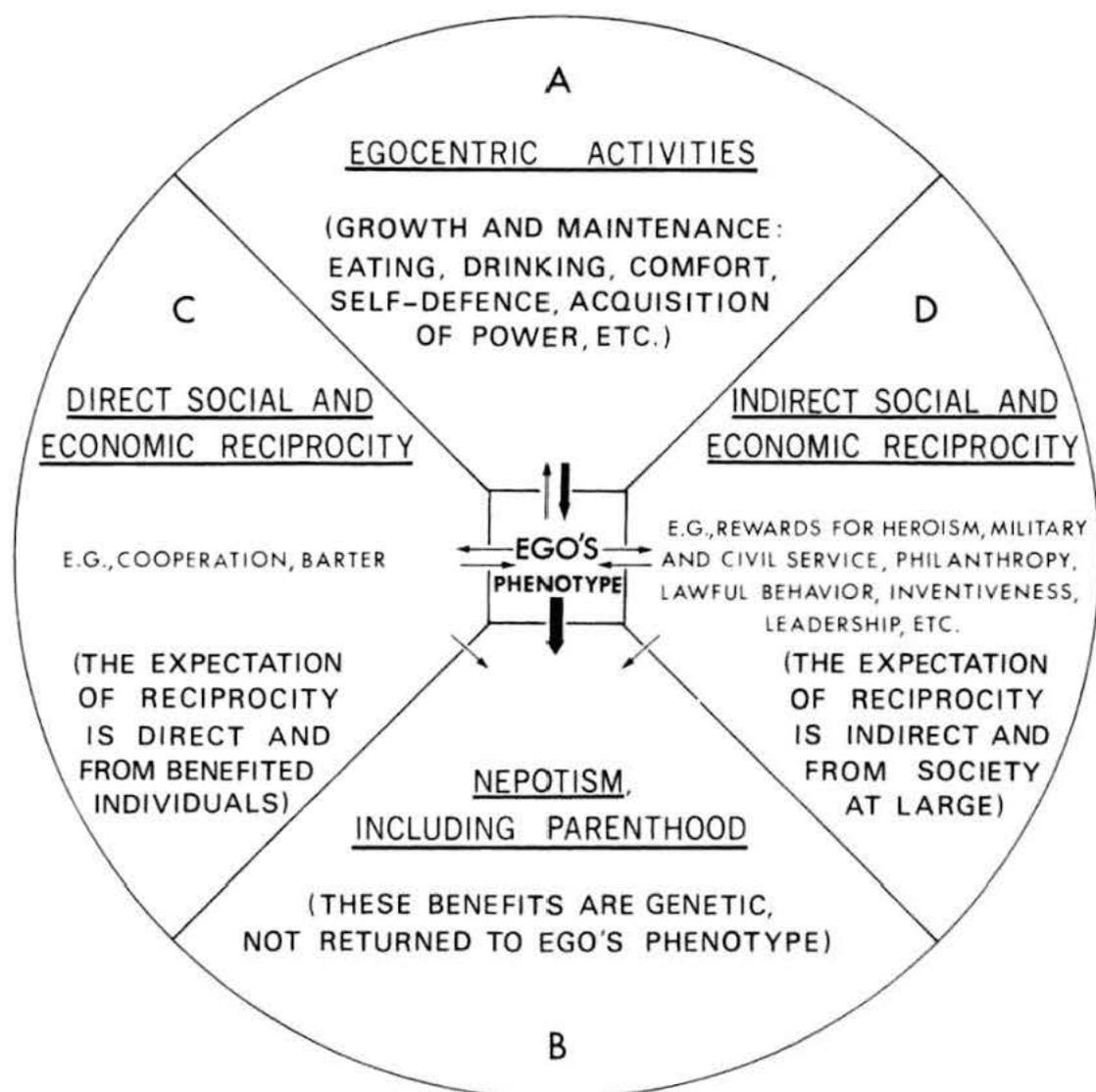


FIGURE 1.—The organism as nepotist. The diagram purports to show all routes by which expenditures of calories and taking of risks by humans can lead, both directly and indirectly, to genetic reproduction. Reproduction will be maximized when the benefits from egocentric activities and reciprocal transactions maximally exceed their costs, and when their benefits are channeled to the closest relatives with the greatest ability to use the benefits to maximize the reproduction of their relatives in turn. I suggest that as sociality increases in complexity, during evolution, from a relatively nonsocial beginning (A), following nepotism (B) only to offspring, nepotism to nondescendant relatives becomes relatively more important, then (chiefly in humans) direct reciprocity (C), then (probably only in humans) indirect reciprocity (D). Expansion of nepotism to nondescendant relatives and increasing group size must, in human history, have set the stage for an increasing prominence of reciprocal transactions. In large and highly organized states or nations, as compared to simpler forms of social organization, indirect reciprocity must generally be more prominent — indeed, probably a criterion. Simple bands must have been predominantly systems of nepotism to descendant and nondescendant relatives with relatively little complexity in reciprocal transactions. Opportunities to engage advantageously in reciprocal transaction must begin to appear as systems of nepotism among nondescendant relatives become

involving very close relatives) — as opposed to the more inclusive phenomena of marriage systems and patterns — involves anything other than the maximizing of genetic outbreeding (Alexander, *ms*).

It is possible to imagine alternative explanations to Darwinian selection for almost any particular behavioral act or pattern, or to develop such explanations after the fact. Nevertheless, I cannot imagine any single hypothesis, other than a history of natural selection of genetic alternatives, that could account for a general patterning of human behavior which fits the Darwinian model in many different societies and circumstances. If patterns of nepotism among humans match predictions from kin selection, and if patterns of sexual interaction or marriage systems lead to sexual avoidance of at least closer kin so as to cause definite outbreeding patterns, then in my view the independence of culture from what is commonly termed the biological history of humans will be cast into doubt. No additional argument should be required to justify a complete review of Darwinism as a more explanatory theory of human sociality than we have previously suspected.

Although the following discussions are preliminary and rudimentary, and cover but a few aspects of nepotism and incest avoidance, perhaps they will help point the way toward more conclusive and satisfying tests.

NEPOTISM: THE GENERAL MODEL

Not merely offspring, but all of one's genetic relatives, both descendant and nondescendant, represent potential avenues of genetic reproduction; for sexually reproducing organisms there are no other avenues. Fig. 1 diagrams the various routes by which an individual may secure benefits to be translated into reproduction via nepotism. Fig. 2 diagrams appropriate recipients of nepotism. As Fig. 2 implies, and as every human knows, individual humans are surrounded by a variety of genetic relatives and interact more or less regularly with them. These relatives overlap with us in varying degrees of need, dependency, or ability to translate assistance from us into reproduction.

It does not matter — to respond here to a social anthropologist's comment — that relatives are actually just individuals treated in special

extensive and complex, which also increases the potential for cheating by recipients of nepotism. Selective pressures leading to larger groups thus represent pressure for increased engagement in reciprocal transactions, and increasingly elaborate cheating and ability to detect and thwart cheating. Aside from fairly small groups, only other competing groups of humans seem an appropriate source of pressure for increasing group size and complexity (Alexander, 1971, 1974, 1975, *in press*).

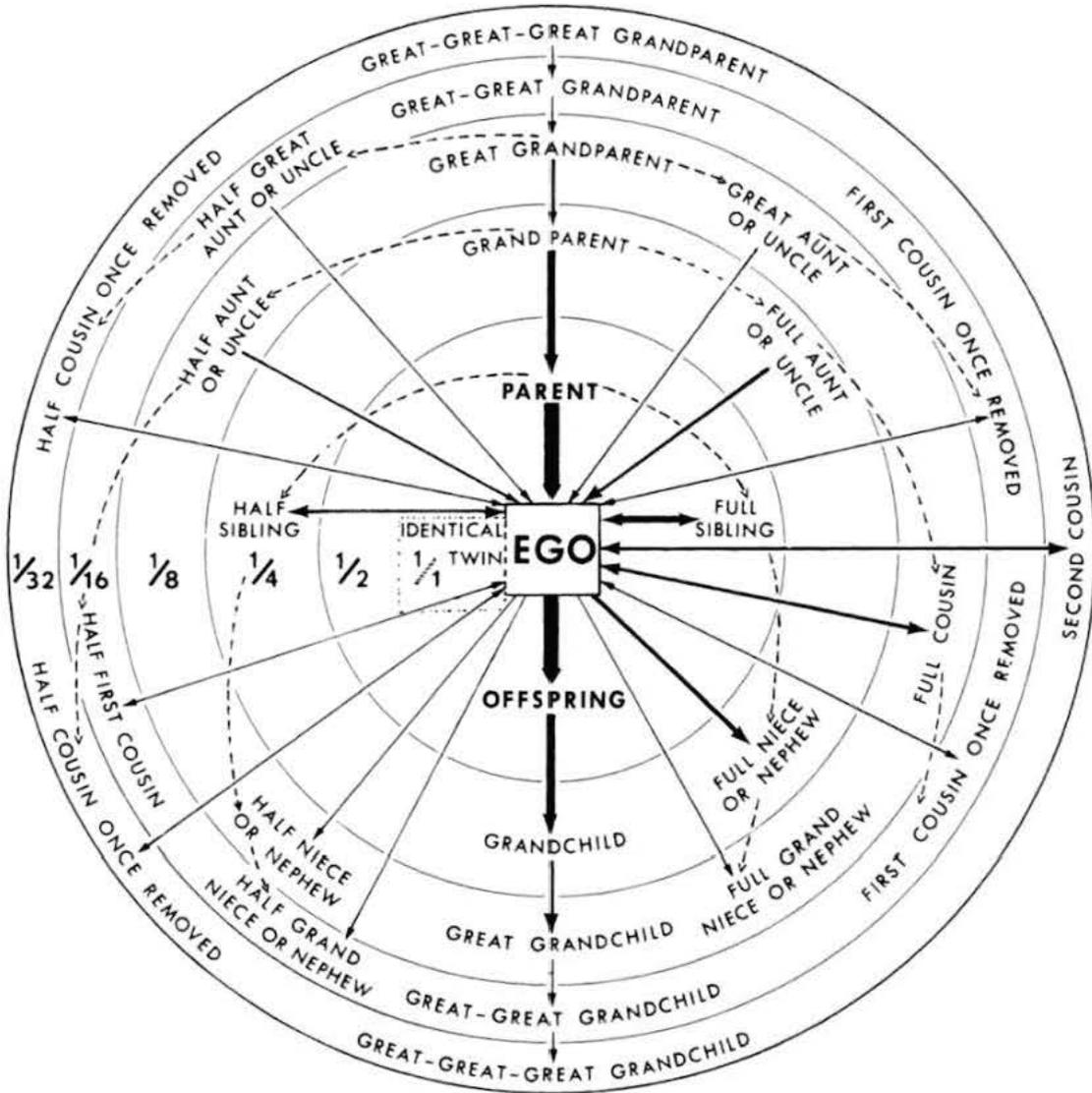


FIGURE 2. — Genetic relatives potentially available to an individual, Ego, for reproductively self-serving nepotism. Arrows indicate likely net flows of benefits. Half the genes of parent and offspring are identical by immediate descent. Other relationships are averages. Dotted lines indicate closest relatives other than Ego, 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 non-overlap. 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.

fashions because of known genealogical connections. One does not need to *know* who his relatives are, and what are their varying degrees of relatedness to him for kin selection to work; he only needs to *behave* as though he *knows*.

The basic prediction from an evolutionary model, then, is that human societies should be extraordinarily complex networks of nepotistic interactions, and that every individual should from birth find itself imbedded in such a network. Of course, we know already that in some sense this is true. Every human society known operates as a kinship system, with genetic relationships among the participants an essential feature, and social anthropologists have always regarded it as their central role to examine these kinship systems and analyze their structure and functions.

From these facts, several general predictions about human nepotism seem evident, and a very large number of subsidiary predictions begins to emerge. For example, we expect that patterns of kinship will be centrally important in human societies, with predictable intensities and kinds of behavior toward different genetic kin. We expect keen ability to sense differences in need, and changes in need, and to respond to them. Similarly, we may expect cleverness in detecting availability of nepotistic benefits, and in diverting them to personal benefit, even sometimes by deception. Such deception may take two forms: (1) efforts to insinuate one's self into the role of a closer than actual relative and (2) efforts to exaggerate one's need or ability to use sought-after benefits in reproduction. In turn, we should expect that individuals with nepotistic benefits to dispense should become very sensitive to all such efforts at deception, and very clever at avoiding nepotism unlikely to yield maximal reproductive returns.

To maximize genetic reproduction through relatives an individual human need not be consciously aware of the various degrees of genetic overlap of those relatives with itself, of the relationship between genetic reproduction and nepotism, or of the prediction from natural selection that organisms evolve to maximize reproduction through nepotism. As with nonhuman organisms one only needs to behave as though aware of these things.

The Darwinian proposition of reproductive maximization not only is not an everyday fact in the consciousness of humans, but instead, when suggested, is almost inevitably denied vehemently, and most often regarded as repugnant, or even ludicrous. Ultimately, if a Darwinian approach to human sociality is to be successful, it must have the power to explain why such reactions are typical, and why they are so intense.

Following is a preliminary list of predictions about human sociality, which I believe follow from a Darwinian model. Some are trivial, individually, and almost circular because we already know they are true owing to our immersion in the human system of sociality. But collectively they are not weak. Moreover, I believe that the list can be expanded to one hundred or more, and to discover eventually that, say, 95% or more are met, would certainly not be trivial.

SOME DARWINIAN PREDICTIONS ABOUT HUMAN SOCIALITY

1. When abilities of potential recipients of nepotistic benefits to translate such benefits into reproduction are equal, then closer relatives will be favored over more distant relatives.
2. When genetic relationships of potential recipients of nepotistic benefits to a potential giver of benefits are equal, then relatives with the greater ability to translate benefits into reproduction will be favored. (These two predictions, which represent the major assumptions of kin selection, are a restatement of Hamilton's 1964 generalization, quoted earlier; numerous subsidiary and more specific hypotheses flow directly from them.)
3. Relatives of the same degree are likely to be distinguished, nomenclaturally and otherwise, only when their abilities to translate benefits into reproduction are consistently different (Thus, uncles and aunts are usually distinguished from nephews and nieces).
4. Cooperativeness and competitiveness between particular sets of relatives, such as full siblings, may vary across essentially the entire spectrum of possibilities, depending upon their opportunities and needs to use the same resource (e.g., parental care or mates) and the value to each of having a cooperative individual available (Thus, the phrase "sibling rivalry" simultaneously connotes a high level of competitiveness and implies that it has an unusual or surprising aspect).
5. Because some kinds of genetic relatives, such as monozygotic twins, have been produced and reared only rarely during human history, their responses to one another are likely to develop so as to reflect some relationship other than the real one (Thus monozygotic twins might be expected to behave like siblings of very similar ages, although such siblings were probably also rather rare during human history as a result of lactation, post partum sexual taboos, and infanticide).
6. Outer limits of effective nepotism may be clarified by drawing limital relatives inward, nomenclaturally and otherwise, and pushing

others outward (hence, some of the apparent inconsistencies in kin nomenclature).

7. Labels usually designating kin may be applied to nonrelatives in the course of establishing, stabilizing, or guaranteeing social reciprocity (hence, classificatory systems of kinship).
8. Older offspring are likely in many circumstances to be reproductively more valuable than younger offspring, and to better serve their parents' interests in the course of serving their own interests according to their age and dependency relationship to their siblings (leading to primogeniture). Younger dependent offspring, on the other hand, may be given full attention with fewer reservations deriving from the probable subsequent appearance of additional dependent young (hence, may be "spoiled").
9. In polygynous societies male offspring with predictably great likelihoods of success will be favored over all others (Trivers and Willard, 1973; Alexander, 1974; Dickeman, in press).
10. Offspring that are abandoned or destroyed are likely to have been of low reproductive value, either because of their phenotypic attributes or because of the timing or the situation of their appearance (Alexander, 1974; Dickeman, in press).
11. Nondescendant relatives may sometimes be better avenues of reproduction than descendant relatives (leading in some cases to adaptive celibacy).
12. Because parent-offspring sociality has been continuous in human history, interpretations of adoptions and quasi-nepotistic behavior toward other species, such as dogs and cats, must be interpreted in terms of the alternatives available to the involved parties; and proximate motivations, or physiological causes, are only to be understood as molded by a long-term selective history.
13. Potential recipients of nepotistic benefits are usually in a better position to gain by cheating than are potential givers of benefits:
 - a. by deceiving about the closeness of their relationship to potential givers of benefits.
 - b. by deceiving about the extent of their ability to translate benefits into reproduction.
14. Relatives by marriage are in a particularly favorable position to gain by cheating their affluent inlaws, since they do not gain directly by the distribution of any benefits to their spouse's relatives.
15. Interactions between young individuals (dependents, or individuals with high reproductive value) and their very old relatives (with low

- reproductive value) remain nepotistic for the old individuals but assume the form of social reciprocity for the young individuals, since old individuals have less and less likelihood of turning nepotistic benefits to reproduction outside the immediate situation.
16. Lowered confidence of paternity causes a man's sister's offspring to assume increased importance as recipients of nepotistic benefits, and in extreme cases to exceed spouse's offspring in this regard (hence, the importance of "mother's brother" to dependent children in many societies — Alexander, 1974, and below).
 17. Erratic confidence of paternity may lead to emphasis upon phenotypic attributes of putative offspring in determining whether or not to accept them as suitable objects of paternal care (hence, perhaps, the frequent attention to the question of whether or not a baby resembles its father).
 18. Sexual activity with spouse's siblings or sibling's spouse leads to asymmetry in the genetic relatedness of putative cross- and parallel-cousins (hence, their separate treatment and nomenclature, concentrated in polygynous societies — Alexander, 1974, and below).
 19. Larger social groups provide more opportunities for social cheating, and on this basis are likely to be typified by greater emphasis on reciprocal transactions, as opposed to nepotism.
 20. Selective forces, such as the value to individuals of preventing the loss of races in balance of power involving their own social group (eventually nation) with its neighbors, may lead to reciprocity rather than nepotism being the cement of group-living (hence, perhaps, a de-emphasizing of particularly extrafamilial nepotism, and the removal of the upper limits of group size imposed by nepotism; and perhaps as well the particular forms, intensities, and influences of religions in successful large nations).

SOME TERMINOLOGICAL PROBLEMS

Because the biological and social sciences have for so long gone their separate ways, it is important to establish the relationships between their different concepts and approaches. Three major focal points of anthropologists and others analyzing human sociality have been those commonly termed (1) kinship systems (2) exchange systems, and (3) marriage systems, the last including the rules and patterns of incest avoidance. Social biologists may assume that these systems are equivalent to their own interests in (1) nepotism, (2) reciprocity, and (3) the composite re-

sults of sexual competition, sexual selection, sex-differential parental investment patterns, and genetic outbreeding. While this may have been true at some times during anthropological history, or in the writings of some social scientists, it is generally an inaccurate interpretation of current investigations. The "kinship systems" of modern anthropologists are not merely systems of nepotism, but include both nepotism and reciprocity, as well as the results of sexual competition, sexual selection, parental investment patterns, and genetic outbreeding. Exchange systems and marriage systems are each usually discussed so as to include all of the same phenomena. This discordance is heavily involved in current disagreement over the applicability of evolutionary theory to understanding human history; when the argument is made that "kinship systems are not based on biology," it usually means that they are demonstrably not merely systems of nepotism. It does not follow, however, that human kinship systems do not accord with the principles of evolutionary biology.

These disparities between the concepts of social and biological sciences may have come about partly because the sciences of anthropology, psychology, and sociology developed without the particular analytical approach that now seems appropriate to evolutionary biologists. Also contributory, I believe, are conscious and unconscious tendencies within human societies to mix or intricate nepotistic, reciprocal, and sexual interactions — for example, to employ terms and practices that ordinarily reflect genetic kinship to emphasize or guarantee reciprocity in situations explicitly not involving genetic kin. Here I have adopted the attitude, or hypothesis, that it is useful to interpret the systems examined by social scientists in terms of the systems conceived by biologists concerned with natural selection. Thus, each time I attempt to analyze some aspect of a kinship or other human system, I will try to dissect it into the components of sociality that seem important from a selectionist view of behavior. I have attempted to diagram the relationship among these different systems in Fig. 3.

Figure 3 implies that parental behavior is the primary evolutionary source (or preadaptive basis) of the altruism of nepotism, and that within-family nepotism is similarly the primary source of extrafamilial nepotism. Nepotism in turn is a likely source of systems of reciprocity (Alexander, 1974). Social cheating, which is potentially rampant in reciprocal systems, is also possible in nepotistic systems (especially by potential recipients of nepotistic benefits); hence, as with reciprocity in general, it may often originate in nepotistic systems (Alexander, ms).

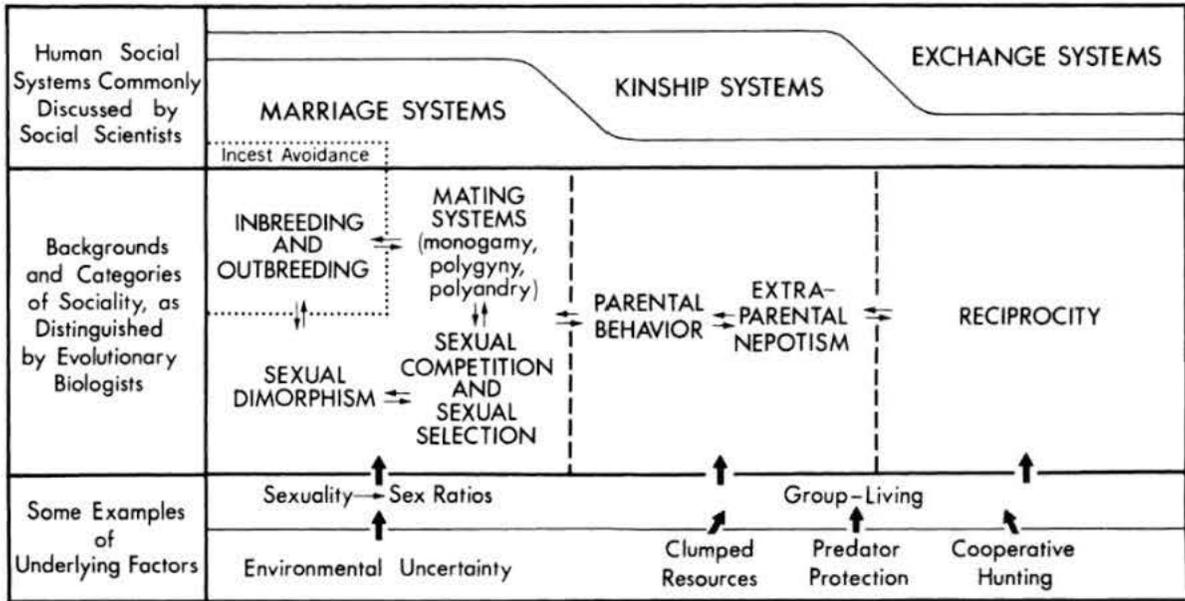


FIGURE 3. — The overlapping relationships of three major systems in human sociality (top) commonly discussed by social scientists, as indicated by the manner in which they apparently correspond with various social and parasocial phenomena (middle) of interest to evolutionary biologists. The viewpoint is adopted here (see text) that the three aspects of human sociality illustrated are appropriately viewed as expressions of the biological phenomena underlying them, and that analyses of human sociality will be facilitated by so identifying them and by more clearly distinguishing them from one another on this basis. The examples at the bottom of the diagram are intended to illustrate how the social phenomena studied by evolutionary biologists can be linked, through the effects of natural selection, to underlying nonsocial features of organisms, and ultimately to identifiable attributes of the extrinsic environment.

THE HUMAN NETWORK OF KIN

When humans began to live continuously in social groups within which they could distinguish numerous relatives of differing degree, two new selective forces were added to their social lives, as compared to those of most other species. First, extrafamilial relatives became reproductive resources as both sources and objects of nepotism, and second, genetic outbreeding beyond the limits of the nuclear family became possible because knowledge of the differing degrees of relatedness of extrafamilial relatives became potentially available to every individual.

The diagram of relationship shown in Fig. 2 effectively conveys the fact that, normally, every individual lives out his life embedded in a network of near and distant kin. The importance of degrees of genetic relatedness is illustrated by the fact that every kind of relative has an accepted name. In other words, leaving aside for the moment that nomenclature varies among societies, the words on the diagram were all

taken from the communicative signals of one society of the human species, and they are well understood and widely used by the members of that society. Such different names for different relatives are used within essentially every segment of society, even when large groups of relatives or clans are so powerfully cohesive as to behave like single families and as to use the word "family" or "clan" to denote the boundaries of kinship. Each individual is not only a member of a particular "family" or "clan" but in Ego's terms a particular kind of relative within the group.

Every person will also realize that the word "family" usually refers to individuals indicated inside the first circle surrounding Ego — parents, offspring, and siblings. All of these relatives, in a monogamous family, are related to Ego by the same amount, either exactly (parents and offspring) or on average (all others). Hence, there is a genetic correlate for the generalization "family," and for the tendency to refer to other individuals on the basis of whether or not they are members of the family.

Similarly, every individual recognizes that at some level toward the outside of the diagram he and his family tend to stop treating relatives in a special fashion, or even referring to them as relatives. Most people in a modern technological society, for example, may know of the existence, at least, of all of their first cousins, but few could count, let alone name, all of their second or third cousins, or their cousins once or twice removed (Schneider and Cottrell, 1975). At these points relationships are usually treated as trivial, although the precise relationship of unusual, famous, or wealthy distant relatives is often remembered and repeated. In general, however, distant relatives, even of differing degrees, tend to be combined under some label such as "distant cousins." In other words, variance in relatedness among associates increases beyond the limits of the nuclear (especially monogamous) family. Then, for practical purposes, it decreases again beyond some level such as that of first cousins; and these changes in variance and effective variance are signalled by tendencies to combine near and distant relatives under the general terms of "family" and "distant cousins," respectively. Between these two extremes relatives tend to be grouped according to (1) relatedness (e.g., sister or brother versus aunt or uncle versus cousin), (2) usual degree of dependency relative to Ego (e.g., aunt or uncle versus niece or nephew), and (3) sex (e.g., aunt versus uncle, niece versus nephew). These kinds of groupings, which are not greatly different from those distinguished by Kroeber (1909), are obviously consistent with a Darwinian model.

CLASSIFICATORY KINSHIP

Kin terms like "mother," "father," "brother," "sister," "aunt," "uncle," and "cousin," are frequently, and sometimes formally and consistently, applied to individuals that clearly do not have the genetic relationship to Ego of such relatives in Fig. 2. Especially when such designations are formal and institutionalized within societies, they are part of what anthropologists refer to as "classificatory" systems or aspects of kinship nomenclature; for an effort to analyze another aspect of such designations in Darwinian terms, see Alexander (in press). The widespread existence of classificatory designations like those above has been used to deny or deprecate the likelihood of a biological background for kinship systems.

Here I will argue the opposite. Suppose that I as an individual, or the members of my society generally, should wish to adjust the apparent social distance, or the privileges and responsibilities, of some particular members or classes of members in the society. First, that such shifts are even possible indicates a certain regularity within society. Second, that terms commonly denoting classes of genetic relationship are employed to create the adjustments indicates that the regularity is based on genetic relationship. After all, if I should wish to draw inward, socially, a particular individual, what reason is there for me to use a kin term like brother except that brother ordinarily refers to someone with the close relationship that I wish to create? The existence and nature of at least some classificatory aspects of kinship thus strongly support, rather than negate, the notion that genetic relationships and nepotism represent the basic cement of human sociality.

This argument calls attention to the fact that the nomenclature of kinship and sociality may be employed at two or more levels. For example, distant relatives may be termed "brother" by certain kinds of associates or interactants in a given society. It does not follow that individuals in such relationships will necessarily be treated like true brothers in every possible social circumstance, or, at least of all, actually confused with one's true brothers. Conversely, it does not follow that true brothers will, frequently or ever, be referred to by a term specifically designating siblings. Just as one may call anyone "brother," and otherwise treat him like a brother or not as circumstances dictate, one can also know his own brothers, and treat them accordingly, with sparse or no use of a specific kin term. The true significance of use of a kin term, or failure to use one, may thus be confusing to observers of a social group, and even to some participants in the system. Indeed, as everyone

is aware, a term like "brother" may very well be used deliberately to deceive either the individual designated by it or anyone else who may observe the designation.

Complications of these sorts in no way suggest that the principles of natural selection have not influenced the history of the structure of human sociality. Instead, their analysis tends to reinforce the idea that when we employ such principles we are finally on the correct route toward understanding our individual and collective tendencies and motivations.

KINSHIP AND CULTURE AS GROUP PHENOMENA

It is significant that in human social systems, *individuals*, particularly those of close genetic relationships, are designated or named according to their particular relationship to Ego rather than solely in a fashion designating them as a member of a given group or society. Anthropologists argue that culture is a group phenomenon, and in some respects it certainly is; class or team designations in which individuals tend to lose their separate identities are clear evidence of such group functioning. But the meticulous delineation of individual genetic and social relationships within human society also indicates quite clearly that the structure of human social systems, at least historically, has not been such as to erase individual functions completely, or disallow competition at the individual level. The prominence of individual designations of kin, which causes the diagram in Fig. 2 to represent a familiar situation to anyone who examines it, supports the validity of a biological approach to the analysis of human sociality which assumes an emphasis on reproductive competition at the individual level.

It is almost impossible to find an anthropological description of a kinship system which appears to contradict the arguments made above, even though the likelihood of a match to so many Darwinian predictions by chance alone seems vanishingly small. The disagreements appear chiefly in the interpretations by social scientists of what they found, and in analyses strongly influenced by theory. Here I quote from Beattie (1960, pp. 49-51) the kind of passage one may locate in almost any anthropological study, which contains information touching upon nearly all of the points discussed so far; and which takes on new meaning when viewed in terms of the Darwinian approach developed here.

"Nyoro kinship terminology is classificatory, like that of many simpler peoples for whom affiliation with a particular group of kin is important. This means, usually, that terms which one applies to relatives in one's own line of descent are also applied to certain

other relatives who are in collateral lines of descent. Thus one's father's brother may be called 'father,' his son may be called 'brother,' and so on. Even a father's sister (who is a member of one's father's group and generation) may be called 'father,' and the Nyoro term for this relative can be translated 'female father.' As far as one's patrilineal relatives are concerned, this classificatory usage means that all of them, however distant the connection, are 'brothers,' 'sisters,' 'fathers' (both male and female), 'grandfathers,' 'children,' or 'grandchildren.' And to call them by these terms means that one should behave toward them, to some extent at least, as one would toward one's nearest agnatic kinsfolk in these various categories. In Bunyoro this usage even extends to people with whom no genealogical relationship at all can be traced, for any member of one's own clan (and clans are widely dispersed and often no real genealogical relationship can be traced between clansmen) is regarded as an agnatic relative, and placed in the appropriate generation. One of the effects of this classificatory usage is to enhance and stress the unity of groups of agnates, for it implies that the same kind of cooperation and mutual support should be extended to and expected from all its members, whatever the degree of relationship. Indeed it would be unseemly to inquire about the exact relationship; Nyoro say that where clansmen are concerned the important thing is friendship, not the degree of relationship.

"But the classificatory system is not restricted to one's agnates. A man's mother's sister (who of course is not his agnate, since her link with him is not through his father but through his mother) is regarded as a kind of mother, and is so referred to. His mother's sister's children, like his own mother's children, are called 'brother' and 'sister.' Even his mother's brother is a kind of 'mother' (even though he is a man), and he is called 'male mother.' This is not so strange as it sounds, when it is remembered that the most important thing about your mother's brother is that he is a member of the same agnatic group or lineage to which your mother belongs. In quite a real sense *all* the members of your mother's agnatic group are 'mothers': your attitude toward them is quite different from your attitude toward your 'own' people, the group of agnates of which you yourself are a member. In systems like the Nyoro one, where one's father's people (and so one's own) and one's mother's people belong to quite separate and distinct social groups and are quite differently regarded, it would evidently be most misleading to translate the words for both father's and mother's siblings (that

is, brothers and sisters) as 'uncles' and 'aunts,' as we do in our system. We use, for instance, the same term, 'uncle,' for both father's brother and mother's brother, because we think of them both as the same kind of relative. To Nyoro, on the other hand, they are as different as they can be, for one's father's brother is a member of one's own group, while a mother's brother is a member of an entirely different group. And a Nyoro's expectations and obligations in regard to members of these two distinct groups are quite different.

"These ways of classifying kin provide a means of placing in a few simple categories a great many of the people whom a Nyoro peasant is likely to have dealings with in his everyday life. Everybody he meets is either a member of his own clan or he is not. If he is, he must be treated as a father, a brother, or a son, depending on their relative ages. If he is not, he may be a member of a clan with which the speaker is related through either kinship or marriage. Thus he may be a member of his mother's clan and so a kind of mother, or of a grandmother's clan and so a kind of grandmother, or of his wife's or his brother's wife's clan and so a kind of brother-in-law. Or he may belong to a clan in which there is another member with whom the speaker or one of his clansmen has made a blood pact, in which case friendliness and mutual help are prescribed. In all these cases there is a ready-made set of behavioral categories, labeled with kinship or affinal or 'blood-partnership' terms, through which amiable personal relations may, and should, be established and maintained. In these ways, the Nyoro clan system, combined with the classificatory mode of designating relatives, provides for the extension of a few quite simple relationship categories over a very wide social field."

ANALYZING HUMAN KINSHIP SYSTEMS

Reasons for the general rejection by social anthropologists of the premise that human kinship systems operate on the basis of biological relationships seem much more complex than a simple rejection of Darwinism, owing to the assumption of an obligate determinism and the ontogenetic problem, hence a fear of social Darwinism. Of course, the general failure to accept Darwinism as a guiding theory meant that there were no compelling theoretical reasons for being skeptical about dismissing biological causations. Also possibly contributory was the tendency by anthropologists to focus on group functions in culture, which tended to downplay possible advantages of kinship systems to indi-

viduals. Additionally, there was the wide suspicion among humans of interpretations of their natural history which give primacy to either individual selfishness or reproductive functions. Finally, numerous apparent violations of a biological basis for kinship systems have been described, a few of them prominent, essentially universal, and seemingly dramatically opposed to predictions from genetic considerations.

These apparent violations seem to fall into at least two general categories. The first, mentioned earlier, involves the fact that systems of reciprocity appear to have grown up largely employing, in confusing fashions, terms derived from, or implying genetic relationships that obviously are not accurately reflected by them.

The second category of violations includes complex genetic relationships that remained incompletely analyzed, hence, in some cases, were wrongly interpreted. Two such violations are perhaps most prominent of all, and most frequently used to indicate the futility of analyzing kinship systems according to genetic relationships. They are, respectively, (1) the phenomenon commonly termed "mother's brother" and (2) the asymmetrical treatment of cross- and parallel-cousins, nomenclaturally as well as in regard to nepotism and incest avoidance. I have already initiated an examination of these two apparent inconsistencies (Alexander, 1974); here I analyze them somewhat further. Unless we are able to explain them convincingly on biological grounds, we will certainly be unable to proceed.

Because amounts of nepotism are difficult to quantify or compare (analysis of wills is a possible exception), and because complete accounts of sexual liaisons are not a practical goal, the two major sources of information will be the nomenclature of kinship and the patterns of marriage. The writings of anthropologists offer some support for this compromise. Thus Lowie (1917) says the following about kinship nomenclature:

"Generally speaking, the use of distinct words for two types of relatives is connected with a real difference in their social relations to the speaker. Thus, a majority of primitive tribes draw *no* distinction between the father's sister's daughter and the mother's brother's daughter. But among the Miwok of California, where one of the cousins may be married while the other is within the prohibited degrees, a discrimination is made in language. Again, in many regions of the globe an altogether special bond connects the maternal uncle with the sister's son, and accordingly we find that he is very often sharply distinguished from the paternal uncle in nomenclature.

"On the other hand, we can very often explain very naturally the use of a single word for two or more relatives whom we designate by as many distinct words. The Vedda of Ceylon, for example, call the man's father-in-law and maternal uncle by the same term. The reason is that here a man commonly marries his mother's brother's daughter; the mother's brother *is* his father-in-law . . ." (p. 98-99).

"Terms of relationship are, in some measure, indices of social usage. Where relatives whom other people distinguish are grouped together, there is some likelihood that the natives regard them as representing the same relationship because they actually enjoy the same privileges or exercise the same functions in tribal life. Where relatives whom other peoples group together are distinguished, there is some probability that the distinction goes hand in hand with a difference in social function" (p. 100).

Similarly, in his cross-cultural analysis of incest avoidance, Murdock (1949) says the following about marriage patterns (p. 301):

"Extended incest taboos — or exogamous rules, as they are frequently called — ordinarily apply alike to sexual intercourse before marriage, to extramarital sex relations, and to marriage. . . . Identity in the three rules is so general . . . that the few exceptions can be safely disregarded in most statistical tests. This is fortunate since it enables us to use marriage rules, which are reported nearly thrice as often in the literature, as representative of all types of extended sexual prohibitions."

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, usually termed the "avunculate," is often a general feature of society. It has always puzzled students of culture although various explanations have been offered (e.g., Radcliffe-Brown, 1924; Harris, 1971). A close examination of the situation reveals the following curious fact, of significance for a Darwinian approach, and illustrated in Fig. 4:

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 $\frac{1}{4}$ like him in genes identical by descent; those of his half sister are $\frac{1}{8}$ like him. Only by a remote

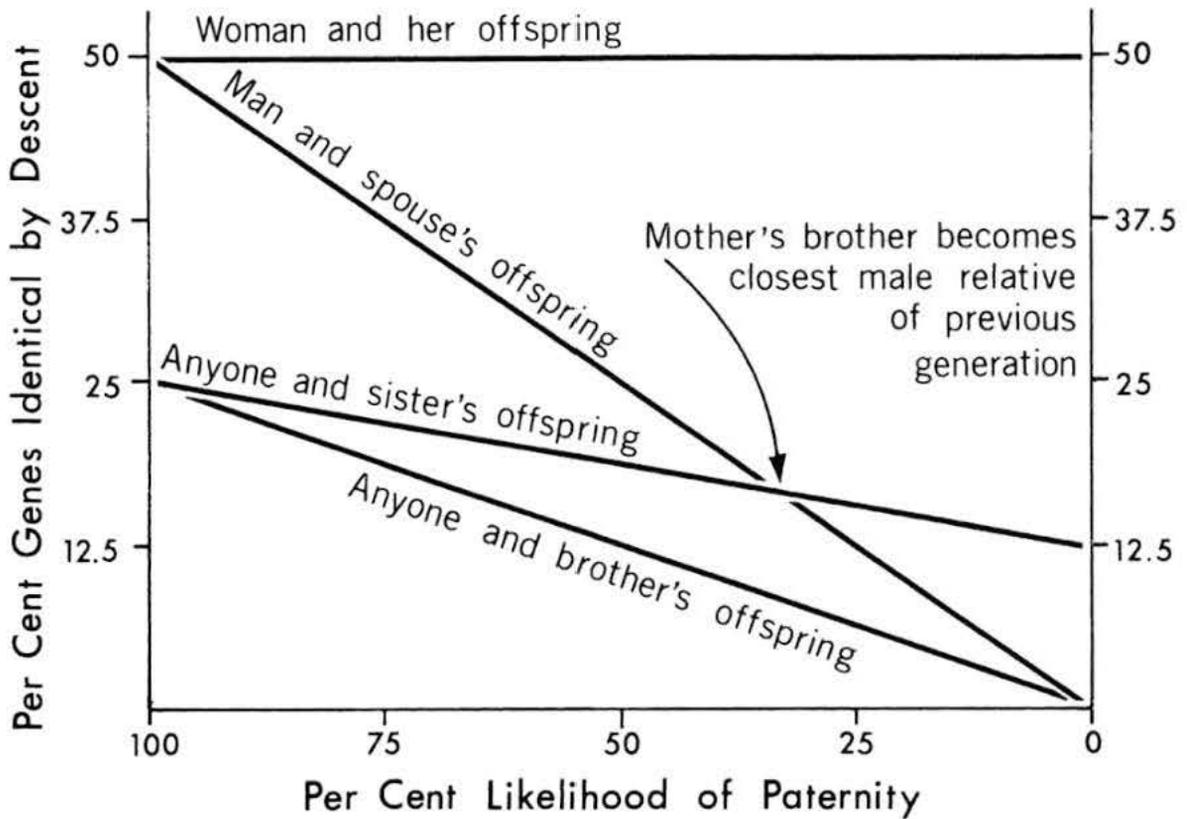


FIGURE 4. — Genetic relationships with putative offspring, and with various kinds of nephews and nieces, with variations in confidence of paternity. Lowered confidence of paternity may be caused by such circumstances as husbands and wives living apart or long absences of husbands on hunting or military trips. Low confidence of paternity may be expected to lead to increased deficits in paternal care by mother's spouse, thus increasing the value of care given by mother's brother. Tendencies by men to discriminate among their spouse's offspring on the basis of phenotypic similarity or difference to themselves, or on the basis of other evidence of philandering by the spouse, will lead to the favoring of some of spouse's offspring over others, and to an increased favoring of sister's offspring over those rejected. Hence, the point at which mother's brother becomes prominent in a society can actually be moved far to the left of the intersection of the lines indicating relationships to spouse's and sister's offspring. The location of this point will also be influenced by the value of paternal care, as opposed to maternal care, and by the extent of differentials in male ability to dispense paternal benefits (e.g., if rich uncles are likely, tendencies to seek their assistance might also be likely).

To simplify the diagram I have kept confidence of paternity and confidence of full (verses half) sibship equal; they need not be.

accident of meiosis or an almost equally remote mistake in maternity can the offspring of a man's sister be totally unlike him (the latter mistake is not quite so remote in technological societies in which women give birth in large hospitals while under anesthesia). His spouse's offspring, on the other hand, are either $\frac{1}{2}$ like him (in genes idb) or totally unlike him; they will be intermediately related to him only if his spouse

has philandered with one of his relatives. 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 parental benefits to her offspring which may otherwise suffer from lack of paternal assistance.

If low confidence of paternity is general throughout a society, a man's sister's offspring because of the high confidence of maternity, can become his closest known relatives in the next generation. Thus, if paternity is on average correctly ascertained only $\frac{1}{4}$ of the time, then a man's spouse's offspring will average $\frac{1}{8}$ like him (and 3 of 4 will be totally unlike him), while his sister's offspring will average $\frac{5}{32}$ like him, and all will approach this degree of overlap. In making these calculations one has to take into account that lowered confidence of paternity will also lower the average relationship between brothers and sisters. I have assumed that if likelihood of paternity is $\frac{1}{4}$, then likelihood of siblings having the same father is $\frac{1}{4}$; other assumptions are also possible.

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, any individual male may suffer from a personal lack of confidence of paternity to the extent that his nieces and nephews, whether offspring of his brothers or his sisters, may be his closest relatives in the next generation. This alone does not mean that such relatives are the most appropriate targets of his parental care, since if his low confidence is unusual (i.e., other males are confident), his nieces and nephews may be expected to have fathers willing to care for them. Whenever general living conditions or other society-wide circumstances lead to a general lowering of confidence of paternity, however, only a man's sister's offspring, among all possible nephews and nieces, can become his closest relatives in the next generation. Moreover, children in such societies will generally fail to receive intense parental care from their mother's spouse. In consequence, so long as adult brothers and sisters tend to remain in sufficient social proximity that men are capable of assisting their sisters' 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. We can add that to the extent that paternal and maternal care are differently appropriate for the two sexes of offspring, and (as might be expected in some regards) paternal care is more appropriately directed to males, mother's brother may be expected to attend more to sister's sons than to her daughters.

For an example of living conditions leading to lowered confidence of paternity, associated with a prominence of mother's brother, consider Alland's (1972) account of the Abron in Africa (p. 105ff):

“. . . the married couple stays apart. The man is in residence with his father (or in some cases with his maternal uncle). . . . The woman lives in the house of her mother and her mother's sisters, with her sisters and the children of her mother's sisters. . . . If a man has two or more wives, they will live in different houses, since a man is not permitted to marry sisters. . . . On the death of the last surviving senior male of the same kin group related through a line of women . . . [the ownership of his house] passes on to the eldest son of the eldest sister of these men. This follows the standard inheritance pattern of the Abron which, as I have already indicated, is matrilineal (from man to man through a line of related women). The pattern of inheritance extends to land holding as well. A man does not inherit from his father but from his maternal uncle. . . . In many such societies the maternal uncle is occupied with the discipline and the father is free to play a supportive role. . . .”

A parallel relationship between prominence of mother's brother and confidence of paternity is clear in the writings of Fortune (1963) on the Dobu of New Guinea:

“Each villager, male or female, owns a house site and a house. . . . The husband in every marriage must come from another village than that of his wife. His house site is in one village, his wife's house site is in another. . . . [A] father bequeaths his house site to his own sister's son. His own son inherits house site and village status from his mother's brother in his mother's village (p. 2). . . . The couple with their children live alternately in the woman's house in the village of the woman's matrilineal kin, and in the man's house in the village of the man's matrilineal kin (pp. 4-5). . . . ‘Those-resulting-from-marriage,’ if they are men, are always abnormally uneasy about their wives' fidelity. Now when a woman is in her own village, she has her kin next door and only too ready to eject her husband if he dares to lift a hand against

her, or use foul language to her. She has no great dependence on her husband for care of her children, since a woman can nearly always get a new husband for future help, and her brother ultimately provides for them in any case. Consequently she behaves very much as she likes in secret (p. 6). . . . Dobuan folklore is full of husbands pathetically packing up their goods and going home to their mothers and sisters after a child has informed them that their wife has been consorting secretly with a male member of a distantly related *susu* of her own village (p. 7). . . . Jealousy normally runs so high in Dobu that a man watches his wife closely, carefully timing her absences when she goes to the bush for natural functions. And when it is time for woman's work in the gardens here and there one sees a man with nothing to do but stand sentinel all day and play with the children if any want to play with him (p. 7). . . . The chances of divorce are high. The oldest Dobuan in my main genealogy had had eight successive marriages, one of the youngest men in the genealogy had had four, one other youth, three, and this is fairly typical of an overwhelming majority of Dobuans (p. 9). . . . A Dobuan tends to think of his sister first of all his ties when the question of breaking ties arises. Dobu practice the avunculate, inheritance passing from mother's brother to sister's son, but this is from no great sentiment between a man and his sister's son. Rather the sister enlists the brother in the interests of her children (p. 62). . . . Every woman claims by right the inheritance of her brother for her male children (p. 3)."

Similarly, this correlation is prominent in some of the matrilineal societies discussed by Schneider and Gough (1974), and generally in cases of prominence of mother's brother (Murdock, 1967).

Fortune's description of the Dobu raises the question of how the institution of mother's brother became prominent in different societies, and how it acquired its relationship to matrilineality and lowered confidence of paternity. Any woman might be expected to turn to her brother for assistance upon loss of child support by a spouse as a result of separation or divorce. She seems less likely to obtain adequate assistance from a brother who is encumbered with the full care of his own offspring. This means that the shift from paternal care to the avunculate, where it has occurred, could have involved (1) young and childless brothers, (2) brothers estranged from other wives, (3) unusually wealthy or powerful brothers, or (4) brothers who are for other reasons unlikely to be successful with their own offspring (e.g., see Dickeman, in press), contributing to the support of sister's offspring. Such a

practice would in certain cases (e.g., the Dobu) tend to relieve women of the necessity of maintaining less than optimal marriages, which in turn could reinforce the strength of the avunculate and the solidarity of kin relationships through mothers, and further weaken the institution of marriage. It is difficult to see how a woman could gain from her spouse having a low confidence of paternity, but she is not as constrained to provide confidence of paternity for him if she can depend upon her brothers and other relatives for child support and other assistance.

Men would ordinarily gain reproductively from being able to tend their own offspring rather than those of sisters. But under certain conditions — such as when inheritance of resources such as land and cattle is very important, and living conditions, absence as a result of military requirements, or other factors cause lowered confidence of paternity — it is easy to understand how shifts toward prominence of mother's brother, matrilineality, fragility of marriage bonds, and lowered confidence of paternity might go together, in patterns entirely consistent with a Darwinian model of human sociality. I emphasize that men may sometimes gain from favoring juveniles less closely related to them than their own offspring, and that much nepotism may be dispensed to sisters' offspring in ordinary situations, owing to the generally greater potential for power among males, causing brothers generally to assume responsibility for sister's welfare and that of her family. These circumstances commonly may occur without the extreme shift which I wish to emphasize, leading to cases in which sister's offspring are actually favored over spouse's offspring. Prominence of the avunculate obviously does not require that a man's sister's offspring average a closer relationship to him than his spouse's offspring.

ASYMMETRICAL TREATMENT OF COUSINS

Cousins are the offspring of siblings. Offspring of full siblings, which share both parents, share on average $\frac{1}{8}$ of their genes, *ibd*; offspring of half-siblings share $\frac{1}{16}$ of their genes (Fig. 2).

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), cousins are usually not subdivided in this fashion, causing these terms to be novel for most persons other than anthropologists; but cousins are so divided in many other societies and in many different parts of the world (Murdock, 1967).

In general, close relatives are more likely to be objects of nepotism,

and less likely to be objects of sexual behavior, than are more distant relatives. In cases 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 prominently analyzed with regard to cousins as has marriage behavior, the nomenclatural asymmetry implies that parallel-cousins also favor one another in nepotism over cross-cousins.

As is typical of human social patterns, these practices are not entirely consistent. Thus, the asymmetry of treatment and nomenclature and reversals in a few societies (with parallel-cousins rather than cross-cousins favored in marriage) have been used prominently and frequently to emphasize the inappropriateness of assuming a biological background for kinship nomenclature and behavior. Since cross- and parallel-cousins are genetically similar to exactly the same degree, it is asked, why should they be treated differently (e.g., see Lowie, 1920; Levi Strauss, 1969)?

To examine this question as an example in the search for biological sense in human cultural practices, we may consider first the likelihood that the assessment of genetic overlap is really correct for the societies in question. It will only be correct, of course, when true (genetic) parents correspond exactly to functional (social) parents. But deviations occur, and in a given society some kinds of deviations may be more likely than others. In a monogamous society with carefully kept records, perhaps deviations will be minimal, and they would seem to have little possible effect on cousin marriages. So we expect societies with long-term monogamy to be symmetrical in regard to the treatment of cousins, hence, not to distinguish them.

But many societies, even today — and nearly all nontechnological societies — permit polygynous marriages, or did so within recorded history. The evident antiquity of group-living in humans, the universality of polygyny (sometimes deriving from promiscuity) in multi-male primate social groups, and the prevalence of polygyny even recently (Murdock, 1967) all indicate that polygyny has likely been a prevalent marriage system in most societies during most of human history. Moreover, in most polygynous societies, sororal polygyny is prevalent — that is, the different wives of one man may be sisters to one another. Additionally, in association with polygyny commonly resulting in many

less powerful men, and particularly younger men, being mateless, older, more powerful men may accumulate wives in excess of the number they can actually retain and pass them to younger brothers still unable to acquire wives on their own (Chagnon, 1968).

In a sororally polygynous society, sisters' offspring will often be half-siblings. If brothers share wives to a significant degree, or if older brothers transfer wives to younger brothers, brothers' offspring will also average a closer relationship than will cross-cousins. That is, there will be less possibility of knowing precisely who has fathered particular babies, and the potential errors involve brothers. In polygynous societies, then, what seem to be parallel cousins may actually have the same father, and in fact they "are usually themselves called siblings in primitive languages" (Lowie, 1970:76). "Parallel-cousins" in such societies will thus on the average be genetically more closely related than cross-cousins (Harris, 1971; Alexander, 1974), and this fact must somehow be explained away before we can dismiss the differences in incest rules for cross- and parallel-cousin unions as genetically meaningless or owing solely to the particular whims or idiosyncracies of different groups.

Numerous asymmetries in genetic overlap between paternal and maternal relatives are possible, and they may correlate closely with tendencies to distinguish them in ways that European monogamous (hence, symmetrical) societies do not. It is worth stressing that the actual origins, or any particular (proximate) reasons given, for the existence of such rules in any society are not in themselves sufficient to cast doubt on the significance of such correlations. They may be as irrelevant to the question of reproductive significance or function as is, say, variation in the ontogenetic background of two bird songs to the fact that each protects the territory of the possessor.

If incest avoidance is principally involved in the greater favor with which cross-cousin marriages are viewed, as contrasted with parallel-cousin marriages, then several predictions can be made about symmetry and asymmetry in the encouragement and discouragement of cross-cousin versus parallel-cousin marriages, and likewise of marriages between parallel-cousins with brother-fathers and those with sister-mothers.

In monogamous societies of long standing, in which marriages usually last a long time or for the lifetimes of the partners, cross- and parallel-cousin marriages should be most symmetrical. For at least two reasons they may not necessarily be symmetrical in any given case: (1) monogamy may be recent and (2) communal living of an asymmetrical sort (e.g., brothers with their wives in the same household, or sisters

with their husbands) may lead to a greater likelihood of parallel-cousins being half-siblings. The reverse can only be true (cross-cousins more closely related than parallel-cousins) if brother-sister incest occurs. If the argument is valid that culture is reproductively adaptive, then only when incest rules do not promote outbreeding should cross-cousins be called siblings when parallel-cousins are not.

A general failure of symmetry in cousin treatment alone might, on account of the great likelihood of a history of polygyny, support the notion that reproductive history is important in interpreting human culture. In cases of ancient monogamy, one should expect parallel- and cross-cousins not to be distinguished at all, as is true of the Andaman Islanders (Radcliffe-Brown, 1964) and all of Murdock's (1967) 28 societies in or derived from modern Europe. Asymmetry should be greatest in systems of sororal polygyny in which men are permitted to make secondary marriages with brother's wives, or when sororal polygyny is prevalent and men cannot take brother's wives.

Considering the extremes, then, asymmetry in cousin treatment should be concentrated in societies favoring or specifying sororal polygyny, and symmetry should be concentrated in societies practicing monogamy. Almost half (211) of the 423 societies in Murdock's (1967) ethnographic sample (of 565), usable for this purpose because the relevant data are there, treat parallel- and cross-cousins symmetrically or do not distinguish them, and half (212) treat them asymmetrically or distinguish them. But 75 of 79 societies (95%) favoring or prescribing sororal polygyny treat parallel- and cross-cousins asymmetrically, while only 35 of 101 monogamous societies (35%) do so ($p < 0.0001$). Alternatively, using Murdock's (1967) standard sample of 186 societies, substituting where data are not available for a few societies indicated in the sample, one finds that only 5 of 15 monogamous societies (33%) treat cousins asymmetrically, while 7 of 8 sororally polygynous societies (87.5%) treat them asymmetrically ($p = 0.0177$: Fisher's exact probability test; Siegel, 1956). These data do not include information on whether or not men are allowed to make secondary marriages with brothers' wives because Murdock does not include this datum.

There are actually two kinds of symmetrical treatment of cross- and parallel-cousins, those in which all are referred to as cousins and never classified as siblings (60 societies) and those in which all cousins and siblings are referred to by the same terms (132 societies, of which 23 are monogamous). In the latter case cousin marriages are obviously not allowed. Of 94 monogamous societies with the relevant data available, 73 (80%) disfavor or forbid all cousin marriages, so it is not sur-

prising that 35% of the monogamous societies treating cousins symmetrically refer to them as siblings and forbid them to marry. The single exception to asymmetrical treatment of cousins among the eight sororally polygynous societies in Murdock's standard sample, used above, is the Papago Indians of Mexico (Underhill, 1939), who are described as disfavoring all cousin marriages and refer to both cross- and parallel-cousins as siblings (hence, this is not really an exception, although I have so treated it in the test — see below).

Another possible explanation for asymmetrical treatment of cross- and parallel-cousins, also consistent with a Darwinian model but not distinguishable by the tests I have described, was suggested to me by William Irons. He notes that favoring relatives of the same sex when the sex is in a position particularly to benefit from the kind of assistance one can give could lead to a lineal bias in which, for example, mother's sister, as well as mother's sister's offspring, were favored over mother's brother and his offspring. It seems to me that this might be especially true (i.e., also prominent) in cases of sororal polygyny, where sisters would benefit from cooperating, sometimes to have their own way against a powerful husband. But we would be hard-pressed to separate these two effects. Moreover, the explanation suggested by Irons might account for preferential nepotism; it would not account for sexual or marital avoidance.

So far I have mentioned two respects in which kinship terms referring to cousins seem not to reflect genetic relationships: (1) parallel-cousins are sometimes called siblings and (2) all cousins are sometimes called siblings. These two departures from genetic kinship seem to reflect the two general categories mentioned earlier, which together may explain a great deal about the background of human kinship conventions. In the first case the apparent deviation is not deviation at all but a closer genetic fit than the model observers had been applying to call it a deviation. The second case appears at first to be a genetically arbitrary decision to serve some particular purpose or function. Such arbitrary decisions may be responsible for much kinship nomenclature. In this case, however, if the function of incest avoidance is served by genetic outbreeding, then referring to all cousins as siblings is not genetically arbitrary if it reflects a closer genetic relationship than in those cases in which cousins are not called siblings, or if it leads to greater outbreeding in societies in which it is less expensive or for other reasons advantageous to avoid first cousin marriages.

Other deviations from genetic relationships in kinship terms are related to those discussed above. Thus, father's brother and mother's

sister are sometimes called father and mother, respectively. As we have already seen, father's brother may indeed be father, and mother's sister in sororal polygyny will have offspring $\frac{3}{8}$ like those of mother. Cross-cousins are sometimes called by names applying to other generations, such as aunt, uncle, niece, or nephew. This effectively removes them from the marriageable category by referring to them as relatives that are related by $\frac{1}{4}$ and characteristically are involved in incest taboos. Similarly, marriageable cross-cousins may be called cousins, and non-marriageable cross-cousins may be called siblings. In each case we will wish to know eventually if there are reasons for suspecting that nomenclatural practices deviating from those apparently genetically appropriate reflect historical variations in genetic differences not yet obvious to us.

In some societies, such as nomadic tribesmen in North Africa, parallel-cousin marriages are preferred (Murdock, 1967); this tendency may actually exist throughout most Arabic-speaking populations (Irons, Dickeman, pers. comm.). The preference is asymmetrical, involving the offspring of brothers, not sisters, and inheritance passes from generation to generation through male offspring. So this system of marriages tends to keep herds and other goods intact and within the family and this has in fact been given by participants in the system as the reason for its maintenance. It is not difficult to suppose that the conflicting costs and benefits of nepotism and marriageability (one marries a more distant relative but nepotistically helps a closer one), which both seem often to focus at the cousin level (one terminating with closer relatedness, the other with more distant relatedness) may involve a delicate balance that can be tipped by special circumstances. Thus, the costs of inbreeding may sometimes, and perhaps with these herdsmen, be outweighed by the benefits of inheritance of wealth or goods. Similar circumstances may prevail in royal lines, notorious for their tendencies to inbreed quite closely. With royalty it is the crown that must be retained at all costs, and its retention may depend upon royalty marrying royalty even when the only royalty available is within the nuclear family.

In these two prominent cases, then, of mother's brother and the asymmetrical treatment of cousins, a Darwinian model for the natural history of human behavior is not only upheld, but it leads to directions of investigation not previously taken, yet apparently yielding significant promise for the solution of problems that have long perplexed students of human sociality. At the very least we may consider that we have good reason to continue our analysis of the relationship between human behavior and natural selection.

A COMMENT ON INCEST AND MARRIAGE PATTERNS

Incest avoidance may be regarded as an aspect of mate selection whereby, in general, close relatives of the opposite sex are unavailable or disfavored, while more distant relatives are favored or specified. Members of one's nuclear family are nearly always excluded as possible mates, and, in humans, certain close relatives, just outside the nuclear family, are nearly always either excluded or disfavored. Other relatives only a little more distant may be suitable, preferred, or prescribed mates. Distant relatives or nonrelatives may also be suitable, preferred, or prescribed mates. If fairly close relatives are preferred or prescribed, those more distant may as a result be more or less incidentally disfavored or excluded.

Genetic outbreeding does not necessarily imply that only the most distant possible relatives, or nonrelatives, are suitable marriage or sex partners. Restricting one's sexual or marriage partner to increasingly distant relatives involves increasing costs (Figs. 2, 5). Thus, fewer individuals are available, greater distances may have to be traveled to locate them, and greater risks may be involved in securing them; deleterious partitioning of reproductive resources may also result from extreme outbreeding.

On the other hand, close inbreeding also has disadvantages. Thus, with outbreeding fewer deleterious recessive alleles are exposed, there is less chance of reproductive devaluing of relatives because of sexual competition (Hamilton, 1967), and reproductive resources may be advantageously partitioned, for example, to those levels at which they are likely to undergo maximal inflation of their value. The complex patterns of marriage regulations in human societies may thus be largely interpretable as aspects of nepotism in which genetic relatives are constrained against competition, for mates and other resources, which devalues collective effects on the inclusive fitnesses of parents and other relatives. This explanation of marriage patterns and rules focuses attention simultaneously on individual interests in obtaining mates and resources and collective or societal interest in minimizing competition deleterious to the inclusive fitnesses of individuals related to the competitors. Rules or practices resulting from such collective interests must often be compromises based on differences in interests, and differences in power or influence; frequently, the most satisfactory or practical compromise remains the same from one generation to the next. In this case a Darwinian model appears to draw together the phenomena of individual interests and cultural collectivity (including its continuity) in a fashion

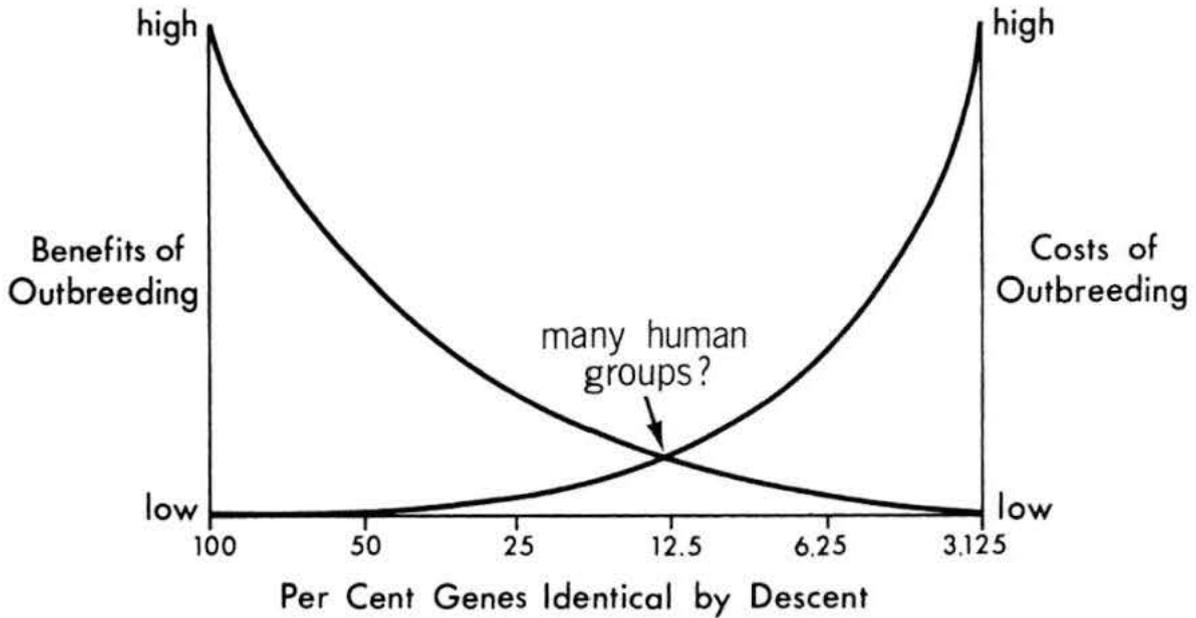


FIGURE 5. — Relationship between the benefits and costs of outbreeding (see text). It is inferred that they tend to balance near the level of first cousins in most human societies. In monogamous species in which, unlike the human species, relatives outside the family are not distinguished, the cost of outbreeding will rise sharply beyond the level of 50% genes identical by descent because it will include the cost of adding a method of distinguishing closer and more distant extrafamilial relatives. For polygynous families the same cost will be incurred largely outside the 25% level if half-siblings are reared together, hence can be excluded as mates with no additional cost of recognition.

not previously accomplished with cultural or genetic models that ignored inclusive fitness (Alexander, ms.).

Since the costs of inbreeding diminish outward and the costs of outbreeding mount with its degree, the two lines necessarily cross at some point (Fig. 5). I suggest that in most human societies the lines cross somewhere near the level of first cousins, farther out when more distant cousins are readily available, and closer in when the particular heritable resources involved are deflated rather than inflated in value as a result of extensive partition. Thus, we may expect nomads with few heritable goods, such as Australian Aborigines, to marry further out. Herdsmen and farmers, and members of titled or royal families, in particular, might tend to marry in. A very large number of factors may be involved in the exact degree of inbreeding and outbreeding, or in the selection of marriage partners at given levels of inbreeding and outbreeding. The important point is that with human marriage patterns, as with kinship systems and inheritance patterns, analyses based on cost-benefit assessments from a Darwinian model are called for, and they are feasible.

CONCLUDING REMARKS

In 1975 I wrote as follows: "That man has evolved his characteristics as a result of selection that never lost its potency at the individual level leads to the argument that civilization, and all of the notions regarding social interactions that derive from it and from which it is derived, like justice, morality, and ethics, to some large extent comprise specifications of the limits to which the collective members of this or that society will permit individual members of society to go in the course of reproductive competition. . . . the argument that group-living intensifies reproductive competition between individuals and requires continual pressure from some outside selective force such as predators to persist . . . implies that human society is a network of lies and deception, persisting only because systems of conventions about permissible kinds and extents of lying have arisen." I identified the triple paradox, referred to earlier, that "the only organism capable of at least a feeble analysis of its own attributes must use the very attributes to be analyzed to carry out the analysis, when a central one of those attributes is a rather strong tendency to reject the results of all such analyses!"

In this paper I have furthered the paradox by noting that another of our human attributes is the ability to initiate cost-benefit analyses, conscious and otherwise, of supposed human behavioral traits or tendencies identified for us, and, if we do not like the results, to cancel the traits or alter the tendencies. No other organism has this ability, hence is so potentially confusing to would-be investigators of its nature.

But we have still not specified the ultimate paradox. It is that the demonstration of the Darwinian model of human behavior, unless we are exceedingly careful, may not be the kind of enlightened behavioral modification described above, but the rejection of the model, through emotional arguments and the insistence that a Darwinian view, if accepted, necessarily leads to the destruction of society or its domination by evil and self-centered minorities. Thus to reject explanations of our sociality, solely because of society's historical framework of self-deception, would be to thwart any notion of a true human philosophy. It would be the greatest of all ironies that we should spend so much of our energies educating ourselves to enlightened adjustment and elimination of activities deemed personally and collectively undesirable, and promotion of those similarly deemed desirable, yet turn from such modifications to righteous and passionate denials when the very basis of sociality is exposed by the same kind of education.

A Darwinian model seems to me to be established beyond doubt as

an appropriate hypothesis for the background of a significant, if not the major, fraction of the proximate behavioral tendencies and motivations of humans. Assuming that I have properly interpreted the evidence on this point, presented here and elsewhere, we may now ask in which of two directions shall we move: Toward further tests of the Darwinian model, and its use where appropriate in conscious, rational, and collectively agreed-upon adjustments of the human fate? Or toward indignant and fearful denials of this and any other testable model of the background of social structure? Which alternative will we ultimately demonstrate to illustrate the true uniqueness of humanity?

A theory is the more impressive the greater is the simplicity of its premises, the more different are the kinds of things it relates and the more extended is its range of applicability.

—*Albert Einstein*

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