REVIIEWS

A COMPARATIVE REVIEW


Few recent books have been reviewed as many times in rapid succession, or with as much vehemence in both defense and derogation, as On Aggression by Konrad Lorenz (1966, Harcourt, Brace and World) and The Territorial Imperative by Robert Ardrey (1966, Atheneum). The principal reason for this attention — and for the disagreements — is that Lorenz and Ardrey have tried to write about one of the most sensitive and important questions facing man: his nature as determined by and determinable from his evolutionary history. The two books have often been reviewed together because they share the basic theme that man is an aggressive animal and that this aggressiveness is in some way a product of the evolutionary process. On Aggression is a personal commentary from a professional zoologist with an extensive background of training, thought, and investigation in behavioral biology. Ardrey, on the other hand, is no biologist, but he has produced a fascinating narrative that is remarkably well-documented. Unfortunately, one of its fascinating aspects in the disarming ease with which it travels back and forth between major insights and ridiculous oversimplifications. Both men write in ways tending to rekindle old, pointless arguments of the instinct vs. learning variety. Although they profess to be presenting evolutionary arguments, both men have mixed into their discussions some peculiarly evolutionary or antievolutionary themes.

Man is indeed an elaborately aggressive organism, and the nature of the evolutionary background for this aggressiveness is a legitimate problem. He is also probably the most extensively altruistic of all organisms. Ardrey and Lorenz take the evolutionary basis of his aggressive tendencies as their major themes, but, in general, seem to muddle the problem of evolving his altruistic tendencies. Critics argue that the prominence of these seemingly opposed tendencies in man's behavior indicates that the characteristic that really evolved was merely the capacity for either behavior, as the situation demanded. They contend that the developmental basis of such behaviors in man is too complex, and that they are too indirectly related to the genotype, for selection to accumulate genes directly correlated with either aggression or altruism as such. We believe that this view, too, is an oversimplification. It would be naive to try to explain man's preoccupation with sex without reference to natural selection; perhaps it is only a little less naive to do so with aggression.

The nature of the evidence on which reasonable answers about man's evolutionary history can be based and the problem of what it means for man to make discoveries about himself regarding such attributes as aggression and altruism are the important questions that arise from reading Lorenz's and Ardrey's books. Several previous reviewers have concentrated on detailed criticisms; we would like instead to consider the general question of the role of aggressiveness and territoriality in man's evolution and build an hypothesis on what we think are appropriate attitudes toward these human attributes. We will also try to identify what we believe are flaws in Lorenz's and Ardrey's arguments.

It is a significant step forward that the questions receiving attention today are not whether man evolved but how he evolved. Doubt seems no longer to exist in the minds of reasonable and knowledgeable persons that man is a product of evolution — a result of the same basic process that has produced all life. A major consequence of this realization is that whatever characteristics may be construed to be uniquely or most decidedly human are thereby automatically categorized as producible through natural selection.

If the size of his brain is used as the chief index to man's evolutionary divergence (and this seems reasonable not only because of the importance of brain function in specifying man but also because brain size increases correlate with paleontological and archeological evidence of increasing complexity of social organization and various cultural phenomena), then there seem to be at least three major puzzles concerning man's evolution from a nonhuman primate:

1) How could his brain increase in size so rapidly from australopithecine to modern man (50-150,000 generations)?
2) What caused the increase in brain size to go so far beyond that of all other primates?
3) What caused the brain apparently to stop increasing in size some 50-100,000 years ago?

Regardless of the indirectness of the relationship between man's genotype and those aspects of his phenotype that we generally refer to as "intellect," we must conclude that variations in intellect were subjected to unusually intense selective action, that this selection was consistent across a long period, and that it carried man's intellectual capabilities right up to their present condition.

Let us consider the basic process by which natural selection operates. First, it always involves competition between alternate genetic elements within species. Even in interspecific competition, evolution occurs as a result of some variants within one or both species outreproducing the other variants. Although selection actually works through favoring certain individual organisms, the result is change in gene frequencies in populations.

There seem to be three possible kinds of intraspecific competition or three different levels of intensity at which selection can operate on alternative genetic elements:

1) Differential reproduction without direct interaction, and no confrontation between competitors.
2) Partial or complete exclusion of competitors from the best (or only) sources of food, mates, and shelter through aggressiveness and territoriality.
3) Elimination of competitors or potential competitors by killing them; this could include cannibalism, or the elimination of competitors with food being obtained, without additional risk or energy expenditures.

Of these kinds of intraspecific competition, the first would usually result in the slowest evolutionary change, the others, in order, in increasingly rapid change. The questions we would ask about man's evolution are (1) which kinds of competition were involved, (2) which were most likely predominant, and (3) what were the sizes and compositions of the units among which each kind of competition operated? In other words, which operated only among individuals and which among social groups, such as families, of different sizes and complexities?

Differential reproduction without direct competition occurs in every species of organism, whether or not the other forms of competition also occur. Exclusion of
competitors through aggression or some form of territoriality is widespread among animals with complex behavior — such as vertebrates, arthropods, and cephalopods — and may be universal among such organisms during times when food, shelter, or mates are in short supply. Nearly all modern primates seem to be territorial.

Killing of competitors and cannibalism are rarely observed, and it is usually difficult to obtain evidence whether observed cases represent evolved functions or incidental results from other kind of selective action. Few animals seem to be cannibalistic — none as much as man's fossil record suggests was the case during his evolution. On the other hand, reviewers of these books who emphasize that little intraspecific violence occurs in most animals in the wild are simply reminding us that responses to aggression also evolve. That ritualization and threat can be effective in establishing dominance without injuries or death is only evidence that inhibition of aggression as well as aggression is subject to natural selection. Aggressive interactions are also crucial when they are conducted solely by threats; such ritualization, on the other hand, is only effective when, on the average, the subordinate gains by giving in. When commodities (food, shelter, mates) are in sufficiently short supply, no advantage is to be gained by giving up. Unlike Lorenz and many other behavioral biologists, we do not find it reasonable or necessary to consider either inhibition of aggression or altruistic behavior as "species" adaptations, evolved to assist the species at the expense of the reproduction of the individuals showing such responses.

The chances seem remote that man evolved without a significant amount of intraspecific aggression occurring continuously and, in fact, guiding his evolution to some extent. We would go further and agree with Lorenz and Ardrey that a more elaborate and extensive array of intraspecific aggressiveness may have been involved in man's evolution than in that of any other animal. This is not to say that any particular kind or instance of human aggression at present may not have grown out of a purely cultural context. We are simply agreeing that, during a long period — perhaps all — of man's evolution, aggressive behavior was directly favored by selection. Under these circumstances there must have been increases in the frequency of many genes that increased the effectiveness of aggression. As with most other human traits, and all human behavior, it is difficult to understand the developmental and hereditary basis of aggressive behavior in any individual or any particular instance; selective action on such a trait must operate in exceedingly indirect fashions. Aggressiveness may easily be modified by culture, and discernible variations in aggressiveness based on genetic differences may be rare or absent among men today. These facts, however, cannot be used to deny the possibility of a genetic background for either the general intensity and quality or the prevalence of aggressiveness in humans. Neither do such conclusions lead us to the remarkable parallels Ardrey draws when he supposes, for example, that a scientist who "place[s] at the disposal of the machinery of war the most sophisticated attainments of his discipline" is "fill[ing] out from the particularity of his learning the generality of that open instinct, the territorial imperative, and, having done so... [acting] according to the finished pattern with the predictability of a capricorn beetle."

Excluding certain social insects, man is the only warping species, and one of the few that commonly engages in interindividual death battles. Perhaps only in man are all of the necessary abilities for such behavior combined. Other animals never developed necessary equipment for killing conspecifics, lack ability to organize for group warfare, lack the ability for recognizing and sparing near relatives, or have been unable simultaneously to resolve the conflicting necessities of intragroup (or family) tolerance and intergroup hostility. In any species engaging in the more violent kinds of intraspecific competition, ability to recognize and spare close relatives would be highly favored. Such an effect, moreover, would have been facilitated by man's tendency to live in small bands or family groups. Members of one's own band could automatically be treated as relatives, or tolerated and even assisted; those of other bands could equally automatically be treated as competitors or the enemy.

Let us take a closer look at what early man was presumably like in order to understand better the significance of the above suggestions. Sometime during his early evolution man became more carnivorous than any modern primate. He hunted his food, and this would have placed a selective premium on individuals capable of improving their weapons, their bipedal locomotion, and their ability to hurl weapons at elusive prey.

Up to this point, there may have been relatively mild selection favoring larger brains (by which is implied — properly, we believe — more complex brain function). Cooperation among individuals of a family in hunting could have favored effective communication systems which would have, in turn, allowed for passing on more cultural information to offspring. Such families, with the favorable genetic endowment of larger brains and thus better ability to absorb and remember past experiences and to associate cause and effect relationships, must have been better hunters and also better at transmitting to offspring the benefits of experience. There must also have been sexual selection in the same contexts, for it would certainly have been to the advantage of females to choose among potential mates those whose intelligence and hunting prowess would cause the maximum survivorship of their offspring. One way or another, family groups evidently increased in size, consisting of more than a pair of adults, and perhaps in some cases three generations of individuals, all of which had more in common, both genetically and culturally, than they had with members of other such groups. The degree of inbreeding may have been rather high within such groups. This could have resulted in the rapid fixation of certain genotypes and favored intensive outbreeding within groups, owing to the prevalence of genes deleterious in the homozygous condition, perhaps leaving an effect in incest taboos of modern man.

As males in family groups aged, they would be unable to maintain dominant positions. However, it may have been of advantage to younger members of the group to tolerate such individuals, thereby benefiting from their experience and wisdom. Such behavior would not only select for long adult life but make for greater cohesiveness between generations and cause groups to increase in size without fragmentation and to persist longer. Cooperation between parents and grandparents might allow surer recognition and encouragement of offspring in culturally transmissible skills such as tool making and hunting. It could free younger adults for hunting and other essential activities, and it would allow a longer period for passing on the accumulated culture to each successive generation. Such processes as these should rapidly incorporate into a stable and long-persisting group not only genes for greater intelligence but also any useful cultural attributes introduced into the group. Under such conditions, "postreproductive" becomes a difficult term to define.

The social structure of early man was also probably conducive to the development of elaborate intraspecific aggression. Each family group would have differed from every other one in cultural as well as genetic traits, to a degree depending upon its stability and cohesiveness. The individuals of such groups were surely able to recognize members of their own group, and, further, to recognize some of their closer relatives (at least their own offspring) within the group. Direct aggression between family groups could have resulted in rapid shifts in gene frequencies.
in the population as a whole. On the other hand, altruistic behavior toward other individuals within groups would also have been favored by selection, both because of the necessity of belonging to a group and because it would result in the favoring of genetically related individuals. Intragroup cooperativeness does not preclude intragroup competition, as, for example, in baboon colonies today.

Elaborate parental behavior, which includes both recognition of relatives and a kind of altruism (toward one’s offspring), and elaborate aggressive and territorial behavior go hand-in-hand in a wide array of animals. They are almost universally linked. It seems to us that man’s altruistic tendencies, as well as his aggressiveness, could have been favored by ordinary natural selection. There is no need to involve the supernatural or to speak of “species” adaptations. We do not understand Ardrey’s tendency to divorce aggressive and reproductive behavior; aggressive and territorial behavior cannot evolve unless it enhances reproduction, and there is no evidence making this argument problematic in any way. We certainly disagree with Lorenz’s conclusions that man failed to develop inhibitions to aggression and that this was because for a long period of his history he was unable to kill his fellow man.

Let us consider in more detail the extent and nature of intergroup aggression in early man. As a result of spatial isolation of family groups and an exclusive kind of social organization such as occurs in many primates (and man) today, each family group would have been to a large extent a gene pool and micro-culture of its own. Different groups might be expected to have varied in average intelligence, in the degree of intragroup cooperation, and in the nature of weapons, hunting ability, and experience.

If shortages of essential commodities such as food and shelter were the rule, then when groups contacted one another, we suppose that one usually attacked the other, killing the males and possibly the young, and appropriating the females. The successful band in these battles could accumulate experiences increasing the probability of success in subsequent encounters. Repetition of intergroup interactions should select for greater intelligence, increasing aggressiveness between groups, and, simultaneously, increasing cooperativeness and altruism within each group.

In short, we visualize a situation in man’s early hunting ancestry in which reproductive individuals characteristically lived in groups, and in which some groups, possessing higher frequency of individuals of greater intelligence, were able by intragroup cooperation and communication to exterminate and replace adjacent groups. Such a process could bring about increasing uniformity among surviving groups, by assimilating intergroup genetic and cultural variation faster than it could be produced, and ultimately decrease the profit to be gained from direct intergroup strife. As this condition was approached, more cohesiveness among splintering bands might have led to sizeable tribes and nations with a corresponding extension of the allegiances of individuals.

What forces could have promoted cohesiveness in band structure? Large predators eliminate lone individuals or small groups among modern primates that live in tightly organized bands. This may be the only kind of selective action that has produced large bands in primates. Intragroup competition, promoted by recognition of near relatives deriving from complex parental activities, would run counter to increases in band size and cohesiveness. Advantages deriving from cooperation in killing large game have often been used to explain development of large bands of primitive men. This not only presumes a dependence upon large game, but it does not seem likely to explain groups of more than a dozen or so able-bodied hunters. Furthermore, as man’s weaponry improved and his behavioral complexity increased, the minimal size of groups effective in this context would decrease, not increase.

For long periods during man’s evolution organized bands may have served as protection against, not other species of predators, but other bands of humans. In such case there would be no theoretical upper limit on band size. If intraband selection worked continually against increasing band size and cohesiveness, then we would expect that reduction of intraband friction resulting from lowered population density (for example, from disease), tendencies toward agriculture, and, eventually, the development of means of protecting large groups within which each family had its own territory (armies and farms) would result in shifts toward increased isolation of small family groups and coincidentally toward monogamy.

To return now to the three questions given at the outset, we believe that man’s brain size increased so rapidly and diverged so far from the brains of other primates (1) because man’s chief competitors all during his evolution were other men and (2) because the competition was of a most direct and extensively aggressive sort, an increasing amount of it operating between family groups of growing size and complexity and with increasingly effective cultural transmission. We believe that brain size stopped increasing when culture became so elaborate and social groupings so large and complex that recognition of allies largely lost its association with degree of genetic relatedness. The result would have been a re-direction of altruistic behavior previously directed toward genetic relatives until its selective advantages were reduced or nullified. As a result, genetic variations reflected in variations in brain size or complexity would largely lose their selective advantage, and evolutionary increases in brain size would level off.

From the preceding discussion, several useful questions arise for the continued investigation of man’s evolutionary history: What was the breeding and social structure of known groups of early man, and how much group interchange occurred? How were new bands formed? What was the extent of intergroup aggression? How was intragroup competition expressed? When did cultural means of recognition of fellow band members or tribesmen arise? Were males and young and old members of competing groups ordinarily killed by victorious bands? Were males more often eaten in cannibalistic ceremonies? Was the degree of cooperation between bands a function of the degree of their genealogical relationship? Not all of these questions can be answered in regard to primitive man, but they provide a frame of reference. They are the same questions that should be asked, but often are not, with regard to the behavior of other primates and so-called “primitive” men still in existence today.

To conclude, the story of man’s evolution seems to have been that of individuals becoming able to recognize themselves as members of larger and larger groups of increasing complexity of social organization. The altruistic tendencies of man most likely arose directly out of the interplay between increasingly elaborate intergroup aggressiveness and intragroup cooperativeness originating in parental behavior; the same process was more than likely fundamental in the rapid evolutionary increase in man’s brain size. Man’s tendency to become involved in wars was almost surely directly favored by selection for a long period of his evolution and, therefore, in some important sense, is not a kind of degenerate or degraded behavior resulting from civilization.

Finally, we do not believe, as Ardrey and Lorenz both imply, that knowledge concerning man’s evolutionary history, regardless of the revelations it may involve, can in any way restrict what man is able to accomplish in manipulating his own behavior toward any desired end. Knowledge of our evolutionary background cannot close doors; it can only open them. If man’s history did involve “narrow red in tooth and claw,” it is no less to our advantage to comprehend where we have been, and possibly of very great benefit in insuring that we realize whether it may be that we wish to go and the best way of moving in that direction.

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