Richard Wrangham

Killer species

Human social behavior varies so much that our plasticity can sometimes seem infinite. But human variation has obvious limits when we compare ourselves with our primate relatives. Napoleon may have claimed that he always had to give in to his wife, the Empress Josephine, but there are no human societies that follow the lemur pattern of all males invariably subordinating themselves to all females. Nor do women anywhere entice all their male counterparts in their community to mate with them every month, as female chimpanzees do. Just as other species have their particular social tendencies, in other words, so does ours. Features characteristic of human society include social communities composed of individuals who associate at will, multilevel ties among communities, mothers forming mating bonds, coalitions of males fighting over territory, and so on.

That all humans share some characteristic social tendencies may be unremarkable in comparison with other species, but it provides valuable insight into behavioral evolution. In this essay I will focus on a few features we share with our closest ape relatives, but that are otherwise found rarely. In particular, we share the tendency for coalitions of related males to cooperate in defending a shared territory; and we kill our enemies. These are unusual patterns in other primates, so the question is why they should be prominent in humans and our close kin.

One hypothesis is phylogenetic inertia, the nonadaptive retention of an ancestral trait. Phylogenetic inertia is a possibility whenever closely related species behave alike. For example, horses and zebras both live in groups of unrelated females and single stallions within larger herds. Breeding wolves and coyotes live as isolated monogamous pairs aided by nonbreeding helpers. Male hornbills of many different species imprison their mating partners in a secluded breeding hole. There are many such examples of social systems corre-

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lated with phylogeny, and in theory these could result from species failing to adapt their behavior to new circumstance.

However attractive the notion of phylogenetic inertia might seem, it suffers from the problem of explaining why adaptive changes in social behavior should be constrained. The hypothesis of adaptive socioecology is therefore a strong a priori alternative to phylogenetic inertia. Adaptive socioecology posits that a similar lifestyle is the key to similar behavior among closely related species, whether it be grass-eating for horses and zebras, den-living for wolves and coyotes, or a shortage of suitable nesting holes for different species of hornbills. Adaptive socioecology rests on the notion that social systems can change rapidly in response to a novel ecology.

Baboons offer a particularly tidy example of adaptive socioecology, because even within a single species genetically based differences in psychology have evolved in apparent response to a specific ecological change. East Africa's olive baboons live in lush grasslands where the abundance of food permits large, cooperative groups of female kin that aid each other in competition against other females. Too large to be monopolized by a single male, a group generally includes ten or more unrelated males that join as adolescents. Female olive baboons respond to the plethora of males by mating widely within the group, thereby garnering protection for their offspring from the numerous possible fathers. A rich food supply thus promotes large, multimale groups of promiscuous and kin-bonded females.

Hamadryas baboons, by contrast, occupy semideserts in northeast Africa and Arabia. They resemble olive baboons closely, being only marginally smaller, with somewhat more colorful males. In their dry habitat, food is so sparse that in bad seasons the large groups fragment by day in search of forage. But females can't survive without a defending male, so each stays in a small subgroup with a single male, to whom she becomes faithfully bonded and whom she allows to herd her when other males are near. To prevent other males from stealing their females when the subgroups reunite at sleeping sites, males form defensive alliances with each other. A poor food supply thus leads to small families of acquiescent female hamadryas attached to a network of bonded males.

The contrasting baboon social patterns conform to the respective ecological pressures. These differences could in theory emerge merely as the baboons' developmental response to their immediate environments, but there is evidence of strong genetic influence. Thus even after many generations in captivity, baboons of the two subspecies form the same kinds of social groups as their wild ancestors. The same differentiation is dramatically echoed among naturally occurring hybrids in Ethiopia, for which physical features and behavior are correlated. Females that look more like olive baboons, for example, strongly resist male efforts to herd them. By contrast, those that look more like hamadryas readily accept a male's herding. Differences in serotonin levels between males of the two subspecies of baboons conform to the different patterns of aggression.

Olive and hamadryas baboons differentiated from each other around three hundred thousand years ago. Even without any notable anatomical evolution, therefore, three hundred thousand years and a changed ecology are enough for radical adaptation in social behavior, including patterns of grouping, kin relations, and feeding competition.

Why, then, should humans be in the least similar to our cousin apes? Chimpanzees and bonobos are separated from humans not only by five to six million years, but by enormous changes in ecology and ability, including raw biological differences in diet, locomotion, and sexuality, as well as by the refined influences of language and culture. Against this background, significant social similarities with our cousin apes are puzzling. While phylogenetic inertia is an explanation of last resort, adaptive socioecology is at first glance improbable. As we will see, however, hidden ecological similarities suggest that contrary to the apparent differences between humans and other apes, our shared social features derive from parallel ecological pressures.

Though human hunter-gatherers (also called foragers) offer the most appropriate comparison with other species, their lifestyle and social relations differ about as much from those of our cousin apes as any other people's. Foragers dig for roots and collect fruits, hunt large game, cook their food, construct simple housing, and defend themselves with spears or other weapons. They tend to occupy temporary camps for several weeks at a time, housing a group of perhaps twenty to forty people, and they relocate these camps when the women find it hard to get enough food within a reasonable day's walk. The members of a camp are part of a larger social community that might include a few hundred or even a thousand or more people. At certain times of the year this community gathers for a few days, when feasts and ceremonies allow social relationships to be re-formed across the wider network of the tribe. And as is true for every other human society, cultural rules pervade life among such communities. None of this is very ape-like.

Killer species

Chimpanzees and bonobos are the species of apes that are closest to humans. Both are quadrupedal, forest-living fruit-eaters that climb for most of their food, sleep in trees exposed to the rain, and use only the simplest tools (some populations use none). Their communities are limited to the set of individuals that live sufficiently close that they might meet by chance. These communities are formed around a core of related males, and there are no bonds among mates.

Yet different as humans and these apes are, all three species live in social communities with no fixed associations of individuals other than those between mothers and their dependent offspring – a rare trait in the context of most other primates. Accordingly, during the day, individuals of these species can decide for themselves where to go. In practice, among hunter-gatherers most women forage every day in the company of other women from their temporary camp, much as most male chimpanzees spend the day in the company of chosen allies. But in both cases, there are options. A woman might choose to make a tryst, stay in the camp, or walk alone. A male chimpanzee might equally well opt to travel alone for hours or days at a time.

Such individual choice within a defined social network occurs in only one other group of primates: the atelines, South American monkeys distantly related to apes. In addition to community organization, those species share a second rare similarity with humans, chimpanzees, and bonobos: their males form coalitions to defend territory.

There are other ways in which the atelines (spider monkeys, woolly monkeys, and muriqui) are the most ape-like group of monkeys: their large size relative to other South American monkeys, relatively efficient travel, mobile shoulders, and diet of ripe fruit and soft

leaves. It has therefore been suggested that resemblances between the social behavior of atelines and that of the apes have resulted from parallel adaptations for harvesting ripe fruit, a resource that induces intense feeding competition, independent travel, and territorial defense.[1] In line with this suggestion, the protean grouping patterns of humans may be similarly derived from an evolutionary commitment to high-quality foods.

Whatever its precise cause, the combination of social communities with small and frequently changing subgroups appears to be an important precondition for one of the most striking similarities between humans and any other primates: the territorial aggression observed in humans and chimpanzees alike.

Warfare is often defined in a way that suggests it is unique to humans, for instance, as an interaction involving culturally sanctioned plans or weapons or organized fighting between large groups. But of course the behavior that underlies human warfare is not unique, as the chimpanzee case makes clear.

Most encounters between chimpanzee communities involve males. There can be as many as thirty-five males in a community, but the average is ten to twelve, and most parties (temporary subgroups) have about half that number. Interactions with neighboring communities are never friendly and are often dangerous.

But even so, males sometimes seek out opportunities to engage with neighbors. They routinely conduct border patrols and may penetrate beyond the zone of relative safety, looking carefully as they go. Sometimes they climb a tree and face the neighboring range, as if listening for rivals. Occasionally they make deep invasions.

Most encounters that result from these behaviors happen by chance when nearby parties surprise each other at close range – a few hundred yards, say. Calls from strangers prompt immediate tension. Sometimes the listeners briefly freeze, but more often they let out a volley of shouts and quickly move. If they are numerous, they advance. If not, they retreat toward the heart of their territory.[2]

But when they meet at close range and the numbers of males on each side are similar they're more likely to stand their ground. Typically, chimpanzees in the battleground hurtle unpredictably through the brush, pausing after each rush to look and listen tensely around, often standing bipedal with one hand on a small tree. For them one decision might be a matter of success or death. Their pauses allow them to gauge who's where, to find an ally, or to see uncertainty in the enemy. After a stop, alone or in a small tight group of two or three, they charge off on a new run across the battle area. Occasionally one of them gets hit by a passing rusher, but mostly the chimpanzees from each community charge backwards and forwards from safe spots as each side tries to frighten the other into retreat. The air is thick

1 Colin A. Chapman, Richard Wrangham, and Lauren J. Chapman, "Ecological Constraints on Group Size: An Analysis of Spider Monkey and Chimpanzee Subgroups," *Behavioral Ecology and Sociobiology* 36 (1995): 59 – 70.

2 Michael L. Wilson, Marc D. Hauser, and Richard W. Wrangham, "Does Participation in Intergroup Conflict Depend on Numerical Assessment, Range Location, or Rank for Wild Chimpanzees?" *Animal Behaviour* 61 (2001): 1203 – 1216, describe playback experiments showing that when a call is heard from a single stranger, chimpanzees move forward only if there are at least three males in the listening party, and that otherwise they retreat.

with screams and emotion. It's hard to tell exactly what's happening; it's difficult even to identify the males in the melee of speed and power and fully erected hair. Their screams and barks can go on with hardly a pause for forty-five minutes.

In the end, the party with fewer males generally retreats. The result can be important. For several weeks, the losing community tends to avoid an area that would otherwise have provided access to a preferred food; this could mean the difference between a few weeks of eating from a rich fruit crop, and being forced onto a poor diet that causes delayed response and threatens infant survival.

Of more immediate importance, these battles sometimes lead to a lone participant being caught by several of his rivals. The result tends to be remarkably lopsided. While the aggressors are unlikely even to be scratched, the victim may be killed on the spot, or bruised, bitten, and torn so badly that he survives for only a few days or weeks. The same result can follow from border patrols or deep invasions. Overwhelming numbers mean the attackers are safe. Several males each hold a hand or foot of the rival. The immobilized victim can then be damaged at will.

Observations from five study sites now allow the first rough estimates of death rates from intergroup killing among chimpanzees. Between 1963 (when we have Jane Goodall's first demographic data from Gombe) and 2002, a total of about 145 data-years of observation were logged across the five long-term sites. During that time, forty-six intercommunity kills were observed or suspected. Thirty-one involved members of the study communities (twenty-four adult males, one adult female, six infants). When the number of chimpanzees in each community is taken into account, these figures yield a median death rate from intergroup aggression of 140 per 100,000, which rises to 356 per 100,000 if we include suspected cases in addition to those observed or confidently inferred.[3]

The chimpanzee data resemble death rates from war among traditional subsistence societies. Thus, based on a worldwide compilation by Lawrence Keeley, Michael Wilson and I have assembled demographic data for thirty-two politically independent peoples. These include twelve hunter-gatherer and twenty gardening or farming cultures. For hunter-gatherers, annual war death rates averaged 165 per 100,000, about the same as the intergroup killing rate for chimpanzees. For the subsistence farmers, the toll rose to a startling 595 per 100,000, somewhat above the upper estimate for chimpanzees (356 per 100,000).[4] The sampled cultures range from relatively peaceful people such as the Semai of Malaysia to the famously dangerous Dani of New Guinea, among whom at least 28 percent of men's deaths, and 2 percent of women's, occurred in war.[5] Understanding why there is such a range is an important challenge for the future. For the moment, however, we can conclude that

3 Rates are calculated from data presented in Michael L. Wilson and Richard W. Wrangham, "Intergroup Relations in Chimpanzees," *Annual Review of Anthropology* 32 (2003): 363–392. For adult males as a separate class, the equivalent rates are between 0.38 and 1.30 percent per year.

4 Lawrence H. Keeley, *War Before Civilization* (New York: Oxford University Press, 1996).

5 Karl G. Heider, *The Dugum Dani: A Papuan Culture in the Highlands of West New Guinea* (Chicago: Aldine Publishing Company, 1970), 128, recorded for Dani living in the Grand Valley of Balim River in the central highlands of western New Guinea.

death rates from intergroup aggression among small independent communities are broadly similar for humans and chimpanzees.

Shockingly, death rates in the modern era tend to be lower even when periods of major war are included. During the twentieth century, for example, Germany, Russia, and Japan each experienced rates of war deaths that were less than half the average hunter-gatherer rate. The contrast reflects a difference in the practice of war between prestate and state societies. In prestate societies all men are warriors, and all women are vulnerable. In state societies, by contrast, fewer people are directly exposed to violence (even though civilians and children often suffer worse casualties than the military) because armies fight on behalf of the larger group.[6]

There's only one other mammal whose intergroup killing has been observed frequently enough to have been calculated. The discovery would have been a surprise to Konrad Lorenz, a founding father of ethology. Lorenz thought wolves would not kill wolves, because he saw captive dominants treating helpless subordinates in a kindly manner. So he argued that wolves must have been selected for inhibition. He was right in one sense: within social groups, wolves normally control their emotions well. But Lorenz didn't know about wolves in the wild, where food is scarce and every group is surrounded by its neighbors.

Wolves of neighboring groups don't hold back. David Mech and his colleagues studied packs in the glacial uplands of Alaska's Denali National Park, an area they considered to be free of human influences. Based on twenty-two killings in at least seventeen packs, they estimated that 39 to 65 percent of adult wolves were killed by other packs. We can expect variation in such rates across populations, but at least in Minnesota a similar figure emerged: 43 percent of wolves not killed by humans were killed by other wolves.[7]

These data were presented as percentages of deaths from violence, rather than as an annual death rate. Human data have sometimes been compiled in the same way, and show that only the most extreme of human cultures match the killing rate of wolves. The highest human death rate from violence has been recorded in eastern Ecuador, where anthropologist James Yost and colleagues collected data on causes of death for Waorani horticulturalists living in dispersed villages of less than a hundred people. Based on 551 deaths, they found that homicide took the lives of 49 percent of women and 64 percent of men, close to the figure for Denali wolves.[8]

Other prestate societies show slightly lower figures. More such data have been collected from highland New Guinea than from any other part of the world, because many of the people living there continued to practice local war until recently. These people include the Tauna

6 Death rates in the twentieth century were presented by Keeley, *War Before Civilization*. Carolyn Nordstrom, "Deadly Myths of Aggression," *Aggressive Behavior* 24 (1998): 147–159.

7 L. David Mech, Layne G. Adams, Thomas J. Meier, John W. Burch, and Bruce W. Dale, *The Wolves of Denali* (Minneapolis: University of Minnesota Press, 1998).

8 James A. Yost and Patricia M. Kelley, "Shotguns, Blowguns, and Spears: The Analysis of Technological Efficiency," in Raymond B. Hames and William T. Vickers, eds., *Adaptive Responses of Native Amazonians* (New York: Academic Press, 1983), 189–224. The recorded deaths include an unrecorded proportion of killings within villages, so these figures do not correspond exactly to the wolf data.

Awa, with 16 percent of women and 30 percent of men (of 206 deaths) dying from homicide; the Usurufa, with 12 percent of women and 32 percent of men (of 514 deaths); the Mae Enga, with maybe 2 to 3 percent of women and 35 percent of men (of 261 deaths); and the Huli, with 1 percent of women and 20 percent of men (of 769 deaths).

For hunter-gatherers, fewer data are available, but the picture is as expected from the annual kill rate. Homicides occur, but at lower rates than among horticultural farmers.[9] There are the Aché of Paraguay, among whom homicide has been responsible for the deaths of 14 percent of women and 15 percent of men (of 115 deaths); the Hiwi of Venezuela, with 17 percent of women and 14 percent of men (of 124 deaths); and the Agta of the Philippines, with 3 percent of women and 14 percent of men (of 78 deaths).

The point about these figures isn't to claim any particular numerical averages. It's merely to say that with chimpanzees, wolves, and humans the big picture is consistent: in typical populations of these three species, it can be mortally dangerous to meet the neighbors.

That's why they all have war zones.

War zones are the border areas where territories abut, danger lurks, and parties rarely go. Low rates of foraging mean that war zones can become lands of plenty – rich in tempting resources.

The Upper Missouri War Zone, a corridor five hundred kilometers long and two hundred forty kilometers wide, was a focal area for the intertribal aggression of numerous indigenous groups, including the Nez Perce, Crow, and Shoshone. Lewis and Clark described the presence there of "immence [sic] quantities of buffalo in every direction";[10] the herbivores benefited from the low human predation pressure resulting from the dangers of hunting in these contested ranges. So the feared war zone became a game sink. Territorial tension sometimes works the same way today. The Demilitarized Zone (DMZ) separating North and South Korea is so empty of people that it has particularly high biodiversity, and supports large populations of rare and endangered species extinct on the rest of the Korean peninsula. (Conservationists should be worried about the prospect of peace. When peace came to the Upper Missouri War Zone, prey animals were hunted to extinction.)

War zones occurred among hunter-gatherers also. Anthropologist Bion Griffin reports, for example, that the Agta of the Philippines knew where the danger lay. "Hunters are especially aware of the chance of illegal trespassers and assume that they may be bent on raiding," Griffin writes. "In the remotest forest hunting zones, where hunters from more than one dialect group may range, precautions are taken and one would seldom hunt alone."[11]

In Australia, expeditions outside the core of the territory were likewise viewed as dangerous: "The red ochre gathering expeditions . . . were normally all-male parties, and although cordial relationships between groups were

9 Bruce M. Knauft, "Violence and Sociality in Human Evolution," *Current Anthropology* 32 (1991): 391 – 428, has stressed the evidence that rates of war are higher among horticulturalists than among hunter-gatherers.

10 Paul S. Martin and Christine R. Szuter, "War Zones and Game Sinks in Lewis and Clark's West," *Conservation Biology* 13 (1999): 36 – 45.

11 P. Bion Griffin, "Forager Resource and Land Use in the Humid Tropics: The Agta of Northeastern Luzon, the Philippines," in Carmel Schrire, ed., *Past and Present in Hunter-Gatherer Studies* (New York: Academic Press, 1984), 106.

sought, fighting appears to have been a common hazard faced by traveling parties. One entire party, with the exception of one man, is recorded as having been ambushed and killed in about 1870, whilst in about 1874 all but one of a group of 30 men were 'entombed in the excavations.'"[12]

Among chimpanzees, evidence of a game sink in war zones comes from the group size of their favorite prey species, red colobus monkeys. Groups averaged 46 percent smaller in the core of the territory than in the border area, according to primatologist Craig Stanford. He attributed the difference to the lower hunting pressure in the border areas, where chimpanzees feared to go.

Meanwhile, David Mech describes how except during periods of extreme food shortage, the threat of encountering hostile neighbors keeps packs of wolves out of border areas. White-tailed deer therefore occur at particularly high density in the zones of wolf-pack territorial overlap. Mech believes that these war-zone populations of deer are critical for the long-term relationship between predator and prey, since they provide the stock for recolonizing the over-hunted areas in the core of the wolf territories. Wolf war zones, in other words, provide conservation areas rather in the style of the Korean DMZ.

It's not the abutment of territories that makes a war zone. Redtail monkeys in Kibale also live within territories, but they do not kill members of neighboring communities and they do not avoid the territorial borders. They use the territory fully, right up to the border, and merely defend their ranges with chases when they meet neighbors. What makes a war zone is not a territory, but the risk of being victimized at its edge.

War zones also aren't known among bonobos, or, for that matter, among most primates or most mammals or most animals. In the great majority of species, territorial encounters involve display, chases, and occasional grappling, but not outright killing. There are only a select few species whose territorial boundaries are places of death and avoidance. The question is why this selection should include chimpanzees, wolves, and humans.

A strong evolutionary rationale for killing derives from the harsh logic of natural selection. Every homicide shifts the power balance in favor of the killers. So the killers have an increased chance of outnumbering their opponents in future territorial battles, and therefore of winning them. Bigger territories mean more food, and therefore more babies.

This unpleasant formula implies that killing is favored by two conditions. It pays whenever resource competition is intense, and whenever killing can be carried out at low risk to the aggressors.

All animals face resource competition. In the wild, for example, female chimpanzees lose weight during poor seasons and are often so short of food that they must wait for an abundant fruiting season before they can conceive. All hunter-gatherer populations show similar evidence of intermittent food scarcity, such as reduced growth during poor seasons.

Persistent food shortages suggest that a larger territory will always pay, and long-term data from Gombe confirm it. During two decades the territory of the Kasekela chimpanzee community varied in size. Shifts in the balance of power with neighboring communities may

12 The quotation is from R. G. Kimber, "Hunter-Gatherer Demography: The Recent Past in Central Australia," in Betty Meehan and Neville White, eds., *Hunter-Gatherer Demography Past and Present* (Sydney: University of Sydney Press, 1990), 160–170.

have been responsible for these oscillations. When the territory was small, the chimpanzees had inadequate food. Individuals lost body weight and tended to travel in the small parties typical of periods of low food supply. Females then had long intervals between births, and offspring survival was low. When the territory was larger, everything changed. Male efforts at expanding the territory led to gains for both sexes. With a better food supply, all adults gained weight, females reproduced faster, and the young survived better.[13]

The Gombe study nicely shows the importance of a larger territory. But it doesn't show anything special about the killer species. Any territory-holding group can be expected to fare better if its neighbors' power declines, allowing its territory to expand. By the same process seen in Gombe, a group of any species that gets a larger territory can be expected to have improved food and better reproduction. This principle should apply as much to bonobos and redtail monkeys as to chimpanzees, wolves, and humans. But bonobos and monkeys don't kill.

So resource competition is a necessary condition for war-zone killing, but it's not enough on its own. The second condition is the sufficient one. Killing must be cheap.

The special feature of the killer species is that when parties from neighboring territories meet, there is sometimes an imbalance of power so great that one party can kill a victim without any significant risk of any of them getting hurt themselves. For chimpanzees and wolves, the imbalances of power come entirely from their protean grouping patterns. For hunter-gatherers, the same applies, but there is an extra twist from human inventiveness. For modern humans, imbalances of power come not only from being able to form a larger subgroup than the enemy's, but also from striking the first lethal blow – such as by throwing a spear, flaming a hut, or flying an airplane into a building.

Among chimpanzees, the most likely victims of homicide are adults found alone or immediately abandoned by their friends after being cornered by members of a hostile community. Among wolves, the evidence is less direct, but 90 percent of kills in Denali occurred in winter. At that time, the probability of a lone individual meeting a party of at least three other wolves is forty times higher than in the summer.

Support for the supposed importance of power imbalances comes from the species that don't kill. Bonobos and monkeys live in relatively stable groups, with individuals rarely in parties so small that they might be overwhelmed by neighbors. Those species have diets that allow parties the luxury of permanent association.

But among humans, power imbalances are routine in intercommunity conflict, and the predominant tactic of war for small-scale societies is unambiguous. It's hit-and-run or ambush. Anthropologist A. R. Radcliffe-Brown recorded the attitude of the Andaman Islanders, hunter-gatherers living east of India. "The whole art of fighting," he wrote, "was to come upon your enemies by surprise, kill one or two of them and then retreat . . . . They would not venture to attack the enemy's camp unless they were certain of taking it by surprise . . . . If they met with any serious resistance or lost one of their own number, they

13 Jennifer M. Williams, Anne E. Pusey, John V. Carlis, B. P. Farm, and Jane Goodall, "Female Competition and Male Territorial Behavior Influence Female Chimpanzees' Ranging Patterns," *Animal Behaviour* 63 (2002): 347 – 360.

would immediately retire. Though the aim of the attacking party was to kill the men, it often happened that women or children were killed."[14]

Similar tactics have been described for hunter-gatherers around the world. In Australia, Walbiri men who surprised enemy camps were said to have killed or driven off the enemy males, and to have carried away any women they could find. In the Arctic, by contrast, raiders would normally kill everyone, though they might spare young girls. Raids typically involved fifteen to twenty men, and could take ten days to complete.[15]

That hunter-gatherers would have raided each other may seem surprising in view of the reputation of forager societies like the Kalahari Bushmen for living peacefully. Scrutiny of early records of contact with hunter-gatherers, however, shows widespread evidence of primitive violence, even in the Kalahari. And material culture supports the picture. Archaeologist Steven LeBlanc has recently drawn attention to the shields of Eskimos that attest to the occurrence of battles. Australian Aborigines also had shields as well as weapons used exclusively for warfare, such as a hooked boomerang and a heavy spear. Both in the Arctic and in Australia there is clear historical evidence for a combination of raids and battles.[16]

The principle that underlies the mayhem is simple, then. When the killing is cheap, kill. In any particular instance it may or may not lead to a bigger territory, but from the perspective of natural selection, the specific case is less important than the average benefit. The integrating effect of selective pressures on emotional systems requires only that killing should lead to benefits sufficiently often. Just as the first male fig wasp that emerges from pupation will immediately attempt to kill any other males he finds in the same fig, so the defenders of territory benefit by taking advantage of opportunity. The killers don't have to think through the logic. They may think of their action as revenge, or placating the gods, or a rite of manhood – or they may not think about it at all. They may do it because it's exciting, as seems the case for chimpanzees. The rationale doesn't matter to natural selection.[17]

What matters, it seems, is that in future battles the neighbors will have one less warrior. So those who killed will become a little more powerful as a result.

Why, then, do humans, chimpanzees, and wolves share the unusual practice of deliberately and frequently killing neighbors? In each species the violence makes sense. Protean grouping patterns allow individuals to attack only when they have overwhelming power. Such tactical success allows them to kill safely and cheaply, and thereby win a likely increase in resources over the succeeding months or years. Killing thus emerges as a consequence of having territories, dispersed groups, and unpredictable power relations. These driving variables, in turn, appear to result from ecological adaptations, whether to a scattered fruit supply or to the challenges of hunting

14 A. R. Radcliffe-Brown, *The Andaman Islanders: A Study in Social Anthropology* (Cambridge: Cambridge University Press, 1948), 85.

15 Azar Gat, "The Human Motivational Complex: Evolutionary Theory and the Causes of Hunter-Gatherer Fighting, Part I: Primary Somatic and Reproductive Causes," *Anthropological Quarterly* 73 (2000): 20 – 34.

16 Steven A. LeBlanc, *Constant Battles* (New York: St. Martin's Press, 2003).

17 Klaus Reinhold, "Influence of Male Relatedness on Lethal Combat in Fig Wasps: A Theoretical Analysis," *Proceedings of the Royal Society of London* B 270 (2003): 1171 – 1175.

vertebrate prey. The implication is that because of our particular evolutionary ecology, natural selection has favored in the brains of humans, chimpanzees, and wolves a tendency to take advantage of opportunities to kill enemies.

This doesn't condemn us to be violent in general. Indeed, within our communities humans are markedly less violent than most other primates, and in some ways humans are specially peaceful. Nor does it mean that intergroup aggression is inevitable: rather, it predicts little violence when power is balanced between neighboring communities. Nor, again, does it mean that gang attacks on members of other tribes or religions or clubs or countries are necessarily adaptive: in evolutionary terms, they may or may not be. Nor does it mean that women are incapable of violence, or are inherently less aggressive than men: it suggests instead why the circumstances that favor aggression are not identical for men and women.

What it does imply, however, is that selection has favored a human tendency to identify enemies, draw moral divides, and exploit weaknesses pitilessly across boundaries. As a result, our species remains specially predisposed to certain types of violent emotion. That selection operated in the context of a hunter-gatherer world that has all but disappeared. But if its legacy is that we are biologically prepared by natural selection to be killers, an understanding of the neural basis of intergroup violence should be a research priority.