

Primate Aggression and Evolution: An Overview of Sociobiological and Anthropological Perspectives

JAMES J. MCKENNA

Attempts to explain the nature and causes of human aggression are handicapped primarily because aggression is anything but a unitary concept. Aggression has no single etiology, no matter which mammalian species we consider or what kind of causation (developmental or evolutionary) we stress. Nevertheless, forensic psychiatrists are asked to evaluate instances of human aggression in ways that would send shivers up the spines of researchers who have been wrestling with the issue for over fifty years. This is not to say forensic psychiatry should be abolished nor to suggest behavioral scientists have not made progress in discovering causes of species aggression in general¹ and human violence in particular.² But especially when predictive models are considered it does mean we are far from achieving highly reliable results.³

Particularly when one person is asked to assess the motivational state of another who has committed a serious aggressive act it becomes more evident just how much more data we need. Strangely, if a forensic psychiatrist were asked to testify in a case in which, let us say, one monkey attacked another, the testimony would be based on more complete information than a case involving a human. This is because a plethora of context-specific data on nonhuman primates are available. These data illuminate a wide range of social, ecological, and endocrinological circumstances under which animals will be expected to act aggressively. Data on humans are much more complex, and sometimes they are absent altogether. For obvious ethical reasons scientists do not purposefully nor directly experiment on humans (biochemically, surgically, or hormonally) to determine how and when aggression can be induced. Moreover, among humans culture and biology are so tightly wedded that the task of identifying and isolating the most salient aggression-eliciting factors is formidable, if, indeed, there is such a thing. If this is not discouraging enough, consider that the data available on human aggression, especially motivation, often lead in diverse directions without any indications about which direction may be most fruitful to explore.⁴

Perhaps I have painted an overly pessimistic picture. Just as forensic psychiatrists analyze and present conclusions about the mental states of accused aggressors, so also do researchers make use of a wide range of principles and assumptions in putting forth their hypotheses on primate

McKenna is Associate Professor of Anthropology, Department of Sociology and Anthropology, Pomona College, Claremont, CA 91711.

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aggression. It is to these theoretical assumptions emerging after years of cross-species research on this subject I wish to turn. I will concentrate on explanations of human aggression that use data collected on nonhuman primates — the order of mammals to which humans belong as do prosimians, monkeys, and apes. By exploring this cross-species (primate) perspective I hope to elucidate the complementarity of variables (both evolutionary and developmental) that coalesce to produce instances in which animals act or threaten to act to injure fellow species members (conspecifics).

In part, this review will be historical, making extensive reference to sociobiology, a rapidly changing and extremely controversial new field that seeks to establish the degree to which genetic processes underlie animal (including human) behavior. Moreover, I should like to make clear why anthropologists sometimes have a difficult time coming to accept some sociobiological notions. While data collected about other species contribute to our understanding of human behavior and to the evolutionary processes influencing this behavior, these data alone cannot fully encompass it, or account for all of its present manifestations and character. It may well be that among human beings aggression is used mostly to achieve political, economic, and ideologically inspired goals somewhat different from the goals (mates, food, shelter) natural selection had in mind. If this is true, we must face the fact that while the cross-species and evolutionary perspective may help us understand how aggression first emerged and its past biological role, these perspectives may be irrelevant in informing us how it can be eliminated or controlled.

Aggression Defined

In its simplest form, human aggression may be defined as a sequence of behavior in which one or more individuals inflict, threaten to inflict, or attempt to inflict harm on another. Ethologists also might add that ordinarily aggressive acts are accompanied by physiological changes in blood chemistry due to the secretion of adrenocorticotrophic hormones. Moyer describes in detail how changes in blood chemistry, including the production of testosterone, can act to sensitize the neural system for aggression. This contrasts with the effects of administering estrogens that can sometimes act to desensitize or inhibit aggression. Among humans there is evidence that nonhormonal influences may act to induce aggression, most notable among them the condition of low blood sugar (hypoglycemia). Turnover rates of such neurotransmitters as serotonin, norepinephrine, and dopamine also may be implicated in facilitating aggression. Of course, this assumes animal models are suggestive of how human neurological functioning affects our aggressivity. It is clear that what amounts to endocrine-brain-chemistry interactions, especially causal relationships affected by the social environment, are by no means clearly or sufficiently understood. This remains a rich area for future research.^{5,6}

While the above definition referring to underlying physiological variables may be sufficient for most kinds of animal aggression, it is important to point out that human aggression is not always so easily defined. For example, socioeconomic and political conditions (the denial of human rights) can be as injurious to the psychosocial health of an individual as violence can be damaging to the limbs and organs of the body. Is this aggression? And as Lorenz pointed out years ago, only humans are in the technological position of being able to remove themselves from contact with individuals with whom they aggressively interact. Individuals can pull the trigger of a loaded gun or drop a seven-hundred pound bomb from a fighter jet and never directly experience or witness the results of their actions, such as the tearing and/or burning of their victims' flesh. The physiological concomitants of aggression — especially performed in a political context — may not always exist, nor will the aggressor necessarily be in a position to coordinate the degree of continued aggression with the degree of appeasement offered by the victim. In animal societies, appeasement gestures given by a victim often preclude the likelihood of fatalities.⁷ In any event, the physical component in animal aggression (internal physiological changes and individual-individual contact or proximity) is an important part of the definition of aggressive interaction, but for humans such physical components are not always, nor necessarily, part of the aggressive event, having the effect of muddling our definitions of them.

Aggression Research: A Brief History

We probably can agree that aggressive behavior among humans and animals is exceedingly conspicuous and for some species at least, it is anything but infrequent. Because of this — and the fact that we all have experienced it in one way or another — it is not surprising to find that people have strong opinions about why aggressive behavior exists and what functions it performs. Researchers and lay persons can easily bring to mind images of animals competing aggressively for mates, for food, or for other resources needed for survival and reproduction. It is easy to intersperse these images with others as, for example, men battling on a football field or in a boxing ring for the acquisition of land or a crown, respectively; and if Darwin's often misused phrases are brought to mind ("nature red in tooth and claw" and "struggle of the survival of the fittest") one can appreciate immediately the powerful preconceptions many of us take to the study of this behavior.

No wonder intellectual positions on the origins and causes of aggression historically have conflicted in rather dramatic, if not extreme ways. For example, the preeminent ethologist Konrad Lorenz proposed in his now classic *On Aggression* that like other animals humans experience a buildup of aggressive energy causing us to seek out appropriate eliciting stimuli in environments capable of releasing it. The longer the time since the last aggressive act, the more likely this seeking-out or "appetitive behavior" will occur. The threshold value needed to evoke aggression will decrease as

the time since the last instance of aggression increases, so the theory holds. According to Lorenz, the expulsion of aggressive energy, that is, the "consummatory act," restores the organism to a temporary equilibrium until, excess neural-hormonal energy builds, setting in motion again the chain of events leading to aggression.

Lorenz's "spontaneity model" of aggression suggests that an aggressive drive exists apart from other drives such as sex and must be considered an inevitable, though not welcome, feature of human nature. Rather than wasting energy denying it, he argues, scholars and clinicians ought to be examining ways in which it can be redirected into innocuous social arenas as, for example, national and international sporting contests. Lorenz's final point is that human aggression evolved because it was adaptive; it functions now and in the past to protect from over-exploitation the home ranges and territories within which organisms mate, find food, and locate appropriate shelter. Intraspecies violence and warfare so well documented among humans, he points out, reflect past adaptive impulses mismatched (no longer probably as adaptive) in today's highly technological and symbolic dependent world. His prognosis for human survival is bleak. He states

An unprejudiced observer from another planet looking upon man as he is today, in his hand the atom bomb a product of his intelligence, in his heart the aggressive drive inherited from his anthropoid ancestors, which their same intelligence cannot control, would not predict long life for the species.⁷

The spontaneity model of aggression proposed by Lorenz was criticized for being much too uncausal in nature, deterministic in tone, and biological in substance;⁸ the cross-cultural anthropological data assembled to refute Lorenz's contentions dealt it a severe blow. Essentially, these studies showed that universally comparative levels of aggressive behavior occurring within different cultures did not exist. Still, Lorenz's ideas served as a catalyst for a popular best-seller book that portrayed the early social life of humans as being anything but peaceful and loving. In Robert Ardrey's *African Genesis* it was argued (based on Raymond Dart's theory) that the confluence of ethological, paleontological, and archaeological data demonstrates that contemporary human aggression emerges from an inherited proclivity for territoriality and sexual competition. Ardrey made it clear that blame for our tainted, aggressive history could be placed squarely on the backs of our two-million-year-old, bipedal, savannah-dwelling, blood-thirsty, bone-munching ancestors — the African Australopithecines. As he phrased it,

We are Cain's children . . . Man is a predator whose natural instinct is to kill with a weapon. The sudden addition of the large brain to the equipment of an already successful predatory animal created not only the human being but also the human predicament.⁹

Never mind that this scenario has been shown to be quite incorrect, or at very least imprecise;¹⁰⁻¹⁴ but consider this unsubstantiated thesis (as ex-

treme as it was) proved exceedingly appealing to a vast number of readers. Not only did *African Genesis* become a best seller, but also several subsequent, related books did just as well (*The Territorial Imperative* and *The Social Contract* also by Ardrey); in fact, the possibility of innate human territorial imperatives proved to be the favorite topic at cocktail parties for quite some time, and the topic still seems to generate a great deal of discourse.

Ardrey's and Lorenz's theories of innate aggressive drives are not altogether unlike Freud's psychoanalytic model of the origins of aggression — though they are not identical, especially when basic assumptions are considered. Both perspectives argue for internal drives. According to psychoanalyst Henri Parens,¹⁵ Freud maintains that infants are born with a death instinct, a natural self-destructiveness that must be neutralized sometime during the first two years of life. The neutralization of infant self-destructiveness serves as a basis by which the individual begins to direct aggression away from itself toward other objects (including individuals) in its environment. In Parens's assessment "Freud's (1920) second theory of aggression holds that aggression derives from the death instinct and under the influence of the libido (by fusion) and the ego (by neutralization) destructiveness is changed to serve self-preservation, mastery, adaptation."¹⁵ However, Parens's observational studies of neonates have led him to reformulate Freud's theory, insofar as it appears there is an "inherent nondestructive aggressive drive evident within months from birth, well before neutralization of aggression is possible"; moreover, Parens argues that contrary to present psychoanalytic theory of aggression, "infantile aggression is not simply destructive, but serves as a basis by which the infant achieves a satisfactory relationship with the libidinal object" and generally adjusts to its particular environment.¹⁵

While they may be similar, it must be stressed that the working assumptions held by the psychoanalyst and the ethologist are radically different. Frankly, the idea that neonates are born with psychic drives or tendencies in need of repair at birth, or that infants are born with self-destructive tendencies is unpalatable to persons adopting natural selection as an explicating concept. Why would natural selection favor genotypes underlying neonatal precognitive or psychic processes that support innate self-destruction? Natural selection, as will be explained later, would be expected to favor infants whose development is, perhaps, unencumbered by serious psychic ambiguities in need of resolution, especially in light of the vast array of other pressures to which helpless and slow-developing primate young must respond.

Bowlby's reinterpretation of Freudian theories (*sui generis*) and his own comparative-observational methodology may serve as the most appropriate example of how psychoanalysis and ethology can be usefully integrated. For the most part Bowlby's work has been disregarded by psychoanalysts for the very reasons ethologists find it interesting. Bowlby is much less

willing to interpret neonatal psychic processes that cannot be seen, recorded, compared, and tested empirically. Bowlby emphasizes that first and foremost infants must *survive* their periods of locomotor and social helplessness; neonates must develop behavioral patterns that, for example, communicate their needs to caregivers on whom their survival depends. Infants cry, smile, vocalize, appear "cute," and struggle to move not due to conflicts between life-and-death instincts but because to do so increases their proximity to their mothers and other caregivers. Precognitive behavioral systems of infants primarily contribute to the developing differential and discriminating social bonds that underlie attachment. If infants survive this helplessness by virtue of their being "attached" to certain caregivers, as Bowlby argues, then socialization and experience can teach infants how to become reproductively active adults who are psychosocially healthy. If infants do not survive, socialization processes and psychic development become irrelevant.¹⁶

Such notions that humans inherit natural destructiveness or that they are "Cain's children" (the descendants of club-wielding aggressors) obviously affect some responsive chord in us all. Whatever criticisms can be leveled against them, surely these ideas represent a departure from the more prosaic psychological theories about aggression that often stress social learning, cognitive processes, and modeling (see Singer¹⁷ 1971 and Kaufmann¹⁸ 1970 for reviews). The idea of an ancestral killer ape or an inherited tendency for self-destructiveness seem more appealing than considering, for example, the contingencies of the aggression-frustration hypothesis proposed by Dollard *et al.*¹⁹ in the 1930s and refined by Berkowitz (1969)²⁰ and Kaufmann (1970).¹⁸ Recall that the aggression-frustration hypothesis maintains that violence and general human aggression occurs and is often the result of individuals not being permitted to obtain their goals, that is, aggressors suffer from goal interference.

One might think arguments stressing internal, genetically based, aggressive drives among humans have been laid to their academic rest, but this clearly is not the case. In a major ethological analysis of human aggression published recently, ethologist Eibl-Eibesfeldt defended the spontaneity of aggression.²¹ He argues that during the last decade empirical evidence demonstrates neurogenic attacks of rage occur among humans and are caused by spontaneous nuclei activity of the human amygdaloid and temporal lobe neurons of the brain. Moreover, Eibl-Eibesfeldt is critical of the cultural anthropologists who collected and analyzed data on the African hunters and gatherers (especially the Bushmen of the Kalahari) picturing them as mostly peaceful, rarely aggressive, and, thus, unincorporable into Lorenz's spontaneity model of human aggression. Recall that this information was used to counter the Lorenz position that aggression is a human universal. Eibl-Eibesfeldt argues that warfare has been as much a part of the history of hunters and gatherers as it has been of our own more complex urban society. Finally, Eibl-Eibesfeldt agrees that the extent and frequency of human intergroup warfare is unique when compared with other species,

but he adds that since control of space and resources (territoriality) remains (in his estimation) a predominant motivation of human warfare, it attests well to the common evolutionary benefits that such behavior was originally (within our hominid ancestors) meant to provide.

Sociobiology Examined

When the above viewpoints are examined carefully, it is clear the levels at which behavior, in this case aggression, being explained are not the same. Lorenz and Eibl-Eibesfeldt are examining explanations dealing with why aggression is evolutionarily old, *why it evolved*; these researchers are attempting to determine how the behavior contributes to the survival and reproductive success of the actors. On the other hand, Freudian psychoanalysts and social learning theorists (including the advocates of the aggression-frustration hypothesis) are interested in answering an altogether different question; they are interested not so much in why or how it evolved, but in understanding the immediate social, psychological, and cultural environments within which aggression is presumably fostered. They are studying how it occurs as well, which includes reference to the physiological support systems that permit the expression of aggression. The explanations of Lorenz, Eibl-Eibesfeldt, and Freud — to use dramatic examples — are not necessarily in competition nor mutually exclusive if we remember these investigators are answering the “why” question about aggression from different perspectives and from different levels of analysis.²² Sociobiologists attempt to separate these kinds of explanations and seek to evaluate each in terms of the specific kind of data they require. By doing so, and by stressing the ways natural selection has sculpted human behavior patterns, sociobiologists hope to be able to interpret social science as well as natural science data using common evolutionary principles, primarily by reference to natural (including kin and sexual) selection theories explained below.²³

One may wonder why the field of sociobiology, which like anthropology uses evolutionary processes to help explain human behavior, should prove to be so controversial and so difficult for anthropologists to accept as bona fide, but clearly this is the case.²⁴⁻²⁶ There are many reasons why many anthropologists express doubts about sociobiology’s usefulness, but the primary difficulty involves how *directly* the principles of natural selection can accurately be applied to explain human behavior (including aggression). Sociobiologists prefer to consider how certain behavioral predispositions may be inherited — they stem from genotypes passed down from generation to generation — insofar as these predispositions (to be sexy, aggressive, xenophobic, parental, conforming, and so forth) may contribute to an individual’s successful survival and reproduction. Sometimes sociobiologists stress too strongly the ultimate or evolutionary factors that influence human behavior and subordinate important proximate factors. Many anthropologists prefer to emphasize proximate factors (holding

evolution in the background) to consider how behaviors are inherited not through genes but through social institutions that from one generation to the next function to impart values, ideologies, and “appropriate” norms of behavior — all of which, many agree, are culturally based and maintained and only remotely linked to biologically sound reproductive strategies of the past.²⁷

It is not that sociobiologists claim genes determine all we do, think, and say, as some have charged; instead sociobiologists argue that natural selection working on individuals rather than on the groups to which individuals belong can be used to *predict* human social behavior. The sociobiological contention here is that selection has shaped human cognitive and emotional structures to the degree that what we learn and how we learn assures that for the most part we will act in our own genetic self-interest.^{23,28} Furthermore, as a primary force of evolutionary change, natural selection will favor behaviors that maximize rather than reduce reproductive effort and success. In the process, though, natural selection will not necessarily give rise to behaviors that in the long run contribute to the success of the species as a whole.

The idea that behaviors including aggression will evolve if they somehow contribute to the survival and reproductive success of the actors hardly should be considered a radical idea or one that challenges existing thought in any of the sciences including anthropology. This idea is essentially what Darwin proposed in *The Origin of Species*, published over a hundred years ago in 1859. Darwin proposed that the process of natural selection was the primary mechanism or force by which change occurred; certainly, he thought, it is well known that individuals of the same species (conspecifics) tend to vary from each other — sometimes dramatically, sometimes only slightly. It is this variance in attributes (morphological, structural, physiological, anatomical) that distinguishes organisms on which, he argued, natural selection worked. If certain of these attributes, or combinations of traits, conferred some advantage on individuals in their struggle to survive, then these same individuals should be more likely than those who do not possess such characteristics to survive and reproduce their own kind.

In this fashion Darwin introduced the notion of differential reproduction — the cornerstone of the modern synthetic theory of evolution. Though Darwin was not able to correctly identify exactly what was passed on from one generation to the next, that is, the underlying cellular (genetic) structures including the chromosomes and the genes that reside on them, he suspected they existed; also, given the reproductive benefits of certain traits, he predicted that through time some traits will be selected for in a population or organisms at the expense of others. Hence, individuals and the species to which individuals belong should evolve in the direction of a more perfect adaptation to the environment in which they exist; the alternative is extinction. This means that those individuals who survive, who successfully compete for mates, and whose offspring survive are those individuals through which species change occurs.

Kin Selection, Inclusive Fitness, and Sexual Selection

Sociobiologists maintain that natural selection can take several different forms and that ways exist by which individuals can increase their own genetic representation in succeeding generations that move beyond the individual's direct and immediate sexual participation. In fact, one rather eminent evolutionary biologist (Haldane) facetiously cheered to his colleagues that he would gladly give his own life (that is, forego entirely his own potential reproductive fitness) either for two brothers or eight cousins! Haldane's comment was made with genetic calculus in mind; obviously he shares 100 percent of his own genes with himself, while with each of his brothers he shares 50 percent of genes by common descent; with each of his eight cousins he shares 12.5 percent ($\frac{1}{8}$) common genes. On a theoretical level at least, two brothers at 50 percent similarity of genotypes equals 100 percent (Haldane's own degree of genetic similarity with himself). Theoretically, at least, eight cousins also constitute 100 percent common genes. Haldane was suggesting that as long as both his brothers (or his eight cousins) reproduced to their potential, in terms of genetic representation in succeeding generations that sum would equal his own ability to be genetically represented had he (Haldane) reproduced himself! The concept of "inclusive fitness" refers to the idea that an individual's reproductive fitness is determined not only by how many offspring he or she reproduces but also by the number of offspring reproduced by relatives with whom genes are shared (albeit fractionally) by way of common descent.²⁸

Haldane's off-the-cuff comment was made in the context of attempting to determine why aid-giving behavior evolved (often referred to as altruism). Darwin wondered why animals should take risks or give up something for the sake of others, since natural selection should favor individuals who give up nothing or who risk little. Natural selection should genetically favor individuals who maximize their own (but not another's) survival and reproductive success. To answer these queries, reference must be made to two related sociobiological concepts: kin selection and inclusive fitness. When selection operates in a way favoring behaviors by individuals that increase the survival and reproductive success of their relatives and these behaviors have an underlying genetic component, this can be referred to as kin selection. Aid-giving behavior and some forms of risk taking — such as a mother or father running into a burning house to save a child, or a healthy dolphin pushing a wounded dolphin brother to the surface so it can breathe, or relatives sharing limited amounts of food in times of shortages — all possibly represent examples of kin selection. These behaviors appear to be altruistic because they represent instances wherein animals fail to act in their own immediate self-interest. But in reality, since the effect of these behaviors is to increase (however slightly) the success of relatives in gaining a resource, the actor (altruist) as determined by the degrees of relatedness of the participants has something to gain (remember Haldane's views). In some instances, kin selection appears to make sense of what appears to be

sacrificial behaviors; this concept reinterprets pure altruism as genetic selfishness — not a particularly appealing viewpoint.

Aggression and sex are inexorably linked in sociobiological thinking.²⁹ For example, sociobiologists reason that males and females ought to have evolved different reproductive strategies since each of the sexes' potential to leave offspring and the energetic costs incurred through copulation are so different. Females are born with a finite number of sex cells (eggs), and compared with males, females experience a shortened reproductive period (due to menopause). Moreover, females also incur substantial burdens when pregnancies occur; they, not males, must carry the fetus to term and, post-natally, they must transport, protect (in some cases), and nurse it. In contrast, males have an unlimited number of sperm continuously being produced throughout the lifetime; males, unlike females, do not experience menopause or infertility. Moreover, males do not necessarily incur heavy costs for their sexual activity (except for the energetic cost of copulation itself), it is not possible for them to become pregnant, nor can they be forced to care for the offspring they sire.

In a recently published book on the evolution of human sexuality, Don Symons³⁰ argues that important differences in the potential for males and females to leave offspring, and in the potential costs of sexual activities, make differences in the sexual emotions (including desires, arousability, and attractability) between the sexes inevitable. He argues that females are (and one would predict this using an evolutionary model) more discriminating in sexual partners than males are, they seek less variety, and desire sex less frequently because the converse would not have been in the female's best reproductive self-interest. Symons argues that natural selection would favor among females genotypes that aid them in discriminating between different kinds of sexual partners — those worth possibly being impregnated by and those with whom mating would not be worth the investment. Negotiations about sexual activity, especially the circumstances within which females commit themselves to sexual liaisons, also would tend to be more important to females than to males since copulation can lead to a pregnancy. The slow-gestating and slow-maturing primates' pregnancies and postnatal care are considerable metabolic, physiologic, and social investments by females. According to sexual-selection theories (the processes of natural selection in which competition for access to mates occurs), females who mate with or "invest" in the best possible partner (most skillful, most clever, most talented in securing control over resources) will be the most successful females — successful insofar as she and her offspring (who presumably also have these abilities to choose appropriate mates) are better represented genotypically than are females with less skilled mate-choosing abilities.

In considering male reproductive strategies, Symons stresses that theoretically males can impregnate many females at little or no cost to themselves. Unlike the female, the male's reproductive potential is so high he can afford not to be choosy in mating behavior. However, this does not

mean that males necessarily have it easy, or that selection has not placed considerable pressure on them. In fact, sociobiologists will suggest that male aggressivity stems largely from the fact they have had to compete among themselves to obtain mating privileges. Consider that the female is often the primary caregiver of infants, and her long-term nursing duties remove her from the reproductive marketplace for considerable periods of time. This places a premium on any one female who may be available to mate at any given time while the number of males available to mate remains relatively constant. Following this sociobiological scenario further, this situation makes females the limiting factor in male reproductive success. Hence, male-male intrasexual competition (that is, aggressive competition) emerges generally under the watchful eyes of the females. Aggressive competition induced by the disparity of available female mating partners possibly has led to increased size and strength among males.

With this theoretical perspective in hand, sociobiologists are especially interested in the discovery of human cultural universals, that is, similarities in human action and thought that cut across the more conspicuous cultural differences such as language, values, religious beliefs, and customs. Using the concepts of kin selection discussed above, sociobiologists attempt to explain why human beings and other animals organize their behavior and social relationships generally along kinship lines, wherein relatives are helped before non-relatives; using sexual selection theories, sociobiologists seek to explain why males rather than females are mostly the more aggressive sex cross-culturally and why males tend to be politically dominant to females, and why in the sexual arena males generally have to prove worthy to females rather than vice versa.

Consider human aggression and how it might be addressed from this line of reasoning. Sociobiologists ask whether aggression permits actors to acquire or retain control of territories containing needed resources. Does successful aggression increase an individual's social status, wealth, and concomitantly, access to mates? How might aggression by an individual increase the survival of his or her offspring and other relatives with whom the aggressor shares genes by way of common descent? In sum, sociobiologists seek to explain biologically what appears to be nonbiological but cultural phenomena. They assume that at the root of most cultural behavior lie sound biological strategies.

Anthropology and Sociobiology; Conflict and Congruence

I began by stressing the difficulty many anthropologists have accepting and applying some of these ideas, including the notion that selection theory offers a heretofore untapped ability to predict forms of human social behavior. This is mainly because early in our careers anthropologists are sensitized to the extraordinary significance of human decision-making abilities, learning, and human behavioral plasticity — all of which owe allegiance (many of us think) only indirectly to genes resting at much lower hierarchical levels. We are aware of our ability to make perfectly irrational,

illogical, and biologically unsuitable decisions. These interrelated human characteristics and talents are made possible by a larger and more complexly organized neocortex. Even among the nonhuman primates on which many sociobiologic hypotheses are being tested, this newer part of the brain is constantly mediating whatever genetically based sexual or aggressive impulses may be sent to it by the older and more primitive limbic system.

In either a simple or an elaborate *social context* humans and other primates depend on learning for their survival. Timing and form of communication, feeding, and sexual behaviors are included here. It is thought the emphasis on delayed social and biological maturity (neoteny) found throughout the primate order is testament to the evolutionary significance of learning. In fact, the evolution of the primate order from an insectivorous grade some 70 million years ago is characterized by a progressive emancipation from direct genetic and/or hormonal control of behavior including, of course, both sexual and aggressive behaviors. This fact has been supported time and time again through experimental investigations from many different laboratories.³¹

To further complicate matters anthropologists are virtually besieged with ethnographic data revealing the power of cultural symbols whose underlying meanings serve to motivate human activities, thereby validating the general social structure out of which such symbols initially are born. With respect to understanding the bases of human aggression, Robert Denton's (1968)³² ethnography of the Semai of Western Malaysia described a tribal society of 13,000 wherein, and due to emotional conditioning from childhood, absolutely no forms of serious aggression occur. Contrast Napoleon Chagnon's (1968)³³ study of the Yanomamo Indians of Northern Brazil wherein aggressivity is found everywhere in the society and is ritualized at different levels: village warfare, mutual chest pounding, head pounding duels, and wife beating are all institutionalized, acceptable forms of aggression. Yanomamo society rewards aggression; the Semai devalue and prohibit it. Due to these studies and others, most anthropologists probably would say that human aggression can be turned either on or off volitionally, abetted or inhibited, sanctified or villified, mostly in accordance with the prevailing sociocultural milieu.

It may seem that anthropologists are a bit two-faced or inconsistent about what they consider the proper approach to understanding the origins and causes of human behavior. On one hand evolution is promoted, but on the other, it is subordinated to culture. To a certain degree this is inevitable because anthropologists have yet to know precisely how to fit together our firm belief in the importance of evolution with our present understanding of the power and independence of socialization, the agency by which cultural values and roles are passed from one generation to the next. Fitting these two processes together is, after all, one of the major tasks in anthropology. And it is the most difficult. We attempt to implement a truly holistic approach or one that deals as much with our primitive hominid and pre-hominid past as it does with our more advanced "human" present. To what

extent are past genetically based behavioral patterns still relevant and operating in the present? At what point in human evolution do biologically sound reproductive strategies give way to (or are compromised by) what sometimes can be interpreted simply as culture choice? Are behavior patterns that emerge because of certain social structures simply paralleling or reflecting what, in the long run, is reproductively useful for the individual? These are all important questions on which anthropologists and now human sociobiologists focus, but perhaps with different amounts of tolerance concerning the extent to which the two groups are willing to use selection theories as explanatory tools.

Biosocial Bases and Functions of Nonhuman Primate Aggression

On at least one point sociobiologists and anthropologists have no trouble agreeing: good answers to the above questions will not be found unless we continue to study the social behavior of other species, especially the behavior of prosimians, monkeys, and apes.

One question frequently asked anthropologists who study these forms is why on earth should time be spent scrambling under forest canopies observing and recording the social behavior of nonhuman primates when what anthropologists are really interested in is human behavior? Why not observe and record only the interactions of human beings? The usual response to this logical query is simple. To analyze our own social system in a more objective, non-prejudicial, and holistic way, we consider how the social systems of closely related species emerge within the context of particular environmental pressures. By doing so we may be able to elucidate the mechanisms that promote stability of primate groups through time and learn why a dependence on learning and sociality evolved. Moreover, by examining the social systems of monkeys and apes, it becomes more obvious how the various subsystems of a society (through parenting, appeasement, mating, subsistence patterns, socialization agencies, defense) sometimes complement and often influence each other to increase the survival and reproductive success of its members. Perhaps we are too close to our own behavior to recognize in what ways it is adaptive or even maladaptive. At very least, these studies permit us to move beyond an analysis that explains human behavior only in terms of itself. The concept of evolution (change through time) is comfortably used here by anthropologists as a major paradigm around which explanations of the human condition and species behavior must begin. In a very real way nonhuman primates provide an "outside" data base from which human behavior (at least in a partial sense) can be seen to have evolved. We are alerted to the adaptive significance of human action. Though we must be exceedingly careful not to compare too closely, nonhuman primates provide glimpses of the *pre-existing* behavioral and biological organizations out of which human (cultural) behavior emerged. Such "glimpses" might be glossed over or even missed altogether if the cross-species comparison were never employed.

The problems of using contemporary nonhuman primates to make comparisons with humans are enormous. Not only are there at least five million years of evolutionary independence (separation) between ourselves and our closest primate relative (the chimpanzees), but also the environments in which we see primate behaviors (including aggression) are not necessarily the same environments in which these behavior patterns emerged.

But in defense of monkey-ape-human comparisons, consider that it is now firmly established by the molecular data that humans and chimpanzees share 99 percent of the same structural DNA and the proteins coded for. In fact, chimpanzees and humans are phylogenetically closer than are chimpanzees and monkeys.³⁴ Sarich has postulated that present-day chimpanzees and humans diverged from a common ancestor possibly as recently as five million years ago. The paleontological record, especially Johansson's³⁵ astounding finds of 3.6 million-year-old Lucy and cohorts with apelike faces but upright-bipedal posture, supports Sarich's opinions made long before the fossils were located.

Monkey and Ape Aggression: Infanticide

What, then, can be said about nonhuman primate aggression beginning with the chimpanzees, our closest living primate relatives? Unfortunately for those who once believed the captivating and charming life of the chimpanzees living at Gombe Stream, Tanzania (made famous by Jane Goodall) offered some better alternative to human aggression, the news is not good. As is true for many primates, our understanding of chimpanzee aggression, especially intraspecies aggression, has changed quite dramatically during the last ten years. In a recent article, Goodall³⁶ and associates tell of shock to have observed repeated incidents of major violence, including the brutal killings of chimpanzees by chimpanzees — males killing males, males killing females, females helping to kill males, and both males and females killing infants. Some females killed infants specifically to consume them although other food resources were available. The form and level of violence directed toward chimpanzee victims, and its rather systematic form, literally shocked the researchers who, even after twenty years of research on this species, never would have predicted anything quite like it.

It is to infanticide that I wish to direct part of my discussion of aggression. Infanticide refers to a sequence of behaviors in which one (or more) animal purposefully seeks out and successfully kills dependent infants. Obviously, such an act is a significant form of interindividual violence. It is now reported to take place at irregular intervals among a great many primate and nonprimate mammal species, including the forever gentle mountain Gorilla. Not less than 86 instances of infanticide reported for 13 species of primates, thus far, have been documented, although only 12 of these reported instances have been observed firsthand by investigators; the remaining 74 have been inferred by investigators after mysterious and suspicious disappearances of dependent infants have occurred.

The interpretation of infanticide has produced one of the more lively

recent debates among primatologists; in fact it ranks as a major controversy. One school of thought argues that infanticide represents a phylogenetically (evolved) male reproductive strategy that increases the reproductive success or fitness of infanticidal males.^{37,38} That is, one way by which a male can maximize his own reproductive fitness is to eliminate whenever possible dependent offspring of competitor males. The death of a dependent infant facilitates an early return of sexual receptivity (ovulation) of the dead infant's mother. Lactating females are much less likely to ovulate and solicit sexual partners. By hastening the female's return to estrus, accomplished through infanticide, a male may assure that not only might he produce more of his own offspring, but also the chances will be increased that his offspring will be independent of mother before another male enters to repeat the cycle by killing the resident male's infants. This hypothesis concerning the adaptive significance of infanticide was formalized by Hrdy after she observed repeated instances of aggression and infanticide among the Common Indian langur monkeys at Abu, India — several different langur troops were observed intermittently over a five-year period.³⁸ This behavior among the Indian langurs had been reported earlier by several investigators but not by all; especially of interest is the fact that Phyllis Jay Dolhinow studied three different langur troops that lived in quite different Indian environments, but no infanticide was observed.³⁹

Most recently, Hrdy has proposed that infanticide among animals is most certainly not a unitary concept. She suggests that infanticide among langurs may be a facultative trait. That is, infanticide will most likely be expressed when population density is high and habitats are small; infanticide is likely to occur especially when there are numerous extragroup (bachelor) males within the home ranges of langur troops. Hrdy has also suggested that such intense male aggression has forced changes in female sexual behavior and associated sexual physiology. One would expect, also utilizing evolutionary reasoning, that if infanticide asserted a major threat to female langur fitness they would evolve appropriate mechanisms to combat, or at least control, its level. As a response to infanticide, Hrdy speculates that continuous behavioral receptivity emerged, but not necessarily physiological receptivity (ability to conceive) that characterizes some primate species (including Indian langurs).⁴⁰ Continuous behavioral receptivity refers to the female's willingness to be sexually mounted outside of the ovulatory phase of her menstrual cycle. Hrdy suggests this may be a female strategy evolved to confuse paternity and to appease raiding males.

Let me expand on these interesting assertions. For example, one of the evolutionary changes in human sexuality was a loss of estrous or periods of female sexual receptivity that for many species produces delineated birth seasons; also, among human females ovulation is concealed. Unlike many other mammals, among humans ovulation is not communicated by way of external swellings or coloration changes in and around the perineum. Also unlike other primates, human female or male sexual activity cannot be correlated with the ovulatory or preovulatory phase of the menstrual cycle.

In fact, human sexual activity and behavior occurs completely independent of hormonal events of the female menstrual cycle. Hrdy suggests that by keeping the males guessing as to which offspring are theirs and by keeping them sexually attentive across the menstrual cycle so they do not miss the female's ovulatory phase, male infanticidal tendencies should be inhibited. All-year sexual access of males to females and females to males should contribute to male-female bonding that could lead to beneficial economic effects. The very fact that females are not tied to hormonal regimes that determine the nature of their sexuality means, like males, they are able to have sex on a rather situational basis, should it prove useful to do so. Sexual activities initiated by females may be helpful in gaining access to male controlled resources or for purposes of protecting her offspring by establishing affiliative relationships with the strongest male.

Increased Density = Increased Aggression among Humans?

Is there a parallel between increased human violence, particularly in highly dense American cities, such as New York, and the langur situation where increased density seems to create increased aggression? No doubt, the average American would suggest that there is, or must be, especially if this average person were aware of Calhoun's⁴¹ work with rodents in which overcrowding was shown to produce stress, hypertrophy of the adrenals, and increased aggression. And if our average American were also aware of Charles Southwick's⁴² comparison of urban-living Rhesus macaques (monkeys living in India in large numbers around temples and garbage heaps) and rural Rhesus macaques (those living in smaller groups distributed throughout the countryside), he or she would have no difficulty whatever accepting this parallel. Southwick found that urban-living monkeys were much more competitive and aggressive (with scars to prove it) than peaceful rural monkeys. Surely this seems to make an open-and-shut case for the notion that increasing density among primates leads to increasing aggressivity. It is not that simple. The fact is that not all human beings have a problem dealing with high-density living; not all people experience increased aggressivity living in high-density urban centers. Anthropologist Gene Anderson⁴³ conducted research in Hong Kong, Penang, Malaysia, and Singapore, where population densities reach as high as 20,000 persons per acre (one hundred times the average density of New York) and no excessive social pathology or "behavioral sink" occurs.

Anderson demonstrates that particular cultures can determine the effect and even the desirability of crowding by maintaining mechanisms that diffuse its potential negative effects. For example, he found that while these social codes are not written and formalized, different Chinese families can and often do share the same house, but space is allocated so that different rooms of a house serve different social functions. While kitchens and living rooms are socializing rooms, bedrooms are "inviolate" — no outside family members can approach or enter them; time management is very loose and flexible so that people are usually not eating or even present all at once;

noise is not regarded as evil or irritating, but as a "sign of life"; status and respect for others is unambiguous, and anyone can discipline (and is expected to discipline) another's children should they misbehave. Finally, perhaps more importantly, Anderson states, "emotional interaction management is characterized by strong expectancy that unrelated persons will not become emotionally highly involved with each other, at least in public." Neutrality is desired in public space precluding powerful joyful, angry, or sorrowful demonstrations in front of strangers. Anderson's point is not that the Chinese are without stress, conflict, or tension but that "the Chinese have developed [not evolved] ways of managing space, time, and people such that even the most extreme crowding does not lead to any particular increase in social stress or aggression."

Human Infanticide

One very intriguing question to ask (with the above in mind) is whether the infanticide well known to cultural anthropologists studying band and tribal level societies conforms to the reproductive strategy model proposed by sociobiologists. We can ask whether cultural patterns mimic biologically sound behaviors. In a general way infanticide among humans *can* be interpreted to be a beneficial behavior insofar as it often corrects for improperly spaced births; that is, protein and general caloric intake of hunting and gathering peoples does not frequently permit the luxury of nursing two infants simultaneously, or infants born within two years of each other. The positively sanctioned act of killing the too-soon-born or defective infant maximizes the chances that at least one offspring or a future offspring will survive. Instead of investing further in a defective child who may die soon even with the best of care, females of many hunting and gathering societies will terminate the infant's life thereby facilitating a new pregnancy and, presumably, one that will yield a more profitable (genetic) return — so the theory goes. In the sense that raising one offspring rather than no offspring contributes to the fitness of the mother, it appears that such cultural learned procedures conform to, if not directly mimic, what could be described as a sound, biological strategy.

We must consider in more detail what actually causes the human infanticidal behavior. Certainly, no genes are involved here. Instead, this aggression must presently be explained by certain sociocultural mechanisms (institutions) that have an effect on fitness but are not genetically based.

Preferential female infanticide (killing female infants rather than males) occurs in several Arctic cultures as well as cultures involved in chronic warfare. The effect of this kind of infanticide is to raise males at the expense of females possibly because of their increased hunting and fighting skills.⁴⁴ Preferential female infanticide also may act as a check on reproductive growth since females rather than males prove to be the limiting reproductive factor.

Interpretation of human infanticide, especially preferential female infanticide, remains highly controversial;⁴⁴⁻⁴⁶ but irrespective of the competing

explanations dealing with this issue, some important principles emerge when we attempt to apply adaptive explanations of this phenomenon that were developed from animal studies. Among different species the same behavior pattern can evolve or develop for quite different reasons. This means also that while the same behavior pattern may be manifested, in this case infanticide, the mechanisms surrounding and permitting its expression, the socioecological conditions that make it useful or not, may differ significantly between species. For less advanced animals, it might be correct to suppose that genes underlie infanticidal attacks; but among human beings, if and when it does occur, only proper socialization (learning and experience) can inform individuals whether and how it should be performed. Just as cultural conditioning affects differences in the degrees of tolerance that Chinese and New Yorkers exhibit for living in highly dense conditions, we must rely on indigenous religious values and ideologies (cultural mechanisms) to explain the perpetuation of infanticide; we cannot defer to genetic processes, though this does not mean that the performance of infanticide has no effect on reproductive fitness.

All these considerations suggest (1) in interpreting the origins and bases of primate aggression, one of the major problems will be in determining to what degree natural selection is responsible for all its complex and varying manifestations, and (2) it will not be easy to borrow explanations from one species to apply to another since the evolutionary (ultimate) cause of one species' behavior, such as infanticide, may be as different as is its proximate (more immediate) bases. It is important to add that the causes of a behavior always must be analyzed separately from functional consequences, though this idea does not preclude the possibility that cause and function may prove to be related.

Socioecological Context of Aggression

The infanticide debate with its emphasis on evolutionary issues has refocused our interest in the dynamics and interrelatedness of aggression with an individual's socioecology, that is, how it makes a living and survives in a particular habitat as a member of an ecological community. It has confirmed the fact that to learn anything about aggression we must analyze it as it occurs in a precisely delimited environment; aggression must be interpreted not simply within a species-specific context but also within a group or sub-group context.

More than passing reference must be made to an individual's feeding needs, disease pressures, or its species' foraging strategy, to defense and sexual needs. What are the anatomical and physiological adaptations to certain dietary requirements that can make intra- or interspecies aggression useful or costly in an adaptive sense? Questions presently being addressed by primate field researchers having implications for understanding the causes and effects of aggression include the ways competing needs or organisms come into conflict and are resolved through adaptive compromises.⁴⁷ For example, it is generally thought that the leaf-eating langur

monkeys of the Old World, and the leaf-eating howler monkeys of the New World are not as aggressive as are many species of the more omnivorous macaques and baboons — generally there tends to be much less interindividual factionalism, and they seem to be able to sit in close proximity to one another during intense feeding without extensive overt feeding competition, punctuated by aggression. The fact that there is minimal feeding competition among these groups is surprising mainly because leaves are notoriously unnutritional. Relative to seeds, roots, fruits, and other herbs, leaves do not contain much protein. Yet, time and time again investigators find these leaf-eating monkeys living in and sharing the same resources in highly dense numbers, with only minimal aggression being exhibited among them.

Among the more omnivorous macaques and baboons, who consume many different foodstuffs, interanimal squabbles are numerous. How might one explain, then, the lack of aggressive feeding competition among the Colobines and howlers where one might expect it? The answer may rest with the collective metabolic or energetic cost of aggression, relative to what exactly is gained. Consider that langurs (one species of leaf eaters) have exceedingly large, diverticulate stomachs that permit absorption of cellulose from dry leaves and detoxification of certain plant secondary compounds — the poisons (tannins and alkaloids) that help protect plants from hungry herbivores. Detoxifying plant toxins and the process of extracting cellulose from dry and senescent leaves require a great deal of energy. It also appears that howler monkeys (without the diverticulate stomachs) can consume and properly digest certain secondary compounds. Hence, since aggression uses many calories that the langurs and howlers cannot afford to lose, they appear to be willing to switch rather than fight. Aggressive behavior is simply not worth it.

Waser and Homewood⁴⁸ studied two different species of mangabeys, a black-tufted monkey living in an Ugandan forest. One species lived in a microhabitat in which a fairly continuous supply of fruit was available in a small, predictable area. Using some traditional ecological theories, most notably the Horn principle, territorial behavior made possible by aggression could be expected. However, playbacks of alien adult male calls could not elicit any kind of aggressive behavior among this group, nor was any "natural" territoriality observed. Waser and Homewood's explanation for the lack of territoriality included the possibility that too many relatives of group members constituted the membership of neighboring groups. In this case the presence of relatives might decrease the utility of stringently protecting a feeding site from intrusion of other mangabeys since such behavior would deny relatives access to preferred food.⁴⁸ This suggestion by Waser and Homewood may only be appropriate for the mangabeys and the kind of social structure they exhibit; but this example further illustrates that both the presence and the absence of aggressive behavior in groups of primates depend on many interacting variables. As was the case for the Colobines and the howlers, the level of aggression exhibited by group

members is a compromise. In this instance, territorial aggression is probably not as beneficial in the long run as sharing resources with relatives, with whom genes by way of common descent are shared. Their reproductive success, in one sense, contributes to the reproductive success of their seemingly caring-and-sharing kin.

Hormones, Social Experience, and Primate Aggression

Obviously, the kind of naturalistic data on which the ideas above are proposed have particular significance to field-oriented anthropologists. Laboratory studies definitely complement the kind of perspective gained through the field studies. For example, laboratory studies continue to support the idea that learned social statuses, experiences, and roles often exert a more powerful influence over the form and direction of aggression among primates than do male androgens such as testosterone. Dixson's recent review of androgens and primate aggressivity reveals important continuities between human and nonhuman primates, especially with respect to the relative contributions that hormones and the social environment make to the expression of aggressive behavior. For example, Dixson discusses several experiments in which it was shown that artificial stimulation of the amygdala could excite animals and induce aggression; yet it was the animals' social experience with colony mates that determined when, if, and to whom aggression would be directed. When the preoptic region of the monkey brain was stimulated, likewise aggression could be induced but only when an appropriate subordinate was available to be attacked.⁴⁸

Studying the role of the androgen testosterone especially as an activator hormone during puberty, Pavachio has shown that even castration on male Rhesus monkeys does not eliminate attack behavior altogether — and this is after no testosterone is being produced by the testes.⁴⁹ Pavachio suggests that certain peptides as well as monoamine neurotransmitters interacting with steroids may be partially responsible for aggression. Arguing that among the primates social experiences can override hormonal or neurological status Dixson adds, "where the social framework or social structure is unstable, however, or the relationship between two animals is finely balanced then hormonal factors may play some role, for there is evidence that androgen enhances the likelihood that male Rhesus monkeys and talapoins will behave aggressively."⁵⁰ Dixson does not mean to insinuate that androgens are unimportant, for they may have an important organizing effect on the male brain *in utero*, as Jerry Levy has recently argued. Dixson does mean that androgens do not play the central role in influencing primate aggression that they play among rodents.

Of course, the role of testosterone in human aggressive behavior has been of interest, but thus far, attempts to correlate levels of male aggressivity with levels of circulating testosterone have been contradictory. Except for the study by Kreuz and Rose most correlations between testosterone and aggression have proved insignificant (see Hoyenga and Hoyenga²² for review). However, Money and Ehrhardt⁵¹ found that chromosomal females

with progestin-induced hermaphroditism were rated more aggressive than control groups, albeit the measurements of aggressivity and the ambiguity of their gender socialization surely must affect the reliability of these data.

Dominance, Aggression, and Reproductive Success

While the effects of circulating testosterone have always been of interest to primatologists, of more interest is the possibility that an important relationship exists between aggression and dominance. The issue is broadened a bit and placed in a functional context when it is considered that successful aggression may produce high status or high social rank (dominance) and this may be correlated positively with reproductive success. This question has been around for a long time and remains an important theoretical issue not yet resolved. It stands to reason that the most successfully aggressive animals ought to be the most reproductively successful if successful aggression achieves priority of access to optimal food resources and first access to available mates.

Yet a positive relationship between dominance (as measured by successful aggression) and reproductive success has been exceedingly difficult to document in the field and laboratory studies. First, there has been confusion over what exactly dominance means and how one should measure it and determine how long animals retain it. We can now say it is no longer thought of as a pervasive personality trait that one either has or doesn't have. It is regarded as multifaceted and possibly age-dependent; dominance is recognized when — through an individual's own actions, the action of supportive others, or both — the individual regularly wins rather than loses aggressive encounters with particular others.⁴⁷ Most investigators will settle for this description.

But still, both field and laboratory data reveal that whether an animal loses or wins, some contested resource or goal often is determined by the nature of the item being competed for (see Popp and Devore⁵²) and how badly the animal needs to win; interactions between individuals that may result in a dominant animal and a subordinate must be analyzed in a resource-specific context. As Bernstein⁵³ has eloquently argued, it is much more difficult to define and recognize a truly dominant/subordinate relationship existing between two animals, than it is to observe an occasion on which one or the other of a pair is dominant. In other words, a mother might defend her young by attacking a "dominant" adult male if she feels her infant is being threatened; while, in a different context, indeed all other non-maternal situations, she will regularly defer to the same male. Just as Moyer pointed out, not to specify the context in which aggression takes place is virtually to ignore the most important aspect of the interaction; a proper interpretation will be impossible.⁵

There is some evidence for some primate species that, at least in the short run, high status achieved through successful aggression (especially among baboons, vervets, gelada baboons, yellow baboons, and Japanese macaques) can lead to greater chances of survival and higher reproductive

records.⁵⁴ Recently, Wrangham demonstrated that when water resources are in short supply, dominant animals can keep subordinate females from obtaining it, and they die. This occurred while Wrangham was watching vervet monkeys in Kenya.⁵⁵ Surely, nobody will argue that these females' lower statuses undermined their fitness on a rather permanent basis. But such a positive relationship (in this case with negative consequences) between dominance and survival is seldom documented. The only other study showing such a clear relationship between survival and dominance is one conducted by Dittus. He studied the toque macaque monkey in Sri Lanka and found that subordinate animals (usually juveniles) died in great numbers during periods of food shortage.⁵⁶

Among the baboons, while it can be shown that dominant adult males mate with females at optimal periods in their reproductive cycles, Hausfater shows that some change in the male dominance hierarchy occurs approximately every 13 days. Thus, it may be that almost all males have their chance at one time or another to be dominant.⁵⁷ Moreover, Lancaster⁵⁸ points out that longevity, his or her health, and general talents determine fitness as much as behavioral dominance does. With a little bit of luck, individuals can be quite fit indeed — even when successful aggression is not forthcoming. Field data of long enough duration are beginning to be available, and they might provide some answers to these important questions.

Summary and Conclusions

I have attempted to describe some of the issues that complicate the anthropologist's and/or sociobiologist's ability to interpret and understand aggression from a cross-species and evolutionary perspective. It would be naive to assert that human aggression has no biological roots or that natural selection processes have nothing to tell us about this behavior. But it would be equally as naive to assert that aggression can be fully explained by such data; the truth is that among human beings, learned social behaviors (which include learning when to use learned behaviors) make it highly unlikely that the kind of aggressivity we are witnessing today, particularly in urban-complex societies, is inevitable, or the result of misguided aggressive genes collected by our hominid ancestors.

Aside from the role of learning in understanding human aggression and the powerful cultural values and ideologies that guide our learning, it is my contention that aggression has not evolved among primates in the same way that, let us say, the grasping hand evolved. Undoubtedly, in certain situations, both in the present and past, the potential for a human being to successfully act aggressively (intraspecifically) either to protect loved ones, food, or other resources, has been critically important; but to speak about how precisely a human being acts aggressively, and, thus, what in total natural selection is favoring, several factors that move well beyond the physical act of aggression itself must be considered. For example, selection has never favored uncontrolled violence; it will favor individuals whose

cognitive/analytic skills permit them to correctly assess when, to what degree, and how aggression should be performed. In some instances aggression may be useful, but in other instances patience and clever social manipulations may work best. Should aggression occur in a one-on-one encounter? Should it occur by way of coalitions of supportive individuals — and at what precise moment is any aggressive act likely to be the most successful and present the fewest risks? Is the intended victim removed from its allies; is the intended victim more vulnerable because it is old or sick? Humans and their immediate ancestors who could answer these questions most correctly and could then *use* this information correctly would be favored by natural selection.

In other words, there are many situation-specific variables in addition to strength and coordination of fighting skills that must evolve concomitantly. Especially among primates, given their extensive social adaptations and considering that they depend as much on their decision-making abilities as they do on their physical-anatomical structures for exhibiting aggression, we cannot interpret aggression as if it were based on the encoding of a genotype. This is a good reminder that aggression is not inevitable nor the result of a singular, selected genotypes; it is also a reminder that we cannot argue too strongly that, *per se*, aggression genotypes evolve. Rather, we can best support the position that individuals characterized by certain physical attributes who also exhibit particular social and analytic skills will be favored; one of many behaviors that can be successfully performed, when necessary, is aggression. This perspective (and I believe it to be fair and accurate) is quite different from arguing that physical strength underlying aggressive behavior evolves while weaker nonaggressive individuals do not evolve; this perspective is different from the more simplistic one that suggests “weak” individuals are prevented from breeding and passing on their genotypes by their aggressive counterparts. Misused aggression, misplaced aggression, and excessive aggressivity would, undoubtedly, have been selected against, while controlled aggression integrated into other spheres of social behavior could prove valuable.

Indeed, we cannot very easily blame present-day aggressivity on our hominid ancestors; we have both the ability and responsibility to alter social structures and socialization agencies so the kinds of aggressive acts we see today can be eliminated. We can ill afford to wait for changed genotypes to do it for us since, after all, they were never the only basis of aggression in the hominid lineage in the first place.

To briefly summarize some of the points I have attempted to illustrate here: (1) Sociobiology has caused many investigators to shift their analyses from considerations of groups to considerations of the individual. (2) According to sociobiologists an individual's behavior, including aggression, should reflect some underlying genetic processes (either past or present) that guide them in the direction of genetic selfishness. (3) Natural selection has played an important role in shaping individual activities that do not

necessarily contribute to the welfare of success of the group. (4) From a sociobiological perspective male aggressivity may be explained in the context of intrasexual competition and in the context of the conflicts between optimal female reproductive strategies and optimal male reproductive strategies. (5) Evolution has always been of central concern to anthropologists, but precisely how this process articulates with the power of learning and socialization in general is not entirely clear. (6) Human sociocultural systems show tremendous differences in the form and level of aggression exhibited by group members. (7) Even when culturally learned behavior mimics or parallels more genetically based behaviors of the past, which at one time increased reproductive success, we must still depend on cultural frameworks and not biological ones to fully explain or predict that behavior. (8) Social behavior among primates is influenced but not determined by hormones or the gene coding primarily because (as field and laboratory data reveal) learning in a social context continues to be a primary part of our survival. (9) It should be remembered that the same kind of aggression can occur among different primate species, but the causes of that behavior, the mechanisms that maintain it, and the ultimate effects of that behavior might differ. (10) Primate aggression cannot be accounted for only in terms of its functional consequences. (11) Cause and function may be independent of one another, though this does not mean that they are completely nor always unrelated. (12) Primate aggression is analyzable only in a resource-specific context and within a particular species and group context. (13) Cross-species comparisons among the primates are important mostly because they alert us to the kinds of socioecological, socioenvironmental, and biological variables that coalesce to produce different kinds of aggressive behaviors. (14) Mechanisms that supported human or hominid aggression in the past are not necessarily the same mechanisms that support it in the present. (15) Human aggression as it occurs and is expressed today occurs in environments for the most part significantly different from the environments in which specific kinds of aggression evolved. (16) The kind of aggression occurring in our highly technocratic society may be quite maladaptive and not at all similar to the rates and form of aggression as it occurred among our hominid ancestors.

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PRIMATE AGGRESSION & EVOLUTION

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