

How has evolution shaped human behavior? Richard Alexander's contribution to an important question

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Abstract

Richard Alexander has been a major contributor to the development of theory concerning the evolution of human sociality. His most important contributions include (1) a theory of the evolution of morality as a form of indirect reciprocity that aids in intergroup competition, (2) a theory of the relationship between biological evolution and culture, (3) an elaboration of Humphrey's theory of the human intellect as a social tool, (4) theories about human parental investment and nepotism, and (5) theories about scenario building, consciousness, and human communication. He also has offered a hypotheses on a large range of other human traits. He is a biologist and has also made major contributions to theories of speciation, communication, eusociality, and social organization in nonhuman animals and has contributed extensively to the study of a number of specific taxa other than the human species: crickets, katydids, cicadas, naked mole rats, and horses. His contribution to the study of nonhuman animals and evolutionary theory, in general, are sufficient to earn him a reputation as an outstanding leader in biology without reference to his work on humans. The same can be said for his contribution to the understanding of human sociality taken alone.

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1. Introduction

The latter part of the 20th century witnessed great progress in our understanding of how organic evolution has shaped the behavioral and social aspects of the human species. This progress has been built on the formulations of a number of crucial theoretical propositions and has involved a number of hotly contested debates. Richard Alexander played a central role in these intellectual developments. He has pointed to a number of issues and generated a number of important ideas and hypotheses, which continue to provide a framework for much research on the evolutionary foundations of human sociality. In this brief essay, I will point out what I consider Alexander's most significant contributions to our understanding of human sociality and briefly place these contributions in the broad outline of his lifetime work.

Alexander was trained as an entomologist at Ohio State University, from where he earned a PhD in 1954. Early in his career (1957), he took a position in the University of Michigan Museum of Zoology, where he remained until he retired in 2001 and where he is now a professor emeritus. As he neared completion of his doctorate in 1954, he decided that, in his future career as a biologist, he would address broad questions concerning evolution. As he put it: "I am going to proceed, for as long as I can, under the assumption that every trait of life can be explained by the process of organic evolution (in the succession of environments in which it has occurred, of course)" (Alexander, personal communication 2004). To do this, he decided to attack the traits that would be most difficult to explain in evolutionary terms, specifically behavior and, eventually, human behavior. However, he decided to begin with somewhat less difficult questions and then proceed step by step toward the more difficult ones. Thus, initially, he concentrated on behavior in the form of communication in the singing insects, specifically crickets, katydids, and cicadas. His interests in placing the human species in the same evolutionary perspective did not surface in print until he published his 1971 paper "The search for an evolutionary philosophy of man" (Alexander, 1971). By that time, he had already established his credentials as a leader in the study of the singing insects and, at the same time, as an important theoretician in evolutionary biology. His contribution to the study of nonhuman species is exceedingly impressive, and, if he had never written a thing about humans, he would still be in the forefront of contributors to zoology and evolutionary biology. But he did publish extensively on humans and trained a number of students who went on to study human behavior in evolutionary terms. In the remainder of this essay, I will limit my discussion to Alexander's contribution to the study of human behavior.

He authored two books on human behavior, *Darwinism and Human Affairs* (1979) and *The Biology of Moral Systems* (1987), and edited one volume with Donald Tinkle (1981), which contained a long section on humans. He also published a long list of articles and book chapters specifically focused on human beings and human behavior, including a seminal article in 1974 entitled "The evolution of social behavior" in the *Annual Review of Ecology and Systematics*. This latter article was eventually noted by Citation Index as one of the "most-cited" papers, and they asked him to write an essay on why he came to write that essay and why he thought it was so frequently cited. All of what Alexander has written on human behavior is densely packed with ideas (often novel) and with careful arguments about why natural selection at the individual level would or would not favor a particular human trait.

2. Balance of power, indirect reciprocity, and morality

Alexander's most significant contribution to the study of the evolutionary foundation of human behavior lies in the area of ground-breaking hypotheses that have served as the foundation of much of the work that is currently being done on the evolution of human behavior. In my opinion, his single most important idea is the balance-of-power hypothesis, which is the core of his 1987 book *The Biology of Moral Systems*. This idea, or ideas very much like it, had been suggested and explored earlier by a number of writers, including Alexander himself (Alexander, 1979; Alexander & Tinkle, 1981; Bigelow, 1969; Durham, 1976; Humphrey, 1976; Keith, 1949; Wilson, 1973, 1975), but he was the first to explore the idea at length and to tie it to an important human trait—morality. His reasoning was as follows. Human beings have an unusually elaborate form of sociality. Social groups of the size and complex structure of human groups are rare in the animal world, and when they do evolve, they are usually based on kinship. There are two broad categories of reasons for the evolution of large social groups: larger groups are, in some environments, better at gaining food (or perhaps some other resource) and larger groups are better, in some environments, at defending against predators. In the human case, the evidence suggests that defense against predators is the primary driving force behind the evolution of human sociality and that the predators consisted of other human groups. Human social groups have a long history of hostile aggression against other human groups (Chagnon, 1974, 1997; Keeley, 1996; Wrangham & Peterson, 1996), and in this kind of direct competition, larger, better-united groups definitely have an advantage. This created a strong selective pressure for the formation of larger social groups and led to a runaway selection for psychological abilities and propensities that facilitated the formation of larger, better united social groups.

Morality is one of these traits. Morality is an important tool for forming larger, more solidary social groups because it alleviates the problem of within-group conflict. Larger social groups are more prone to internal conflict, and moral sentiments and principles tend to dampen these internal conflicts. It should be noted at the same time that morality is typically something that human beings perceive as relevant to social interaction within social groups. Human beings have a very strong tendency to divide themselves into in- and out-groups, and morality is often not considered relevant to the treatment of members of out-groups. In fact, the moral thing to do is often to mistreat and even attack and kill members of other competing social groups. This is what one would expect as a result of selection for advantages in intergroup competition. Morality has a dark side, and Alexander, in all of his writings, never shies away from pointing out the dark sides of various human traits, a habit that has earned him hostile treatment by defenders of moralizing social science and moralizing humanistic authors. (For example, see Kitcher, 1985. To put Kitcher's book and the "Darwin wars" in perspective, I recommend reading Radcliffe Richards, 2000 and Segerstråle, 2000.)

A closely connected idea is that of indirect reciprocity. Alexander proposed that moral systems are systems of indirect reciprocity. Alexander (1987, p. 93) described indirect reciprocity as "a consequence of direct reciprocity occurring in the presence of interested audiences—groups of individuals who continually evaluate the members of their society as

possible future interactants from whom they would like to gain more than they lose (this outcome, of course, can be mutual).” In such a social environment, in which one is being continually observed by “interested audiences,” selection would favor displaying the quality of being altruistic to other individuals and of being a dependable reciprocator. Alexander expanded on this idea by suggesting that moral rules and codes are formulated by a process of discourse and negotiation among the members of a society or, in some cases, among the more powerful members of a society. In this discourse, different individuals advocate rules that will favor their own reproductive interests, and, eventually, compromise and something approaching consensus is reached. The fact that a large, well-united group has an advantage in intergroup competition provides a confluence of interests among group members encouraging their reaching a mutually satisfactory set of rules governing within-group behavior. He summarized this by saying that moral systems are contractual in character and cited Rawls (1971) as having a similar idea about moral rules and codes. Thus, moral authority is placed in the collectivity.

Many of the ideas developed more thoroughly in the *Biology of Moral Systems* appeared in earlier publications in shorter form. One of these is this idea that the moral authority that provides answers to ought-questions lies in “the entire collectivity of people willing to think on such [moral] problems and to participate in their solution” (*Darwinism and Human Affairs*, 1979, p. 139). This view allows that what is morally acceptable will vary from one society to another and from one historic period to another. It also suggests that the process of change in moral rules occurs because of a process of discourse and negotiation among the members of a social group (or perhaps among the most influential and powerful members). One important aspect of this is that it incorporates the fact of cultural variation and the flexibility of human behavior.

3. Culture and evolution

Another area where Alexander made a very important contribution is in the question of how to incorporate culture into an evolutionary understanding of human behavior. Anthropologists and other social scientists have long argued that culture is unique to human beings, and that, because of the way in which it influences behavior, patterns of human behavior cannot be understood as adaptive strategies the way that the behaviors of other animals can (Sahlins, 1976). Chapter two of *Darwinism and Human Affairs* is one of the best early statements of how the presence of culture is completely compatible with the idea that human beings, like other organisms, strive to maximize their individual inclusive fitness. (A similar argument was made more briefly in Irons, 1979.) They do this by treating culture as a part of their environment and trying as best they can to use and manipulate it to their advantage. The issue of how culture fits into a valid evolutionary perspective is still under vigorous debate (see, e.g., Boyd & Richerson, 1985; Cronk, 1999; Richerson & Boyd, 2004), but Alexander’s view of culture, as expressed in *Darwinism and Human Affairs*, is still very much alive and a part of the debate. This is the view that the form of culture in any human society is completely a result of human beings attempting, in each generation, to do the things

which, in ancestral environments, maximized individual inclusive fitness. This view has become so widely known that people who advocate it often do not cite Alexander's writings on the subject (see, e.g., Cronk, 1999).

4. Intelligence as a social tool

Alexander's view of behavioral flexibility and culture and his view of indirect reciprocity are closely interrelated. Alexander, along with Humphrey (1976), sees human evolution as involving a kind of arms race for intelligence, especially the kind of intelligence that has been labeled Machiavellian intelligence. Because human beings are constantly observing one another and sending each other both honest and dishonest messages, there is an advantage to being a little quicker to understand the thought of others and to manipulate them to one's advantage. Having fixed and inflexible strategies of social behavior would leave one vulnerable to exploitation by those who are more flexible. New strategies and still newer counterstrategies for social interaction are the only formula for success in the environments of ever-shifting confluences and conflicts of interest that are characteristic of human societies. The idea that the human brain is a social tool explains many aspects of human behavior. One of these is the importance of scenario building and its relationship to consciousness. Human beings very often explore multiple courses of action before deciding how to behave, and sharing of these scenarios with close allies is an important way of evaluating which one is most advantageous.

5. Parental care and nepotism

Another trait related to the mind-as-social-tool hypothesis is the vast increase in parental care in humans. Children have a great deal to learn to become competitive adults in human social environments, and a long period of learning, in which they are largely protected and cared for by parents, confers an advantage. This appears to have led to some long-term trends in human evolution. One of these trends is the expansion of the circle of kin who invest in the nurturance of offspring. Human beings differ sharply from their closest relatives, the great apes, in the extent of paternal care. They are also unique among all animals in the extent to which they track more distant relatives—aunts, uncles, nephews, nieces, cousins, grandparents, and grandchildren—and make careful distinctions of closeness and distance (Alexander, 1979, 1987). Furthermore, human beings trace wide networks of relatives by marriage that are not genetically related to themselves but are genetically related to their children. These more distant kin and relatives by marriage are, at times, important sources of aid to oneself or one's children.

The involvement of human males in both direct and indirect child care, combined with the formation of large, intricately, and flexibly cooperating male groups, has led to a number of additional traits, such as concealed ovulation and social pair bonds between men and women combined with elaborate mate guarding. Alexander points out that humans are unique in

having both intricately cooperating male groups and, at the same time, close social bonds between pairs of men and women and high paternity confidence. Also related to the advantage of more extensive parental care are the traits of menopause and the altriciality of the human offspring. Alexander has developed and explored hypotheses related to these traits in great detail.

The balance-of-power hypothesis and the closely associated idea of indirect reciprocity have, in my opinion, not yet been fully explored. There are many other human traits that can probably be explained by these ideas. Among these other traits are religion, art, humor, music, and poetry, to note a few (Alexander, personal communication). All of these traits involve, to some degree, attempts to influence the behavior of other members of one's social group and attempts to portray oneself in a favorable light to "interested audiences." Alexander has explored a few of these himself as have others, but much remains to be done. He is currently turning his attention to religion, which is obviously connected strongly to indirect reciprocity and group identity (manuscript entitled *The Concept of God and the Meaning of Life*). He has also briefly discussed the subjects of humor (Alexander, 1986) and aesthetics (Alexander, 1989).

6. Language and closely related traits

One trait that Alexander has not discussed extensively, but which can be explained by a combination of the balance-of-power and the indirect-reciprocity hypotheses, is the origin of language. Alexander (1979, pp. 82–83, 122, 208–209) did discuss briefly the role of language in consciousness, scenario building, foresight, and communication. Nevertheless, he has given less attention to language per se than to some other traits. It is interesting that Dunbar (1996) has developed a theory of the origin of language, which is built on the balance-of-power hypothesis, without citing Alexander, Humphrey, Bigelow, Durham, Keith, or Wilson (see above). I do not fault him for this. Dunbar is a primatologist, and an excellent one at that. I bring this up only to emphasize the explanatory power of a combination of the balance-of-power and the indirect-reciprocity hypotheses. In developing his version of the balance-of-power theory, Dunbar has studied and built on the large and excellent body of literature dealing with nonhuman primates. He concludes that a common function of social groups is protection from predators and suggests that what happened in human evolution is that other human groups became the predators (pp. 17–19). This led to strong selection for larger and larger groups. This is the balance-of-power hypothesis, although he does not use that label. He then goes on to observe that grooming is the primary way of signaling close social alliance in nonhuman primates and that, as social groups get larger in primates, the time spent grooming becomes larger and, therefore, more costly. He suggests as a hypothesis that, as groups became much larger in the course of evolution, the cost of grooming necessary to hold a group together became prohibitive and that, as a result, grooming was replaced by conversation as the primary means of signaling alliance. One can carry on a conversation with several individuals at once but can only groom one other individual at a time. Conversation required language, and this need for conversation in place of grooming supplied the primary

selective force for the evolution of human linguistic abilities. The form of conversation that was most useful for monitoring the behavior of other members of one's group and, hence, knowing whether their behavior threatened or aided one's own interests was gossip. What Dunbar is saying, in effect, is that gossip was a tool for indirect reciprocity, although he does not use the phrase "indirect reciprocity." The hypothesis of Dunbar about gossip is interesting and goes completely beyond anything suggested by Alexander. At the same time, it is built on the balance-of-power hypothesis and the idea of indirect reciprocity. I see it as relevant to the current discussion because it demonstrates the explanatory power of intergroup competition and indirect reciprocity as a theoretical framework. I also think it is interesting that Alexander uses his hypothesis of indirect reciprocity to explain morality and Dunbar uses essentially the same hypothesis to explain gossip. This suggests that gossip and morality serve the same purpose. On reflection, most of gossip is about the moral failures and accomplishments of other members of one's community, and one of the primary ways in which people discuss and eventually negotiate the moral precepts of their society is through gossip. Morality and gossip are indeed closely intertwined.

7. Final observations regarding Alexander's contribution

I have only scratched the surface of Alexander's rich accomplishments in the development of theory relevant to human evolution. In brief, I might note that there are many other aspects of our species that he has addressed and that his discussion of all of these issues is rich in careful thought and always faithful to the assumption that natural selection at the individual level has been the primary driving force in human evolution. If future researchers want to see how far individual-level selection can go in explaining human sociality, Alexander has given them a rich set of hypotheses to guide their work. Other human traits to which he has given attention include relative hairlessness in adults, frontal copulation, female orgasm, sexual dimorphism, ecological dominance and its implications for sociality, socially imposed monogamy, the combination of high paternity confidence and multimale intricately cooperating social groups, group–group competition as a form of play, the association of low paternity confidence and an emphasis on uterine kinship, and cross-cousin marriage, to mention a few. How many of his hypotheses will stand the test of empirical evaluation is yet to be seen, but, whatever future research reveals about human behavior, he has provided a very valuable set of hypotheses that can guide research, and, at present, much of what he has suggested has been confirmed empirically. His contribution to our understanding of the evolution of human behavior is vast indeed.

I should also point out that he has continued to study and publish prodigiously on nonhuman animal sociality. He has, in fact, expanded his purview beyond the singing insects and made significant contributions to the discovery and description of eusociality in mammals, especially naked mole rats, the social organization of horses, and the interrelations of humans and horses. I recently saw a copy of his curriculum vitae and it contained three single-authored books, one on singing insects and two on humans. It contained a coauthored book on Australian crickets and a coedited volume on social behavior in both nonhuman and

human animals. It further contained 130 scientific articles and book chapters, roughly 40 of which focus primarily on human sociality. Of this large body of literature, I have primarily discussed his two books on human beings, *Darwinism and Human Affairs* and *The Biology of Moral Systems*, and two of his major articles, “The evolution of social behavior” (1974) and “How did humans evolve? Reflections on the uniquely unique species” (Alexander, 1990). The rest of his publications contain a great deal more.

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