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Evolution, Primates, and Subaltern Genocide

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The incident took place in February 1974 and marked the beginning of the end of the Kahama community. A raiding party of three adult males and one adult female from the Kasakela community hiked for over half an hour into Kahama country, where they happened upon a member of the Kahama community. The three males attacked quickly, catching the unsuspecting Kahama male, biting him and stamping on him. Soon the victim stopped struggling and sat hunched over on the ground. Suddenly he attempted to run away, but he was caught by the leg and pulled to the ground. Now all the members of the Kasakela raiding party, including the female, joined in the attack, pounding the prostrate victim repeatedly. One or more of the aggressors ripped the skin from the victim's leg with their teeth. The attack ended as quickly as it had begun. Two months later the victim was seen again. His spine and pelvis were protruding. He had an unhealed gash on his inner thigh, likely the spot where his skin was ripped in the attack. The nails had been torn off his fingers. One toe was partially severed. He had lost part of an ear. He was emaciated. After that sighting, he was never seen again.

This is not an instance of a genocidal attack among humans, but rather an attack by members of a larger, socially dominant group of chimpanzees (based on the demography of the group, and in particular the number of adult males) on members of a smaller, less dominant group in the Gombe Stream National Park in Tanzania.[1] The incident suggests that humans are not the only primates capable of systematic group attack and killing of nongroup members. Consideration of, and comparison with, our closest nonhuman relatives may provide useful insights into genocidal behavior in general, and subaltern genocide in particular. Are humans, for example, the only animal species in which some groups experience "oppression" and seek to gain "revenge" and achieve "liberation" by waging genocide against their "oppressors"? To the extent that humans exhibit such behavior, can we account for it with culture and learned behavior alone? Or is there an evolutionary basis for this behavior?

A reasonable question is: "So what if there are commonalities between humans and nonhumans in the expression of certain types of aggressive behavior?" And additionally, "What difference does it make if genocide has an evolutionary or biological basis or not?" It is important to understand that the strategies developed to control genocide might be different from those employed today, if it could be shown that there was at least a partial evolutionary or biological basis to this aggressive behavior. An evolutionary perspective on human aggression might therefore stimulate new thinking about the formation and implementation of social policy, incorporating an acceptance of the underlying genetic and hence evolutionary basis of our aggressive behavior. Using an evolutionary approach, it might be possible to identify certain sociopolitical and ecological situations where genocide may occur, and at the very least prepare a humanitarian response if it occurs.

An Evolutionary Primer

Many critics of the application of evolutionary theory to human behavior are vigorous adherents to the Standard Social Science Model (SSSM) of explanation. The central theme of the SSSM is that differences between people result from differing environmental conditions, not genetic differences between populations or individuals. Unfortunately, adherents of the SSSM are misinformed about the relationship between genes and behavior. Rather than playing a rigidly deterministic role in shaping behavior, genes may exert more subtle influences—which feel like urges from within that have positive feelings attached to them, as opposed to rigid cause-and-effect relationships. The widespread acceptance of the SSSM is based on its moral appeal rather than on empirical fact. The SSSM has been carefully critiqued,[2] but its appeal lies in its strong stand against explaining differences between races, sexes, or individuals as exclusively the outcome of underlying biological differences. In its most extreme form, the SSSM holds that humans are plastic and the contingencies of the environment shape and channel our behavior with no input from our genetic heritage in explaining modern human variation.

This model has been important in combating social injustices. Supporters of the SSSM are opposed to racism and sexism; by definition, those who challenge the moral superiority of SSSM are labeled "biological determinists." This characterization of all non-SSSM adherents as determinists is patently wrong. Moreover, SSSM adherents argue that those who challenge the SSSM are attacking the basic human behavioral plasticity that is the cornerstone of their view of human nature. This "learning" view of human behavior favored by ardent devotees of SSSM is the intellectual product of the renowned psychologist John B. Watson:

> Give me a dozen healthy infants, well-formed, and my own specified world to bring them up in and I'll guarantee to any one at random and train him to become any type of specialist I might select—doctor, lawyer, artist, merchant-chief, and yes, even beggar-man and thief, regardless of his talents, penchants, tendencies, abilities, vocations, and the race of his ancestors.[3]

Before I enter into the details of the argument about an evolutionary basis for genocide, it is important to have a basic understanding of evolutionary theory. Most people feel they have an intuitive grasp of what Darwinian evolution is all about, but it may be beneficial to review some basic principles. Readers with a solid background in Darwinian thinking are invited to skip ahead to the section "Comparative Data."

Darwin 101

Darwin's central thesis consists of three major points and can be summarized as follows. Where competition exists for scarce resources, those organisms most fit to survive and reproduce will do so in greater numbers than those less fit. Darwin's ideas were not completely novel when he wrote *On the Origin of Species*, and they seem almost absurdly simple today. But there is much more here than first meets the eye. The first aspect of Darwin's theory is that competition is a fundamental aspect of life; it occurs when two or more individuals require the same resources and those resources are in limited supply. Competition exists at several different levels in biological communities, but for our purposes intraspecific competition is of considerable importance.

Intraspecific Competition

Organisms encounter competition from members of their own species, and it is common among animals as well as humans. Intraspecific competition among humans takes a variety of forms, and it is not always the "main event, winner-take-all" strategy that is most successful. Deception, bluffing, and false advertising are all important alternative competitive strategies—very often the strategies that are played out in human subaltern genocide in order to initiate a discourse of resistance and sometimes active rebellion.[4] The first thing to do in understanding competition in an evolutionary sense is to attempt to identify the cause of the original conflict—although identification of the contested resource is not as easy as it may seem at first blush.

Most Fit to Survive

Winning at evolution means more than simply surviving. In fact, survival alone does not even get you entered in the competition. What you really want to do is to maximize your genetic representation in future generations. Is that the same as maximizing the number of children that you have? That is partially the case—but the real definition of fitness has to do with the number of your genes that are present in the next generation.

When one thinks about measuring fitness, the renowned evolutionary biologist W. D. Hamilton (1936–2000), called by some the most distinguished Darwinian since Darwin, suggested that there are two components that must be taken into account.[5] First, there is your direct fitness, the number of your offspring that survive and reproduce. Remember that the only way to win at the game of evolution is to ensure that your genes reach the next generation, producing offspring that in turn produce offspring. By becoming a grandparent, you win at the game of evolution. However, the production of massive numbers of offspring that fail to reach maturity is not a winning strategy in evolution; nor is producing offspring that reach maturity but do so too slowly to make an impact in subsequent generations. It does not matter in the evolutionary calculus how many children you have if none of them reach sexual maturity and mate.

The production of offspring is not the only way one can get genes into subsequent generations. On average, you share about fifty percent of your genes with a full sibling, someone who has the same mother and father as you. This means that if your full sibling has children that survive and reproduce, then you are also winning at the game of evolution without reproducing yourself. Hamilton called this indirect fitness, and it is the outcome of the reproductive efforts of those to whom you are related. Imagine that you are actually helping yourself in the game of evolution if your sibling produces offspring that reproduce—even if you never see them or interact with them, or even know their names. Your total fitness is thus composed of your direct fitness plus your indirect fitness. In most cases, your indirect fitness will not exceed your direct fitness, but it is conceivable that it might.[6] And since it is *total lifetime fitness* that is significant, one could make a relative judgment about fitness based on current reproductive output that would be totally incorrect. This is particularly important to keep in mind for a long-lived species such as our own.

Greater Numbers of Survivors

The final piece of the short version of Darwinian evolution emphasized that where competition exists for scarce resources, those organisms that are most fit survive and reproduce in greater numbers than those that are less fit. It means that while individuals live and die, it is a species that undergoes extinction. Not all individuals with certain characteristics favorable to a particular environment will necessarily survive and reproduce; there are many non-Darwinian factors (unpredictable environmental change, random chance, and so on) that can affect survival. What Darwin meant is that if you possess characteristics that are fitness-enhancing in a particular environment, you will survive in greater numbers than those not possessing those favorable characters.

So is there some absolute number of individuals possessing a particular phenotype that must survive in order for you to win at evolution? How many grandchildren must you have to ensure that you are a winner in evolutionary terms? Must you produce 1.8, 2.4, 4, or even 7 offspring to "win"? Unfortunately, there is no absolute number that ensures you will win in the competitive arena of evolution. The only thing you must do is to produce more viable offspring that reproduce themselves than your local competition. It is not the number of offspring produced by competitors that are distantly removed, but ones with whom you compete daily.

Exactly What Is Evolution?

Evolution is one of the central concepts in biology, and because its definition is so simple and elegant, people are easily deceived into thinking that it is something it is not. The concept of evolution is widely deployed, yet there is a fundamental problem with how it is used. For example, many assume that evolution is somehow progressive. To most people, if something is evolving, there is an unstated assumption that it is improving. Of course, what constitutes improvement is another matter entirely.

The word evolution has its origin in Latin *evolvere*, means to unfold or unfurl. Nowhere in its definition is there a notion that progress is an inherent part of evolution. The hypothesis that there was some driving force in organisms that moved them in a unilinear manner toward perfection can be traced to Jean-Baptiste-Pierre-Antoine de Monet, Chevalier de Lamarck (1744–1829), and his idea of the inheritance of acquired characteristics. The notion that organisms are moving inexorably toward perfection has many implications that are beyond the scope of this chapter, most notably in current ideas about intelligent design and religion. However, it was Herbert Spencer (1820–1903) who suggested that social evolution was comparable to biological evolution and that human societies progressed from undifferentiated hordes into complex civilizations. Ideas about the progressive nature of evolution still hold considerable power in the common conception of evolution. In fact, Darwin did not refer to evolution in the *Origin* until the last page, the last paragraph, the last sentence, and the final word of his book:

> There is grandeur in this view of life, with its several powers, having been originally breathed by the Creator into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved.[7]

So if evolution is not progressive, what is it? As used in evolutionary anthropology, and for that matter in virtually all of science, evolution simply describes genetic changes in organisms over time. The definition has no hidden assumptions about organisms progressing to forms that are increasingly better adapted to their local environment. Genetic changes could produce forms that are better able to exploit their local environment; but just as easily, evolution can produce forms less able to survive. From a statistical perspective, the odds are that species extinction is much more likely than survival.

If this view of evolution is correct, what factors will bring about these genetic changes over time? There are four forces that can cause changes in gene frequency or produce evolutionary change in a population. Natural selection, the differential production and survival of offspring, is the force that most frequently comes to mind. It is certainly important, but the others deserve careful consideration as well. Mutation, the physical alteration of heritable genetic material, is the source of new genetic material in the population and that new genetic material can have positive, negative, or neutral effects. Rather than characterizing mutations as good or bad, it is best to think of them as having potential for both. Gene flow, the migration of fertile individuals and their subsequent reproduction, or the transfer of gametes between groups of individuals, is a lesser known agent of evolutionary change, but one that has had considerable importance in the evolution of early humans and their diffusion from Africa. Finally, there are changes in the genetic makeup of populations that are due to random events that have nothing to do with the process of organisms becoming better adapted to their environment, and this is called genetic drift.

Another evolutionarily important concept with which almost everyone has a passing familiarity is adaptation. This is the outcome of natural selection, since such selection is the only evolutionary force that can "choose" one phenotype over another. It is important to remember that natural selection is an evolutionary force that does not "know" if an organism possesses an underlying genotype that will be more successful than other genotypes in the population. Natural selection can only "see" the variation expressed in the phenotype. An individual could be the carrier of the most adaptive trait imaginable in a particular environment; but if it is not expressed, it cannot be selected. When we speak about an organism being "adapted" to its environment, we are really saying that it possesses a suite of traits or characteristics, expressed in the phenotype, that increase its fitness relative to individuals without those traits. We can talk about both process and outcome: about an organism becoming adapted to its environment, and about an organism possessing adaptations to an environment.

Underlying Assumptions of Darwinian Evolution

First, for a character or trait to be called Darwinian, there must be some phenotypic variation in the population under study. A phenotypic trait is one that is observable, and is the outcome of an interaction between the underlying genetic basis and the environment. What is of particular concern here is that there must be variation in the expression of the trait. Without variation in phenotype there would be no raw material on which natural selection could operate.

The genetic basis for all traits, whether they are expressed phenotypic traits or unexpressed traits, is the genotype. Not all of the genetic variation present in an organism is expressed in the phenotype. The variation in phenotype can be due to underlying genetic variation, as well as variation introduced by the environment. Indeed, the second assumption that must be met before a trait can be considered a Darwinian trait is that some proportion of the phenotypic variation must be due to underlying genetic variation. This is not the same as saying a trait is genetically determined, just that a proportion of the variation in the phenotype is due to underlying variation in the genes. That one can see variation in genetically identical offspring demonstrates that not all variation is due to genes.

Finally, to be considered Darwinian, a trait must have some effect on the fitness of the individual possessing it. While many traits fulfill this condition, a nontrivial number are simply adaptively neutral. These neutral traits are maintained in populations because there is no selection pressure against them.[8] Without fitness consequences for the possessor, no trait can be called a Darwinian trait; while perhaps interesting to specialists in genetics and evolutionary biology, the discussion of neutral traits is beyond the scope of this chapter.

Comparative Data

I have attempted to lay the foundation for the serious consideration that there are aspects of modern human behavior that should be called Darwinian evolutionary traits. Indeed, an evolutionary perspective has been enormously helpful in understanding such disparate aspects of human behavior as our reproductive strategies,[9] our parenting behavior,[10] and our tendency toward aggression, violence, and warfare.[11]

This perspective is important if we are to assess the possibility that genocide in general, and subaltern genocide in particular, may have an evolutionary basis. My goal in this section is to present comparative data on intraspecific killing in other animals, and to evaluate its importance for our discussion of subaltern genocide. The data are restricted to mammals, and to cases of individuals killing members of their own species in particular. (While intraspecific killing is well known in birds, insects, and fish, I have excluded those data based on their presumed phylogenetic distance from humans. I have also excluded cases of interspecific predatory behavior.)

I categorize intraspecific killing into three types: infanticide,[12] intragroup killing, and intergroup killing. Infanticide is a fascinating behavior: at first glance it seems to run counter to Darwinian principles, but on further examination it can be seen as a classic Darwinian trait.[13] Male infanticide in animals is a straightforward fitness-maximizing strategy whereby males will attack and kill infants sired by other males. The net result of the loss of a dependent infant is that mothers soon return to a sexually receptive state. This type of infanticide typically occurs in species where males immigrate between groups, but it has also been observed in species lacking male migration.[14] Female infanticide is also observed in a variety of animals; typically, the killing of dependent offspring of other females helps to secure additional resources for the perpetrator's offspring. Classifying killings into those perpetrated against members of a social group by members of that group, as distinct from killings perpetrated by nongroup members, also seems relevant. Given that genocide involves the killing of members of one group by members of another, differentiating among the types of lethal aggression seen in mammals seems justified if we are to search for examples that inform our study.

While chimpanzees are the primary focus of this comparative analysis, it is important to note that there are many other primate species, as well as other mammalian species, that form coalitions in order to enhance dominance status, gain access to estrus females, or gain access to preferred food resources. Most of the research on coalitions has been done on nonhuman primates, but there is good evidence that such diverse animals as South and Central American coatimundis, African spotted hyenas, and Atlantic spotted dolphins form coalitions for a variety of reasons. (See Table 8.1.) While the comparative data are instructive, they still leave unanswered questions. If coalition formation is as widespread as it appears among primates, and is as important in chimpanzee society as the field research indicates, then what does that mean for us? An in-depth discussion of coalition formation in humans is far beyond the scope of this paper, but there seem to be some interesting parallels, particularly with the behavior of wild chimpanzees.

Both male and female chimpanzees form temporary as well as long-term coalitions in both the field and captive conditions. Such coalitions seem to be important for both males and females, but for different reasons. Captive, group-living female chimpanzees as well as male chimpanzees form coalitions, but the functions of these coalitions seem to differ dramatically, with males forming coalitions in order to increase status while female coalitions are formed for protection from male aggression.[15] Oddly, however, female chimpanzees have been reported to form such coalitions in the natural setting at only one research site.[16] This suggests that female chimpanzees, like males, have the behavioral potential to engage in such interactions, but do so only when particular demographic and ecological conditions are present. While the precise reasons females engage in coalitions against males in the Budongo Forest, Uganda, are unclear, it may be that by participating in such coalitions, females reduce the levels of future aggression.[17]

In contrast, male chimpanzees routinely form coalitions that have been observed at several different field sites. Chimpanzee males form dyadic as well as triadic coalitions to enhance or maintain dominance status.[18] On one occasion, in the Kasakela chimpanzee community in the Gombe Stream National Park, the existing alpha male was overthrown by a team of two brothers (Figan and Faban) that left Figan as the top-ranking male.[19] Another coalitionary dominance takeover was observed in the M group in the Mahale Mountains of Tanzania. A deposed alpha male who had remained in the vicinity but some distance from his previous group took advantage of the death of one of the three dominant resident males and allied himself with the less dominant of the two remaining males and ultimately reasserted his alpha dominance position.[20]

Central to the question of genocide are observations of intergroup killing. If there is a parallel to human genocide among animals and in particular primates, it is likely the coalitionary killing observed in chimpanzees (*Pan troglodytes*).[21] Coalitionary attacks have also been reported in white-faced capuchin monkeys (*Cebus capucinus*) and spider monkeys (*Ateles geoffroyi yucatanensis*), but these are much rarer occurrences and do not appear to have the same underlying motivation as seen in chimpanzees. The real question is whether coalitionary killing in chimpanzees is truly homologous with human genocide; or whether certain attributes of human genocide serve to clearly differentiate our behavior from that of our closest primate relatives. The reports of intergroup killing are summarized in Table 8.2.

TABLE 8.1 CASES OF COALITIONARY KILLING BY ADULT NONHUMAN PRIMATES

Species	Common Name	Location	Details	Reference
Cebus capucinus	White-faced capuchin	Lomas Barbudal Biological Reserve, Costa Rica	1. α♂ wounded and evicted from group, later attacked again by group members and killed. 2. Lone nongroup ♂ (2–3 yr) was attacked by several group member males including adults, subadult, and juveniles. Victim was severely injured and died the next day.	(Gros-Louis et al. 2003)
Ateles geoffroyi	Spider monkey	Otoch Ma'ax Yetel Kooh, Mexico	1. Young adult ♂ (6–7 yr) group member attacked by three adult ♂ group members and killed.	(Valero et al. 2006)
Pan troglodytes	Chimpanzee		1. Prime adult ♂ of Kahama community (Godi) attacked by six adult ♂♂, adolescent ♂, and adult ♀ members of Kasakela. Godi suffered severe wounds, never seen again following attack, presumed dead. 2. Adult ♂ of Kahama community (Dé) attacked by three adult ♂ and one adult ♀ member of Kasakela. Dé suffered severe wounds and survived the attack, but was assumed to have died as result of attack. 3. Old adult ♂ of Kahama community (Goliath) was attacked by three adult ♂♂, and one adolescent ♂ members of Kasakela. Goliath suffered severe wounds, never seen again following attack, presumed dead.	(Goodall et al. 1979)

Species	Common Name	Location	Details	Reference
Pan troglodytes	Chimpanzee	Gombe Stream Reserve, Tanzania	1. Prime adult ♂ of Kahama community (Charlie) was presumably killed by party of five adult ♂♂ of Kasakela community. No details of attack available, but Charlie's body found two days later at Kahama Stream. 2. Prime young adult ♂ of Kahama community (Sniff) was attacked by three adult ♂♂ and one adolescent ♂ members of Kasakela. Sniff suffered severe injuries, seen the day after attack unable to move, never seen again, presumed dead. 3. Old adult ♀ of Kahama community (Madam Bee) attacked by four adult ♂♂ of Kasakela community. Madam Bee suffered severe injuries and died five days after the attack.	(Goodall 1986)
Pan troglodytes	Chimpanzee	Budongo Forest, Uganda	1. Prime adult ♂ of Sonso community (Zesta) was attacked by at least two adult ♂♂ of the Sonso community. Zesta suffered fatal injuries and died at the scene of the attack. (Suggested reason for attack was intra-community male sexual competition.)	(Fawcett and Muhumuza 2000)
Pan troglodytes	Chimpanzee	Kibale National Park, Uganda	1. Low ranking adult ♂ of the Ngogo community (GRA) was attacked by at least seven other adult ♂♂ of the Sonso community. GRA was held down during the attack by three adult ♂♂ but not completely immobilized. GRA suffered severe wounds, but survived attack only to die a week or so later from his wounds. (Suggested hypotheses include retribution for past behavior, contests over α status, or sexual access.)	(Watts 2004)

Species	Common Name	Location	Details	Reference
Pan troglodytes	Chimpanzee	Kibale National Park, Uganda	1. Adult ♂ from another community was feeding with other group members (at least two ♀♀ with infants, one adult ♂, one juvenile) when the adult ♂ was attacked and killed by five adult ♂♂ of the Ngogo community. 2. Adult ♂ from Wantabu community was attacked by sixteen adult and three adolescent ♂♂ of the Ngogo community. Attacking ♂♂ did not press the attack continuously. Different ♂♂ participated. Wantabu ♂ died within ten minutes of start of attack. 3. Adult ♂ from another community was attacked by eight Ngogo ♂♂. Both adults and adolescents participated. Injured adult ♂ left area and was not seen again, presumed dead. 4. Adult ♂ from Sebitoli was presumably killed by ten ♂♂ from the Kanyawara community. The attack was not witnessed, but victim was found already dead, surrounded by Kanyawara ♂♂ 5. Juvenile ♂ (from neighboring community) was attacked by ≈ eight Ngogo ♂♂. The victim suffered severe wounds, but was not followed after the attack and presumably died.	(Watts et al. 2006)

Species	**Common Name**	**Location**	**Details**	**Reference**
Pan troglodytes	Chimpanzee	Gombe Stream Reserve, Tanzania	1. Juvenile ♂(≈10 yr) from the Kalande community was attacked by three adult ♂♂ from the Kasekala community. Victim suffered severe injuries which were presumably fatal, although he was not seen after the attack. 2. Adolescent ♂ (≈12–14 yr) of the Mitumba community was found dead. Suffered wounds that were consistent with those administered during chimpanzee attacks. Males from adjacent community Kasekala were within 1 km of site of victim's body.	(Wilson et al. 2004)
Pan troglodytes	Chimpanzee	Mahale Mountains National Park, Tanzania	1. Six adult ♂♂ members of K group killed between 1969 and 1980. Sobongo and Kamemanfu killed by M group ♂♂. All ♂♂ that disappeared were healthy and not senile.	(Nishida and Kawanaka 1985)
Pan troglodytes	Chimpanzee	Mahale Mountains National Park, Tanzania	1. Adult ♂ (Ntologi) of M group was found dead in center of M group territory dead. His death followed numerous coalitionary attacks by former subordinates after his defeat as α ♂ of M group	(Nishida 1996)

TABLE 8.2 EXAMPLES OF SPECIES WHO ROUTINELY FORM COALITIONS

Species	**Common Name**	**Details**	**Reference**
Macaca thibetana	Tibetan macaques	Males form coalitions to maintain dominance rankings against lower ranking males or immigrants.	(Berman et al. 2007)
Macaca mulatta	Rhesus monkeys	Matrilineal kin relations are the basis of coalitions to maintain dominance rank.	(Kutsukake and Hasegawa 2005)
Cercopithecus aethiops	Vervet monkeys	Females formed coalitions to accelerate integration into a new group.	(Hauser et al. 1986)
Cebus capucinus	Capuchin monkeys	Females form coalitions against other females as well as males to maintain dominance hierarchy.	(Manson et al. 1999; Perry 1997; Vogel et al. 2007)
Cercopithecus mitis	Blue monkeys	Females form coalitions with other group females to defend territorial boundaries.	(Cords 2002)
Papio cynocephalus	Savanna baboons	Female coalitions important in determining dominance relationships and access to resources.	(Silk et al. 2004)
Crocuta crocuta	Spotted hyenas	Males form coalitions to rise in status in female dominated heterosexual groups.	(East and Hofer 2001; Szykman et al. 2003)
Nasua narica	White-nosed coatis	Kin-related individuals form bands and direct aggressive behavior toward nongroup unrelated individuals.	(Gompper et al. 1997)
Stenella frontalis	Atlantic spotted dolphins	Formed coalitions of young males for social play.	(Herzing and Johnson 1997)

There are several important things to note about Table 8.2. The most obvious is that there is a decided mismatch in competitive abilities between aggressor and victim. Killing in nonhuman primates is not an individual effort, and more importantly there has been no instance of lethal dyadic aggression observed among any adult apes. This is not to say that there is not aggression between and among individuals, but when it escalates to the level of lethal force, individuals give way to coalitions. In order to kill another, coalitions of individuals are implicated, not single individuals.

Second, an examination of the primates that have been observed engaging in coalitionary killing reveals a strong bias toward chimpanzees. There has been considerable energy expended among primatologists to explain this bias,[22] and a detailed discussion of the ecological as well as social factors involved in chimpanzees' disproportionate levels of lethal coalitionary aggression is beyond the scope of this paper. Suffice it to say that many feel it has to do with the high degree of male philopatry[23] and female migration between male coalitionary bands; but a completely satisfactory explanation remains elusive.

Finally, a careful examination of the coalitionary data for chimpanzees shows that it is males that are the most frequent perpetrators of fatal aggression. It is true that females may participate in these episodes,[24] but they are virtually never the initiators. Males are also the most frequent targets of these lethal aggressive coalitions, especially those from neighboring communities. What emerges is a picture of groups of male chimpanzees periodically patrolling the boundaries of their territory, looking for intruders. When they encounter members from other groups, there is a nontrivial probability that some sort of aggressive encounter will ensue, and in a few cases these encounters have escalated in lethal aggression. It appears that this coalitionary killing occurs when the probability of injury to the initiator is low, and is most likely when the killing is carried out by a group of individuals.

So What About Subaltern Genocide?

We now return to the question posed at the beginning of this chapter. Are humans the only animal species in which oppressed groups seek to gain revenge and liberation by waging genocide against their oppressors? It is clear that chimpanzees engage in coalitionary killing which has on occasion resulted in the extinction of one group at the hands of another; but does this coalitionary killing among chimpanzees exhibit some of the same patterns and dynamics as *subaltern* genocide in humans?

As one might expect, the answer to that question is complicated. Two factors suggest that chimpanzees do not engage in behavior that is directly comparable to human genocide. First, as we have seen, lethal aggression in chimpanzees is not an individual event, but neither is genocide typically committed by single individuals. Among chimpanzees, coalitions of individuals in all observed cases were the perpetrators of the attacks. Second, the attacks are opportunistic and seem to occur only when the cost of the attack to the perpetrator is low and the likelihood of success is high. Certainly, any historian of human genocide will recognize these as major differences.

Given our understanding of chimpanzee behavior, then, it seems likely that the answer to my question is "yes": humans *are* the only animal species in which oppressed groups seek to gain revenge and liberation by lethal aggression against their oppressors. One of the critical points of the discussion is the behavior of groups. The coalitions among chimpanzee males have some extraordinary properties (e.g., longevity of associations, mutual support, sharing of resources), but there seems to be a lack of coordinated action of entire groups. Interestingly, some primatologists have speculated that there may be an element of revenge among chimpanzees, a characteristic motivating factor in subaltern genocide.

Robert Trivers, in his seminal paper on the evolution of reciprocal altruism,[25] used the term "moralistic aggression" to identify a type of behavior that would ensure that an altruist would not continue to engage in such behavior in the absence of reciprocation, to frighten a non-reciprocator with injury, or in extreme cases to kill, injure, or exile a non-reciprocator.[26] It has been suggested that "elements of revenge may enter into it (*the attack*) as may dissatisfaction about the cost/benefit balance of the relationship (e.g., lack of reciprocation). It is these more complex, cognition-based emotions that we most clearly associate with the human sense of justice and morality."[27] Chimpanzees have been characterized as the only species to exhibit revenge where individuals "tend to intervene against individuals who intervene against themselves."[28] Instead of risking injury by retaliating against more dominant individuals, subordinate chimpanzees often wait for opportunities to attack more dominant individuals while they are engaged in conflicts with others.[29] So if chimpanzees are capable of engaging in behavior that we could label as revenge, it is possible that their behavior may have more in common with subaltern genocide than it initially appears.

Like our primate relatives, there certainly exists the potential in modern humans to commit violent coalitionary aggressive behavior, and that potential has a distinctly evolutionary basis. Humans have the genetic potential to act in ways that have been favored by natural selection and evolution, and in some cases that means committing lethal acts against other humans. In most cases, humans lack the physical strength to engage in lethal hand-to-hand combat as do chimpanzees, and hence must rely on tools for our aggressive encounters—which makes our aggressive behavior more deadly than that of any nonhuman. Given that we all have the evolutionary predisposition to commit lethal violence under certain circumstances, why is there variation in the expression of this capacity? Why are not all humans genocidal? What are the constraints that limit the expression of this evolved capacity?

Here we must invoke two additional factors to explain our behavior: our experience during sensitive developmental periods in our early life, and the sociocultural and environmental circumstances in which we find ourselves as adults. It is certainly a widely accepted fact that aggressive behavior expressed in adulthood is influenced by the type of environment in which we grow up, and that the environment has many subtle elements including parents, siblings, early educational experiences, different parenting practices, and so on.[30] This developmental underpinning of aggressive behavior has been well studied by social scientists, and while there is much left to understand, it is clear that growing up in an environment where critical resources (food, shelter, care, comfort) are limited and unpredictable contributes significantly to the likelihood of the expression of uncontrolled aggressive and antisocial behavior as an adult. But is a particular type of early experience the final arbiter of adult behavior? Absolutely not.

Even though individuals may have had a developmental experience that enhances the probability that they will commit violent acts, the last ingredient must also be in place, and that is a sociocultural and environmental situation that allows for the expression of that behavior. There are some environmental conditions that are particularly favorable for the expression of genocide, but these conditions are not sufficient by themselves to cause it.

Conditions Promoting Genocide

Xenophobia

One of humans' great adaptations is a reliance on culture as a fundamental determinant of our social behavior. Humans are successful because we live in groups and have developed cultural traits that enhance the benefits of group living. But there is a cost to sociality, and that is prejudice and intolerance toward nongroup members. It is clear that in our evolutionary past, xenophobia was adaptive and fitness-enhancing. We can imagine that nongroup members posed a threat for a variety of reasons, not the least of which was their potential for commandeering critical resources (food, territory, mates), their potential for providing misinformation about the location of necessary future resources (locations of water holes, game paths, salt licks), and their potential challenge to other cultural beliefs (symbolic identity, supernatural powers) by polluting them with outside influences. It is relatively easy to imagine that the chance meeting of two proto-human bands could have a violent outcome.

On the other hand, we do not greet all strangers with violence and hostility. The difference seems to be in the recognition of kin relationships and immediate inferred intent. Anthropologists have long been interested in rituals and greetings between humans because it is in the context of these encounters that potentially lethal interactions can occur but often do not. For example, among the Tuareg, nomads living in the Western Sahara, encounters between individuals are rare but are culturally defined. Since visibility in the desert is generally good (save for the occasional simoon or scirocco), it is usually quite easy to spot another traveler in the distance. Assessment of the intentions of a stranger begins immediately upon sighting. First, there is an assessment of the posture and riding style of the other, the type of camel, the direction of travel, and so on. Closer approach calls for an escalation of threat assessment techniques and finally, when the two individuals are literally within arm's reach of each other, they start to identify common kin relations.[31] Such rituals of greeting and assessment have long been the providence of anthropologists,[32] and such research has demonstrated not only the importance of first impressions, but the ability of strangers to identify kin relations as a way of avoiding conflict.

The differential treatment of those to whom we are genetically related has a long and distinguished evolutionary history, ranging from bees and wasps to naked mole rats and to the apes. Since we share some proportion of our genes with our siblings, cousins, aunts, uncles, and so on, it behooves us to treat them differently than we would a totally unrelated individual. This differential treatment of relatives enhances our own indirect fitness, as previously discussed.

It is interesting to see how our reliance on culture has amplified and elaborated this potential. Our culture allows us to share fundamental aspects of group identity (kinship, if you will) and in turn to treat members of our group as our kin, whether or not genetic relatedness exists. Hence we have moved beyond the level of groups of individuals who are genetically related, to larger coalitions that rely on culture to trick us into believing all our group members are kin. This trickery has been extraordinarily important in the course of human evolution because it allowed individuals who were not related to form alliances and coalitions that would have been impossible based solely on true kinship. As I have suggested, the cost of this trickery is a widespread intolerance for "nonkin" individuals, but that cost is no different than without trickery. Our xenophobic response to nongroup members was certainly adaptive during the course of our evolution, but what was once highly adapted has proven to be quite costly in modern society. In fact, one would predict that the greater the degree of kin recognition among members of a coalition or alliance, the greater the tendency would be to fight in support of other group members. Rephrasing slightly, it may be that the more susceptible to the trickery of evolution, the greater the potential for intergroup aggression.[33]

Limited Availability of High Value Concentrated Resources

External environmental and social factors also contribute to creating an environment in which subaltern genocide could flourish. In addition to our xenophobic tendencies, living in an environment where there are limited high value resources is likely to exacerbate any predispositions we might have. We know that the distribution of resources plays a vital role in the behavior of our nonhuman primate relatives, and it is the lack of access to critical resources that dictates much of human behavior as well. Subaltern groups are often characterized by their lack of access to critical resources, and it has been suggested that much of the humiliation and envy they suffer is directly attributable to differential resource allocation.[34]

Other Individual and Social Problems

Other individual factors have also been implicated in the likelihood of the occurrence of genocide (e.g., relative importance of social status and authority, degree of acceptance of social identity and acceptance of in-group and out-group boundaries, susceptibility to social influence). In addition, authors have noted that a destabilizing political crisis will also enhance the probability of genocide.[35] While it is unlikely that any of these contributing factors would inevitably lead to populations committing genocide, the confluence of several of them has often proven sufficient.

Relevance of the Comparative Data

It is clear that when environmental conditions are encountered that tip the cost-benefit equation toward benefits, both long and short term, chimpanzees as well as humans are capable of lethal aggression. While genocide as a behavioral practice has been viewed as a struggle between the powerful and powerless,[36] from a chimpanzee's perspective it is clear that any individual will take advantage of an opportunity to enhance its reproductive success. If you are male, it is by recruitment of females, or if you are a female it is by accumulation of resources which can be translated into more or healthier offspring.

The real value of the comparative data is to demonstrate the capacity of all individuals to commit lethal violence under the right set of circumstances. Chimpanzees are particularly calculating in this regard, and only kill conspecifics when the probability of success is high and the risk of injury is low. For chimpanzees, it is not a question of individual fighting ability, but of the combined fighting abilities of a coalition of individuals against a single victim. If this cost/benefit assessment is an intrinsic part of the expression of lethal levels of aggression in primates, then it should not surprise us that humans follow similar paths. This is to say that under the right set of developmental, ecological, and social conditions we all can express violent aggressive potential, as well as extreme submission; it simply takes a particular set of circumstances to elicit the behavior. A culture characterized by rigid status differentials and dominance relationships, widespread poverty, highly concentrated wealth among a small group of individuals, and clearly and rigidly divided cultural groups are conditions that provide the environment in which the human capacity for lethal aggression might be played out. Those individuals who are most disenfranchised economically, politically, and socially are likely to be the perpetrators.

An evolutionary perspective would predict that where such conditions exist, subaltern genocide is a possibility. Moreover, our comparative and evolutionary perspective also suggests that subaltern genocide is possible where groups of people assess the probabilities of success (lethal aggression against the oppressor) and failure (risk of fatal injury) and those probabilities tip in favor of aggression. To state it more bluntly, subaltern genocide is not an inevitable consequence of oppression, but the potential for lethal aggression among the oppressed against the oppressors is a part of every human's behavioral potential. When placed in a particular set of ecological, social, and political conditions, any individual is capable of subaltern genocide.

The Darwinian approach to genocide has a number of strengths that should make it relevant to genocide scholars. It is clear that humans have a long and distinguished evolutionary history of intraspecific violence. Lethal aggression is the ultimate expression of the capacity, but, as I have noted, it is not inevitable. If we can identify situations where there exist significant differences in allocation of resources, dominance and oppression of minority populations, exaggeration and emphasis on cultural themes of nationalism and distrust of nongroup members, then it may be possible to head off genocide before it starts. Failure to fully recognize that all humans have the capacity for genocide will undoubtedly resign us to witness its horror again.

What can we say about an evolutionary perspective on subaltern genocide? An evolutionary perspective tells us that in order to understand something that has such deep historical roots as seen in various forms of genocide, we need to look at the larger picture of human evolution to make any sense out of this seemingly maladaptive behavior. Over evolutionary time, organisms have been favored by natural selection to act in ways that allowed them to survive, reproduce, and see that their offspring reproduced. Any anatomical, physiological, or behavioral trait that aided in the process was carried along with genes into the next generation. Human ancestors who were slightly more willing to aid a relative, even if they recognized the relationship or not, were actually helping their own genes survive. We need not impute conscious choice in the decision-making process to give aid to another; it is simply that those who did offer aid to relatives survived in greater numbers than those who did not. Once the practice of aiding kin was established, it provided a powerful set of rules that would guide much of human behavior.

We also know that because an individual human is no match for a variety of the predators present during our evolutionary history, the only way that humans could be successful was to band together into small groups where they could enjoy considerable advantage over many other larger and stronger animals. In addition, social living provided immense advantages in other competitive arenas with larger groups dominating smaller groups, and groups developing a host of social customs that fostered intragroup loyalty and intergroup hostility. It is easy to imagine that individuals who were the most articulate and persuasive would enjoy high status along with individuals who possessed certain cognitive or physical skills that enhanced the welfare of all individuals in the group. It is also easy to imagine that occasionally there existed a conspiracy of factors creating an environment that was favorable for genocide. Historically, the powerful have generally succeeded in eliminating the less powerful, but there are occasions when the less powerful have banded together to carry out lethal aggression against their oppressors. We have reviewed the evidence that coalitions are an important part of the social fabric for many primate societies and in particular chimpanzees. We have also noted the potential for chimpanzees to engage in coalitionary killing both within their own group but more often of males from other groups. This is not surprising if one accepts the Darwinian argument that any of us have the potential to commit lethal aggression under the right circumstances. To think that the social forces that shape society preclude any particular segment from the predisposition to commit lethal aggression is naïve at best. The important point of this chapter is that we all have the potential to engage in genocide, subaltern or not, under the right set of circumstances.

It should come as no surprise that the oppressed have turned on their oppressors with astonishing ferocity. Where circumstances favor the expression of genocide, we should always be mindful of the potential for the expression of subaltern genocide with considerable rapidity if circumstances allow it. Recognizing the panhuman nature of our behavioral potential for lethal aggression should alert us to the possibility that any human group, if placed in the right environmental, political, and social circumstances, can commit astonishingly brutal behavior.

So what conclusions can be drawn from this discussion of lethal aggression in chimpanzees and its relevance to human subaltern genocide? To answer the questions initially posed: Are humans the only animal species in which some groups wage genocide against their oppressors? It seems that while there are similarities to coalitionary killing in chimpanzees, subaltern genocide among humans is an elaboration on a theme rather than something that is fundamentally distinct from chimpanzee behavior. We know that subaltern genocide may be motivated by similar fundamental impulses, but it is often an individual behavior in humans, and never a behavior committed by single individuals among chimpanzees. No instances of dyadic lethal encounters have ever been recorded among chimpanzees. Of course, our use of weapons changes the cost/benefit ratio of such interactions to allow for individuals to carry out lethal aggression with considerably reduced risk of harm when compared to chimpanzees. It is also reasonable to conclude that human culture and our reliance on learned behavior have shaped and molded the evolutionary predispositions into the forms of genocide seen today. While there is no gene for genocide, there is strong evidence that there are evolutionary predispositions that we share with our closest primate relatives that allow for the expression of this type of violent aggressive behavior, and these predispositions have been elaborated in the context of human culture.

Notes

1. Goodall, *The Chimpanzees of Gombe*, 507–10.

2. Tooby and Cosmides, "The Psychological Foundations of Culture."

3. Watson, *Behaviorism*, 82.

4. Scott, *Weapons of the Weak*.

5. Hamilton, "The Genetical Evolution of Social Behaviour. I" and "The Genetical Evolution of Social Behaviour. II."

6. Imagine the case of one sibling in a large family entering the priesthood. In doing so this individual foregoes the possibility of any direct fitness, but his overall fitness could be considerably greater than zero due to the indirect fitness effects of the reproductive efforts of his siblings.

7. Darwin, *On the Origin of Species By Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life*, 445.

8. Charlat, Ballard, and Mercot, "What Maintains Noncytoplasmic Incompatibility Inducing Wolbachia in Their Hosts," 322–30; Joshi, Castillo, and Mueller, "The Contribution of Ancestry, Chance, and Past and Ongoing Selection to Adaptive Evolution," 147–62; Pyle and Richmond, "Genetic Basis of Aristal Morphology in *Drosophila Melanogaster* and Its Correlation with Behavior," 297.

9. Betzig, *Despotism and Differential Reproduction*; Betzig, Mulder, and Turke, *Human Reproductive Behaviour*; Chisholm, *Death, Hope, and Sex*; Ellison, *Reproductive Ecology and Human Evolution*; Short, "On the Evolution of Human Reproduction," 5.

10. Campbell, *A Mind of Her Own*; Daly and Wilson, *The Truth about Cinderella*; Ellis and Bjorklund, *Origins of the Social Mind.*

11. Buss and Shackelford, "Human Aggression in Evolutionary Psychological Perspective," 605; van der Dennen, *The Origin of War*; Wrangham and Peterson, *Demonic Males*; Wrangham, Wilson, and Muller, "Comparative Rates of Violence in Chimpanzees and Humans," 14.

12. I have excluded infanticide from these analyses because it is clear that there are very different evolutionary strategies in play when it comes to killing of particular infants.

13. Hausfater and Hrdy, *Infanticide: Comparative and Evolutionary Perspectives*; van Schaik and Janson, *Infanticide by Males and Its Implications.*

14. Species include Mongolian gerbils (*Meriones unguiculatus*), wild rabbits (*Oryctolagus cuniculus*), Hanuman langurs (*Presbytis entellus*), meadow voles (*Microtus pennsylvanicus*), howler monkeys (*Alouatta palliata*), lions (*Panthera leo*), crab-eating macaques (*Macaca fascicularis*), chacma baboons (*Papio ursinus*), chimpanzees (*Pan troglodytes*), brown bears (*Ursus arctos*), as well as a variety of other rodents, mammals, and birds.

15. Baker and Smuts, "Social Relationships of Female Chimpanzees," 227; de Waal, "Sex Differences in the Formation of Coalitions Among Chimpanzees," 239.

16. Newton-Fisher, "Female Coalitions Against Male Aggression in Wild Chimpanzees of the Budongo Forest," 1589.

17. Ibid., 1591.

18. Nishida and Hosaka, "Coalition Strategies among Adult Male Chimpanzees of the Mahale Mountains, Tanzania"; Riss and Goodall, "The recent rise to the alpha-rank in a population of free-living chimpanzees," 134; Watts, "Reciprocity and Interchange in the Social Relationships of Wild Male Chimpanzees," 343.

19. Riss and Goodall, "The Recent Rise to the Alpha-Rank in a Population of Free-Living Chimpanzees," 137.

20. Nishida, "Review of Recent Findings on Mahale Chimpanzees."

21. Wrangham, "Evolution of Coalitionary Killing," 1.

22. Roscoe, "Intelligence, Coalitional Killing, and the Antecedents of War," 485; Wilson, Wallauer, and Pusey, "New Cases of Intergroup Violence among Chimpanzees in Gombe National Park, Tanzania," 523; Watts, "Intracommunity Coalitionary Killing of an Adult Male Chimpanzee at Ngogo, Kibale National Park, Uganda," 507; Wilson and Wrangham, "Intergroup Relations in Chimpanzees," 363; Wrangham, "Evolution of Coalitionary Killing," 2.

23. In the study of animal behavior, philopatry (Greek, "home-loving") is the tendency of an animal to return to or remain in a specific location in order to breed or feed. Philopatry can manifest itself in several ways, and can be applied to more than just the area in which an animal was born. Species that return to their birthplace in order to breed are said to exhibit natal philopatry. Species that return in consecutive years to the same breeding site or territory exhibit breeding philopatry or site fidelity. Philopatry is generally believed to be an adaptation to a specific set of environmental circumstances.

24. See the example in the first paragraphs of this chapter.

25. Reciprocal altruism is a form of altruism in which one organism provides a benefit to another without any immediate compensatory benefit, but with the expectation that the altruistic act will be repaid in the future.

26. Trivers, "The Evolution of Reciprocal Altruism," 35.

27. de Waal, "The Chimpanzee's Sense of Social Regularity and Its Relation to the Human Sense of Justice," 342.

28. de Waal and Luttrell, "Mechanisms of Social Reciprocity in Three Primate Species," 114.

29. Ibid., 115.

30. Anderson and Bushman, "Human Aggression," 27; Cairns, "Aggression from a Developmental Perspective"; Constantino, "Early Relationships and the Development of Aggression in Children," 259; Ramirez, "Hormones and Aggression in Childhood and Adolescence," 621; Tremblay, "The Development of Aggressive Behaviour During Childhood," 129.

31. Youssouf, Grimshaw, and Bird, "Greetings in the Desert," 797.

32. Firth, "Verbal and Bodily Rituals of Greeting and Parting"; Goffman, *The Presentation of Self in Everyday Life.*

33. Brannigan, "Criminology and the Holocaust," 257. See Cashdan, "Ethnocentrism and Xenophobia," 761, for an interesting but incomplete test of this hypothesis.

34. Kamola, "The Global Coffee Economy and the Production of Genocide in Rwanda," 571; Niazi, "The Ecology of Genocide in Rwanda," 223.

35. Woolf and Hulsizer, "Psychosocial Roots of Genocide," 101.

36. Freeman, "Puritans and Pequots," 278; Longman, "Genocide and Socio-Political Change," 18; Longman, "Empowering the Weak and Protecting the Powerful," 49; Mirkovic, "Ethnic Conflict and Genocide," 191; Ndikumana, "Institutional Failure and Ethnic Conflicts in Burundi," 29; Newbury, "Understanding Genocide," 73; Uvin, "Ethnicity and Power in Burundi and Rwanda," 253.

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