Nonhuman Intergroup Agonistic Behavior and 'Warfare'

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Intergroup Agonistic Behavior: Introduction

In this article the significance of nonhuman intergroup agonistic behavior for the explanation of human primitive warfare will be assessed. I shall, in other words, explore the possibility of some evolutionary precursors or phylogenetic preadaptations being involved in hominid warfare, by analyzing animal intergroup (or intercommunity) agonistic behavior (IAB).

IAB will be considered to be any intraspecific agonistic interaction or episode of such interactions (e.g., threatening, chasing, hitting, biting, injuring, killing) between more or less cooperating members of two or more spatially separate, distinct and identifiable groups (troops, packs, collectivities, local populations), or between groups and individuals acting primarily as members or representatives of such collectivities.

Similar categories, called ‘Reactive Intergroup Aggression’ (i.e., mainly collective group defense) and ‘Exported Intergroup Aggression’ (EIA), defined as “the regular conduct, by breeding adults, of aggressive, physically damaging cooperative raids against adults in neighboring groups” were suggested by Manson & Wrangham (1987). The latter category was changed to ‘lethal male raiding’ in a later publication (Manson & Wrangham, 1991). Tooby & Cosmides (1988) use their term ‘coalitional aggression’ also in a similar sense.

Many authors simply prefer terms such as ‘intergroup conflict’, ‘intergroup aggression’ or ‘intergroup aggressive encounters’ (e.g., Cheney, 1987; Tooby & DeVore, 1987; Manson & Wrangham, 1991).

‘Aggression’ properly belongs to the individual organismic level-of-analysis; a term like ‘group aggression’ cannot be more than a metaphor because a group does not have a source of behavior and motivation beyond the individual actors. The term is frequently used in the literature, however, and in this chapter I shall adopt it as a synonym of intergroup agonistic behavior.

At this point, it is important to acknowledge that, according to modern evolutionary biology, selection acts at the level of the gene (Hamilton, 1964; Maynard Smith, 1964; G.C. Williams, 1966, 1988; Dawkins, 1976, 1982; Cosmides & Tooby, 1981; Tooby & DeVore, 1987, a.o.). The genes present in any generation are disproportionately those that had, in preceding environments, effective ‘strategies’ for their own propagation. And conversely, the traits individuals express are present because the genes that govern their development have (had) successful strategies of self-propagation. In other words, “genes work through the individual in which they occur, and the individual’s morphology and behavior embody the strategies of the genes it contains” (Tooby & DeVore, 1987).

The only currency in the cold calculus of evolution is reproductive success: the differential contribution of individuals to the gene pool of the population. The individual organism is, in this perspective, just a temporary, ephemeral and mortal vehicle with the only ‘purpose’ to transmit its genes – which have the ‘selfish’ interest of spreading as many replicas or copies of themselves as possible – to future generations. Those genes that have not ‘programmed’
their temporary vehicles with strong urges to reproduce must have been selected against since time immemorial.

Researchers now speak of organisms as ‘strategists’, meaning that individual organisms are selected to manifest any property, behavioral or morphological, however fixed or plastic, that correlates with strategies of genic reproduction. Thus, if one neglects the complications of intragenomic conflict (Cosmides & Tooby, 1981), organisms will be selected to behave as if they were following strategies to promote their inclusive fitness (Hamilton, 1964).

A major implication of this genic-level-of-selection thinking is that characteristics of groups or species are not selected or shaped per se; they are the result of the interactions among individuals whose behavior is controlled by proximate mechanisms, the properties of which correlate with genic fitness.

The interests of different individuals in a group or population will often be in conflict. Therefore, broader patterns of social behavior are not necessarily optimal for any individual or group of individuals, but rather may be the emergent result of the conflicting interests of interacting individuals. Frequently, therefore, the behavior of an individual cannot be understood in isolation; its behavior will be the mutual result of its interests and strategies and the opposite interests and counter-strategies of those with whom the individual is associated.

“Group processes and characteristics are not selected for in themselves (for example, by group selection), but are the emergent product of dynamic processes taking place at the individual strategic level, and must be analyzed at that level. Thus, intergroup conflict cannot be understood in terms of ‘benefit to the group’, whatever that might mean. Instead, the costs and benefits to the individual actors must be analyzed. Thus, ‘intergroup hostility’ may instead be hostility between different male coalitions (as in chimpanzees), or simply hostility between the dominant male of a group and outside males (as is usual in langurs)” (Tooby & DeVore, 1987).

Evolutionarily, ‘aggression’ may be considered to be a proximate mechanism of contest competition (Barash, 1977; E.O. Wilson, 1970, 1975), and mostly consists of acts, or the threat of acts, of an individual organism to reduce the fitness of, or enhance its own fitness at the expense of, another individual. According to the group selection paradigm (the ‘good-for-the-species’ reasoning), the killing or serious injury of one conspecific by another should occur only very rarely in nature. Lorenz (1966) expressed this view as follows: “Though occasionally, in territorial or rival fights, by some mishap a horn may penetrate an eye or a tooth or an artery, we have never found that the aim of aggression was the extermination of fellow members of the species concerned” (This view fits in very well with Lorenz’s view of the functions of aggression, which he indeed considered to be eufunctional at the group or species level). As more and more species have been subjected to extended field observations, however, the reports of intraspecific killings, mutilations, cannibalism, kromism and infanticide (pup-killing), siblicide and fratricide, (group) rape and courtship violence, have been steadily accumulating. Already in 1973 E.O. Wilson could comment that “Murder has now been observed frequently enough in gulls, hyenas, hippopotamuses, langurs, macaques and some other vertebrates to suggest that it is both widespread and, Konrad Lorenz and some other popular writers notwithstanding, far more common and hence ‘normal’ in these species than in man”.


While such behaviors certainly contradict a species preservation paradigm – within which animals are assumed to act for the social good of the group or the preservation of the species – they may be economically explained in terms of genic or kin selection theory. Animals may in fact kill or harm conspecifics when conditions are such that it is in the actor’s genetic self-interest to do so, or, in other words, if the benefits or pay-offs of the behavior in terms of fitness exceed the costs to fitness. Accordingly, aggressive behavior has increasingly come to be viewed as an adaptive mechanism, a strategy pursued when assessment indicates that it will be cost-effective in the competition for reproductive and/or material resources.

An individual enhances her/his reproductive fitness not only by successfully competing for resources, however, but also by directly or indirectly reducing the reproductive fitness of others: by destruction of nests, eggs, and fry; by cannibalism and infanticide or destroying the offspring of competitors; by interfering with mating (sexual harassment) or rearing of young; by keeping competitors in a state of chronic and costly stress; by reducing their social activities and thus their breeding opportunities; by delaying their mating and nesting; by inflicting injuries and wounds which are expensive to heal; by exhausting and lowering their resistance to infection; even by affecting the viability of offspring of competitors in the intrauterine environment (Geist, 1978; Hausfater & Hrdy, 1984; Kevles, 1986; Huntingford & Turner, 1989). To maximize reproductive fitness it obviously pays not only to maximize one’s own reproductive output, but also to minimize that of others, provided that the costs are low.

Costs in this context do not, of course, refer to monetary currency, but are to be understood in terms of time and/or energy expenditure (or limited time and/or energy budgets) which could have been allocated to foraging, feeding, finding mates, copulation and so on.

Animals do not habitually grab their pocket calculators to assess the cost/benefit ratio of their agonistic actions; instead, natural selection has done the necessary calculations for the organisms. It is not necessary to regard the organisms as consciously or rationally contemplating the reproductive advantage of a tidbit, after carefully subtracting the potential costs.

Let there be no misunderstanding that the costs of agonistic interactions in most situations are often extremely, even prohibitively, high (death, fatal injuries, sublethal but extremely costly wounds and lacerations which may get infected, exhaustion and attrition, aggressive neglect, exposure to predation, ostracism and isolation, etc.) So, agonistic interactions are not likely to be engaged in just for the fun of it. A shrewd strategist, designed as such by natural selection, ‘knows’ when the odds are against her/him. There is nothing mysterious in this ‘knowledge’ or ‘intuition’ or whatever one wishes to call it. It might be as simple as a translation of the costs assessment in the level or intensity of fear an organism experiences, so that the assessed cost/benefit ratio is reflected in the fight/flight balance.

Selection theory thus predicts that serious fighting will be over serious matters, and the most serious matter of all – the evolutionary \textit{ultima ratio}, so to speak – is reproductive success. Reproductive success concerns the acquisition, defense and monopolization of mates particularly, and resources and positions of dominance or status, which may contribute to reproductive success, generally.

Combatants assess the probability of a favorable outcome of an agonistic interaction on the basis of the information they possess about each other’s capabilities. Maynard Smith &
Parker (1976) have proposed the term Resource Holding Power (RHP) as a shorthand for the sum total of these capabilities. RHP is intimately connected with the fitness budgets of the opponents (and therefore fluctuating over time). Assessment of each other’s RHP thus defines for each combatant a critical probability of winning above which fighting or escalation is the favored strategy, and below which withdrawal, flight or submission is the ‘sane alternative’. Escalation of a fight ensues when both combatants assess their probability of winning as positive. The stake played for – the name of the game – is the infliction of loss of RHP on the adversary. But, alas, there is always a loser who has to bear the consequences of his/her erroneous, too optimistic, assessment of the situation. Obviously, the information on which the assessment was based, proved to be inadequate, imperfect, insufficient, or plainly wrong. If information had been perfect the prospective loser would not have engaged in the tragic encounter to begin with.

It is now easy to see how cost/benefit considerations, and assessment of RHP and the realistic estimation of the risks involved in mortal combat predict

(a) low-level conflict (e.g., displays, threats, wars of attrition) over resources of low reproductive value;

(b) escalation of fighting only when the stakes are high (for many mammalian species this means almost exclusively mating contests);

(c) the significant sex difference in ‘aggression’ in most sexually dimorphic organisms (males have generally more to gain by fighting than females, or females have more to loose; because females’ conflicts center on food or parental resources, while males’ conflicts are likely to center on the acquisition of mates, the reproductive impact of conflict for male mammals may be many times greater than that for females) and

(d) the individual differences in agonistic strategies among socially living animals.

Consider for a moment a herd of red deer. The females in the herd have, at most, low-level, low-cost agonistic interactions because they do not have to compete for matings and so have reproductively little to gain by escalating fights. The dominant stags, being already in a privileged position, have little to gain either: for them fighting incurs costs without much additional gain. The subordinate, and mostly younger, stags bide their time – growing larger, growing stronger, growing more impressive antlers – and postpone serious confrontations with dominants because the risks of injury are too high now. Their chance will come in the next mating season; in the meantime it is better to keep a low profile than exhaust energy in disadvantageous adventures. So peace and quiet reigns in the herd, until the seasonal sexual competition will turn out to be lethal for some 20% of the males.

But why, one may ask, is it worthwhile for males to fight to the death over females? The simple answer is: it is either that or oblivion. The somewhat less simple answer is: females are the reproductively limiting resource to the males. A somewhat more complicated answer is: the sexes have evolved different reproductive and parental strategies to achieve reproductive success. Males experience more variance in reproductive performance; more males than females in each generation fail to have any offspring in their lives, and the most successful males may have ten times as many offspring in their lives as the most successful female. Because males’ variance is high, great expenditure and risk may be profitable, so risky
behavior and conflict are, in polygynous species, male endeavors. Thus conflicts arising under
the influence of sexual selection (more frequently male in mammals) seem more likely to
escalate to lethal proportions than conflicts arising from other sorts of individual selection.
Through evolutionary history, men have also been able to gain reproductively by coalitional
violence and warring behavior; women almost never have been able to do so (Low, 1990).

The paramount majority of all animal agonistic interactions is apparently an intragroup
phenomenon (i.e., it involves fighting among individuals within the same group, population
or community). Some other species, especially nonhuman primates and carnivores, also
exhibit intergroup agonistic behavior, which may be more or less collective and more or less
coordinated.

Animal ‘Wars’

Animal ‘wars’ are a part of popular Western folklore, and also figure prominently in the
mythologies of peoples all over the world. Except for the social insects (vide infra), most
cases described in the literature, however, concern spectacular forms of defense against
predators or more or less collective and concerted attacks of members of one species on one
or more members of another species.

As Van Hooff (1990) observes: “The ethological literature contains no reports of antelopes,
rabbits or cats joining in an attack against a rival group or a threatening predator”. It is not
always easy to determine what phylogenetic and ecological factors (selection pressures)
underlie the presence or absence of such behavior in particular species (and even local
populations).

Gregarious ungulates living in large amorphous herds depend chiefly on flight to escape from
predators, and they do not generally cooperate in active defense. But ungulates that form
kinship group or harems mutually assist one another against predator attacks. A well-known
example is the perimeter defense by musk oxen against wolves, in which the bulls form a
protective circular shield around the cows and calves (The same circular defensive strategy by
buffalo on the American Plains proved fatal against the bullets of human hunters). Many more
species, including primates, show coordinated group defense and sometimes quite elaborate
and ‘clever’ evasive tactics and complex patterns resembling military maneuvers (see

Less evasive is interspecific mobbing behavior, the active and joint assault on a predator or
raptor too formidable to be handled by a single individual. It occurs in a number of social
mammals, such as chimpanzees frenziedly attacking – and some daredevils even beating up –
a leopard model (Kortlandt, 1965), but the most spectacular examples are encountered in the
avian kingdom. Mobbing in birds is a well-defined behavioral pattern that occurs in a wide
variety of taxonomic groups. The attacks are normally directed at predatory birds, particularly
hawks and owls, when they intrude into the territorial or roosting areas of the smaller birds.
The mobbing of some species can result in severe injury or death to the predator.

Migratory bird or mammal aggregations have been reported on rare occasions to engage in
sanguinary ‘wars’ when meeting another aggregation of the same or a different species.
Letourneau (1895) refers to a ‘war’ between magpies and jays in the 15th century in France,
and a ‘war’ between two huge flocks of starlings is said to have occurred in England in the 18th century (E.O. Wilson, 1975).

These and similar instances of mobbing behavior can be understood as collective and organized defense against organisms which normally constitute sources of threat and danger, or as rather severe forms of interspecific competition. The boundary between inter- and intraspecific defense and competition is less clear in the social insects to which we now turn for a closer look. It has been observed time and again that there are only two kinds of animals that habitually make war: humans and ants. Huxley (1944) was one of the first to draw explicit parallels between the warfare of these Hymenoptera and Homo sapiens.

How Tiny Organisms Wage Huge Battles

Among harvester ants, the inhabitants of one nest set out deliberately to raid the supplies of another group (Huxley, 1944). According to Huber (1861), Sajo (1908) and other early students of ant life, they may employ elaborate tactics, and the battles generally result in heavy casualties. If the attackers win, they remove the stores grain by grain to their own nest.

Harvesters are the only kind of ants to go in for accumulating property, as well as the chief kind to practice ‘war’. From the point of view of parallel evolution, this association of property with war is interesting, as many anthropologists and historians believe that in humans war, or at any rate habitual and organized war, did not arise in human evolution until man had reached the stage of settled civilization, when he began to accumulate stores of grain and other forms of wealth.

Less deliberate ‘wars’ may also occur in some other species, between communities whose nests are so close that they compete for the same food territory. On the other hand, the raids of the slave-making ants are not true war, but a curious combination of predation and parasitism.

There is another group of ants called army ants, which suggests military activity. But the phrase is really a misnomer, for these army ants are in reality simply predatory species which happen to hunt in packs; they are the wolves of the insect world, not the warmongers (Huxley, 1944).

The evolutionary rationale underlying social insect organized defense and warfare, E.O. Wilson (1975) explains, is altruism: because the workers are reproductive neuters devoted to the sustenance of the queen and maximum production of her offspring, their own brothers and sisters, they can afford to throw their lives away. And if the colony welfare is threatened they do just that, with impressive efficiency. The result has been the evolution of elaborate communication systems devoted primarily or exclusively to group defense, together with special soldier castes programmed for no function other than combat.

Huber’s (1861) observation of a great war between two nests of ants of the same species some hundred steps distant from each other is thus recounted by Letourneau (1895):

On the field of battle, some thousands of the ants struggled two by two, holding each other with their mandibles; others were searching for each other, attacking each other, forcing each other to come as prisoners into their city where they awaited an end most cruel. The combatants deluged each other with venom and rolled interlaced in the dust... Often in the
heat of action, one sees the severed head of an ant still suspended from the legs or antennae of the victorious adversary; sometimes it is a dead body which is thus dragged and which does not cease to move its legs convulsively.

Some of the battles between ant species are epic in their proportions. The most dramatic battles known within ant species may be those conducted by the common pavement ant *Tetramorium caespitum*. First described by the American Reverend and myrmecologist McCook (1879) from observations in Penn Square, Philadelphia, these ‘wars’ can be witnessed in abundance on sidewalks and lawns in towns and cities of the eastern United States throughout the summer. Masses of hundreds or thousands of the small dark brown workers lock in combat for hours at a time, tumbling, biting, and pulling one another, while new recruits are guided to the melee along freshly laid odor trails. Very probably, these are contests between adjacent colonies in the vicinity of their territorial boundaries. Curiously, only a minute fraction of the workers are injured or killed. One campaign observed by McCook lasted almost 3 weeks. The longest on record is 6½ weeks.

One of the more dramatic spectacles of insect biology is also provided by the large-headed soldiers of certain species belonging to the genus *Pheidole*. These individuals have mandibles shaped approximately like the blades of wire clippers, and their heads are largely filled by massive adductor muscles. When clashes occur between colonies the soldiers rush in, attack blindly, and leave the field littered with the severed antennae, legs, and abdomens of their defeated enemies.

There can be no question, E.O. Wilson (1975; see also E.O. Wilson, 1971) concludes his extensive survey, that fighting, slave raiding, predation and robbery, parasitism, and even cannibalism are normal among the members of some insect species. In the life cycle of some species of parasitic Hymenoptera, for example, the larvae undergo a temporary transformation into a bizarre fighting form that kills and eats other conspecific larvae occupying the same host insect.

Tiny fig wasps have a mixture of winged and wingless males. The wingless males, which, in their search for females, will never leave the fig they are born in, have savage pincer jaws which they use only for fighting – lacerating and slicing to death other males that they encounter as they stalk the length and breadth of the dark, moist, silent garden that is their only world in search of females (Dawkins, 1996). Hamilton (1996) gives a memorable description: “Their fighting looks at once vicious and cautious – cowardly would be the word except that, on reflection, this seems unfair in a situation that can only be likened in human terms to a darkened room full of jostling people among whom, or else lurking in cupboards and recesses which open on all sides, are a dozen or so maniacal homicides armed with knives. One bite is easily fatal. One large *Idarnes* male is capable of biting another in half, but usually a lethal bite is quite a small puncture in the body. Paralysis follows a small injury so regularly and quickly as to suggest use of venom... One fruiting of a large tree of *Ficus* probably involves several million deaths due to combat”.

Indeed, it has been remarked that there is no bizarre and quixotic form of violence imaginable that does not occur in these social insects.

“What can be concluded from the evidence presented above? Mainly that there is no universal ‘rule of conduct’, any more than there is a universal aggressive instinct – and for the same reason. Species are entirely opportunistic. Their behavior patterns do not conform to any
general innate restrictions but are guided, like all other biological traits, solely by what happens to be advantageous over a period or time sufficient for evolution to occur” (E.O. Wilson, 1975).

The Extent of Animal IAB

Collective defensive behavior is highly differential among animal species. Most of them have neither defense nor offense in their repertoire. In a number of avian species, cooperative territorial defense involves regular patrolling of territorial boundaries and chorus vocalizations by all group members in concert.

Collective defense would be rather pointless if there were no threat or danger of offense. In the remainder of this chapter I shall focus on these (mainly mammalian) species in which intraspecific intergroup agonistic behavior, involving observed offensive episodes, has been clearly ascertained. Intergroup agonistic behavior has been described in the following species:

### Table: Animal Intergroup Agonistic Behavior

- *Turdoides squamiceps* (Arabian babbler);
- *Tursiops truncatus* (dolphin);
- *Helogale undulata* (dwarf-mongoose);
- *Suricata suricatta* (slender-tailed meerkat);
- *Otaria byronia* (southern sea lion);
- *Crocuta crocuta* (spotted hyena);
- *Canis lupus* (wolf);
- *Lycaon pictus lupinus* (Cape hunting dog);
- *Panthera leo* (lion);
- *Acynonyx (Cynaelurus) jubatus* (cheetah);
- *Lemur catta* (ring-tailed lemur); &\#8225;
- *Lemur [Eulemur] fulvus* (brown lemur); *
- *Propithecus verreauxi* (white or Verreaux’s sifaka); &\#8225;
- *Indri indri* (indri); *
- *Saguinus imperator* (emperor tamarin); &\#8225;
- *Saguinus fuscicollis* (saddleback tamarin); &\#8225;
- *Saguinus mystax* (moustached tamarin);
- *Callicebus moloch* (dusky titi monkey); &\#8225;
- *Callicebus torquatus* (yellow-handed titi monkey); *
- *Saimiri sciureus* (squirrel monkey);
- *Alouatta fusca* (brown howler monkey);
- *Alouatta palliata* (mantled howler monkey);
- *Alouatta seniculus* (red howler monkey); &\#8225;
- *Cebus apella* (brown or black-capped or tufted capuchin); *
- *Cebus albifrons* (white-fronted capuchin); *
- *Cebus capucinus* (white-faced capuchin);
- *Cebus olivaceus* (wedge-capped capuchin); &\#8225;
Ateles belzebuth ((long-haired) spider monkey);  
Brachyteles arachnoides (murmiqui or woolly spider monkey); *
Lagothrix lagotricha (Humboldt’s woolly monkey); &#8225;
Presbytis [Semnopithecus] entellus (gray or Hanuman or Ceylon langur); &#8225;
Presbytis [Trachypithecus] johnii (Nilgiri langur);
Presbytis pileata [Trachypithecus pileatus] (capped langur);
Presbytis cristata [Trachypithecus cristatus] (silver(ed) leaf monkey or lutong);
Presbytis senex [Trachypithecus retulus] (purple-faced langur);
Presbytis aygula ((Sunda Island) leaf monkey); &#8225;
Presbytis potenziani (Mentawai langur); &#8225;
Colobus [Procolobus] badius (red colobus);
Colobus guereza (black-and-white colobus); &#8225;
Cercocebus [Lophocebus] albigena (crested or gray-cheeked mangabey); &#8225;
Cercopithecus [Chlorocebus] aethiops (vervet); &#8225;
Cercopithecus ascanius (redtail monkey); &#8225;
Cercopithecus mitis (guenon or blue monkey); &#8225;
Cercopithecus neglectus (De Brazza’s monkey); *
Miopithecus talapoin (talapoin); *
Erythrocebus patas (patas monkey); &#8225;
Papio hamadryas (hamadryas or desert baboon);
Papio cynocephalus (yellow or savanna baboon); &#8225;
Papio anubis (olive baboon);
Papio ursinus (chacma baboon);
Macaca fascicularis (kra or long-tailed or crab-eating macaque); &#8225;
Macaca fuscata (Japanese macaque); &#8225;
Macaca mulatta (rhesus monkey); &#8225;
Macaca radiata (bonnet macaque); *
Macaca sylvanus (barbary macaque);
Hylobates lar (whitehanded gibbon); &#8225;
Hylobates klossii (Kloss’s gibbon); &#8225;
Hylobates agillis (agile or dark-handed gibbon); &#8225;
Hylobates moloch (moloch or silvery gibbon);
Hylobates pileatus (pileated or capped gibbon); &#8225;
Hylobates (Symphalangus) syndactylus (siamang);
Gorilla g. berengei (mountain gorilla);
Pan paniscus (bonobo or pygmy chimpanzee); *
Pan troglodytes ((common) chimpanzee);

Legend:

* = Aggressive intergroup encounters are reported to be (extremely) rare.

&#8225; = Both sexes, or mainly females, actively participate in the conflict (vide infra).

In brackets [ ] the species names according to the recent primate taxonomy by Colin Groves (1993).
**General Observations on IAB**

The presence of one avian species, the Arabian babbler, in the table is, by all means, surprising. Yet, this tiny bird is perfectly capable of what Zahavi (1987) unhesitatingly compared to human ‘warfare’.

Rasa (1985, 1986) reported territorial group aggression in dwarf mongoose. Group meetings in this highly social species are random, and the animals do not appear to patrol territorial boundaries.

Among dolphins, coalitions of young males may harass, attempt to isolate, ‘aggressively herd’ and ‘group rape’ females from other groups.

Among social carnivores, a number of group-territorial species show coordinated lethal attacks. In wolves, family-based packs occasionally invade neighboring packs’ territories, attacking residents; Mech (1977) found that intraspecific conflict accounted for 43% of deaths not caused by humans. Among spotted hyenas, who, like wolves, live in family-based, territory-holding groups, intruders into a clan’s territory are likely to be attacked and killed, and smaller clan subgroups patrol the territory boundaries, confronting other ‘patrols’ (Kruuk, 1972). Neighboring clans sometimes engage in pitched battles over carcasses of prey that one or the other of the groups has killed. The following account is taken from Kruuk’s (1972) protocols (as cited in E.O. Wilson, 1975):

The two groups mixed with an uproar of calls, but within seconds the sides parted again and the Mungi hyenas ran away, briefly pursued by the Scratching Rock hyenas, who then returned to the carcass. About a dozen of the Scratching Rock hyenas, though, grabbed one of the Mungi males and bit him wherever they could – especially in the belly, the feet, and the ears. The victim was completely covered by his attackers, who proceeded to maul him for about 10 min. while their clan fellows were eating the wildebeest. The Mungi male was literally pulled apart, and when I later studied the injuries more closely, it appeared that his ears were bitten off and so were his feet and testicles, he was paralyzed by a spinal injury, had large gashes in the hind legs and belly, and subcutaneous hemorrhages all over... The next morning I found a hyena eating from the carcass and saw evidence that more had been there; about one-third of the internal organs and muscles had been eaten. Cannibals!

In lions, which also live in groups (prides) based on a group of related females and one or more associated males, interpride encounters occur, but lethal injury is rare. When invading males are attempting to take over a pride, there may be lethal injuries, though once one male cedes reproductive rights, aggression typically stops. New males are likely to commit infanticide (e.g., Bertram, 1976, 1978). Coalitions of male cheetahs driving smaller coalitions away from breeding females may inflict fatal injuries (Caro & Collins, 1986).

The following observations pertain specifically to the nonhuman primate species:

1. As may be gathered from the table, the majority of species in which IAB has been documented belong to the primate order. The intergroup behavior of primates is extremely variable – both inter- and intraspecific – and ranges from very relaxed and ‘peaceful’ to lethal raiding.
When two or more groups of primates meet, the resulting behavior may range from complete fusion of the groups (no antagonism), or mutual avoidance, via bluffing and intimidation, threats and displays, fights and chases, to outright killing (Eberhart & Candland, 1981).

In most primate species conflicts between groups are rare. Neighboring groups generally avoid each other. When groups spot one other, the group most eccentric in relation to its home range generally is the first to retreat, or, in case a dominance-subordination relationship exists among the groups (vide infra), the subordinate group retreats (Kawanaka, 1973; Eberhard & Candland, 1981; Cheney, 1987).

Among primates, exclusive use of space is generally maintained by (a) site attachment; (b) site-dependent aggression; and (c) active defense of (exclusive access to) an area’s resources by advertisement and/or eviction of intruders (territoriality). The behavioral mechanisms regulating spacing and grouping may vary within a genus, and even within a species (Robinson, Wright & Kinzey, 1987). For example, in a Callicebus torquatus population in Peru, exclusive use of space is maintained by mutual avoidance and restricting movements to familiar areas. In contrast, Callicebus moloch has been described as ‘territorial’ in that, in addition to groups occupying exclusive areas, spacing between groups is maintained by site-dependent aggression: the probability that a group will attack, rather than avoid, another group depends on the site at which the encounter takes place. In this (and other) species, that probability is low at the center of the group’s own range, increases the closer the group is to the boundary, and then drops off rapidly as the boundary is crossed. The outcome of an aggressive encounter therefore varies with locality. Each group is more aggressive and therefore displaces other groups more easily when it is within its own exclusive area. Groups are most aggressive close to, but on their own side of, the boundary, a ‘doughnut’-shaped aggression field (Waser & Wiley, 1979) that results in the clear definition and reinforcement of the conventional location of the boundaries. Typically, chasing occurs, but physical contact is rare. The ordinal positions of dominance among groups (vide infra) are thus contingent upon their positions on a central-peripheral axis across their ranges (Carpenter, 1974).

As a rule, most primate agonistic group encounters are of the ‘ritualized contact’ type, in which injuries are rare and hardly serious, and fatalities virtually unknown (Eberhard & Candland, 1981). The few times when contact between groups results in a collective skirmish, it seems to be the result of incidental escalation of brawls between peripheral individuals in which others interfere, rather than a deliberately coordinated and concerted enterprise (Van Hooff, 1990).

Observers of nonterritorial groups often comment upon the relative lack of intergroup aggression, even when groups are in close proximity. Chacma and olive baboons are representative of the state of at least several species of primates. In over 2,000 hours of observation by Hall and DeVore, “no aggressive interactions between groups have ever been recorded” (Hall, 1964). Relationships between groups are characterized by mutual avoidance in most situations, and temporary mutual tolerance in special circumstances, such as gatherings at water holes in arid regions.

A number of other primate species have occasionally been observed to mingle peacefully at sleeping sites.

Some non-territorial species have evolved loud calls (‘duetting calls’) that aid in the regulation of intergroup spacing and mutual avoidance (Cheney, 1987).
2. In contrast, when groups defend all or part of their home ranges, most intergroup interactions are characterized by aggression rather than by mutual avoidance. Communal defense of home range or territory against intraspecific intruders seems to be the most common manifestation of IAB in primates and carnivores. However, relatively few primate species maintain true territories; rather, there is some overlapping of foraging ranges in most studied species of Cercopithecoida and Ceboidea. Troops of rhesus, langurs, howlers, and Japanese macaque avoid contact with each other when approaching the overlapping zones. Adjacent social groups in the majority of colobines generally interact aggressively, with adult males usually the most aggressive and frequent participants (Poirier, 1974).

Friendly interactions (play, grooming, copulation) between members of different intraspecific groups do, however, occur in both territorial and nonterritorial species (Cheney, 1987).

Home range size is influenced by both dietary requirements and the spatiotemporal distribution of food (Cheney, 1987). A group’s ability to patrol its range on a regular basis is correlated with the presence or absence of territoriality (Mitani & Rodman, 1979). This is in accordance with the ‘economic defendability’ model of territoriality. Perhaps because large ranges are difficult and uneconomical to patrol, they often overlap extensively with those of other groups. When overlap is great, aggressive encounters occur at low rates, and those that do occur usually concern access to a clumped, desirable resource, such as a fruiting tree, rather than a range boundary. This occurs among e.g., capuchins, red howlers, baboons, and mangabeys (Cheney, 1987).

In contrast to nonterritorial species, most territorial primates have specialized intergroup calls that seem to attract, rather than repel, neighboring groups.

3. Facilitating and/or aggravating conditions of IAB in primates include: extreme crowding, competition for food at artificial feeding sites and other rather ‘pathological’ conditions such as disruption caused by human interference (e.g., Kawanaka, 1973; Mitani & Rodman, 1979), which is generally substantiated by reports on zoo massacres (e.g., Russell & Russell, 1968; Zuckerman, 1932).

4. In primate species which form all-male groups, defense by the leader of the bisexual group against the violent appropriation and abduction of females by the all-male group may result in prolonged and severe fighting with skirmishes and raids lasting for periods of days (Bygott, 1979; Mohnot, 1971).

In capped langurs, intergroup aggression is not related to defense of food sources by either sex, but rather appears to involve attempts by males from outside the group to interact with group females. During intergroup encounters, resident females bite and push females that approach an intruding male. Males appear to use intergroup encounters as a means of defending their own females while gaining access to those of other groups (Stanford, 1991).

Mate defense and the exploration of new breeding opportunities appear to be important functions of intergroup conflict in other primate species too.

In the population of mountain gorillas living in the Virunga Volcanoes of east central Africa, males acquire females by attracting them away from other silverbacks (adult males) during encounters with bisexual groups. Such encounters are characterized by intense male-male
competition, involving vigorous threat displays (e.g., chest beating) and physical fights in 50% of the cases (Harcourt, 1978; Stewart & Harcourt, 1987). Severe wounding (Harcourt, 1978) and probably death (Baumgartel, 1976; Fossey, 1983) of adult males can result. Infanticides may occur during intergroup encounters (Fossey, 1983). The majority of the males Fossey observed carried the scars of furious fighting, and showed missing or broken canine teeth.

5. For some primate species agonistic intertroop or intercommunity encounters may be highly attractive (at least for some individuals, mostly young males) (e.g., Bygott, 1979; Fossey, 1979; Goodall, 1986), and confrontations may be actively sought and provoked (which suggests intrinsic motivation: they seem to be ‘spoiling for a fight’). According to Poirier (1974), a very interesting feature of colobine (genera *Colobus* and *Presbytis*) agonistic intergroup encounters is the fact that they have readily available means of avoiding such contact.

In many Old World species subadult and adult males are involved in these skirmishes. On the other hand, it has become increasingly clear lately that female involvement in IAB has been systematically underestimated. Manson & Wrangham (1991) state:

> Among humans and chimpanzees, males are actively involved in intergroup aggression whereas females are largely limited to a supporting role. This low level of involvement by females is unusual among primates. For example, among rhesus macaques (*Macaca mulatta*) at Cayo Santiago, ‘violent intergroup squabbles... were marked by sustained fighting in line formation... 2-20 animals faced off with individuals of an opposing group and reciprocally lunged, batted, and growled... participants in the line were most often adult females and 2- to 5-year-old males (i.e., juveniles and subadults)’ (Hausfater, 1972). Although physical contact was rare among the Cayo Santiago rhesus macaques, at least 8% of wounds occurred during intergroup fighting. Adult females may be more involved than males and in a number of species are reported to constitute the central phalanx. In an unusually violent intergroup confrontation among olive baboons at Gilgil, Kenya, older males watched the conflict from a safe distance while the younger adult males tried to pull their female troopmates away from the fray...

> Also in most populations of *Presbytis entellus*, adult females (Ripley, 1967), as well as youngsters (Hrdy, 1977) may play prominent roles in intergroup fights.

In primate species defending territories, and those characterized by male dispersal (or female philopatry), female hostility toward other groups and cooperation in intergroup aggression is common, and may involve both resource defense against extragroup females, and, more or less collective, antagonism toward migrant, potentially infanticidal, males. Female antagonism toward extragroup females also occurs in some of the social carnivores.

In monogamous primate species (e.g., Hyllobatidae), females may be as aggressively participating in cooperative territory defense and other intergroup interactions as males (Cheney, 1987).

In primate species characterized by female dispersion, in which the females transfer to new groups, on the other hand, females tend not to participate in aggressive intergroup interactions: e.g., gorillas (Fossey, 1979).
Female involvement in intergroup aggression has been proposed to depend on whether resources that limit female reproduction are defensible through cooperative action. In such ‘matriotic’ species (Wrangham & Peterson, 1996), only females are committed by birth and temperament to the fortunes of their troop.

Accordingly, species in which females cooperate may be expected to be those with female philopatry. This hypothesis was tested by Manson & Wrangham (1991). Their data indicate that female philopatry and female participation in intergroup aggression are indeed correlated ($\chi^2 = 8.26; \text{Phi} = .76; p < .01$). Female philopatry also appears to be associated with female participation in intergroup aggression in social carnivores such as spotted hyenas (Kruuk, 1972) and lions (Packer, Scheel & Pusey, 1990).

6. In a number of primate and carnivore species IAB is accompanied by infanticide, infant kidnapping and, occasionally, cannibalism. In Hanuman langurs and red howlers, for example, a number of infanticides are committed by males who have recently invaded the group. This seems to be the most common pattern of infanticide in primates and lions. For the possible evolutionary rationale behind infanticide, as a male reproductive strategy, see Angst & Thommen (1977) and Hausfater & Hrdy (1984), who also present evidence on other genera and taxa. When a female’s infant is killed, she soon becomes sexually receptive again, and, more often than not, she copulates with the killer of her infant (see also Wrangham & Peterson, 1996).

7. When home ranges overlap extensively, the aggressive defense of a particular resource may be more costly than the simple avoidance of other groups. In such cases, intergroup competition is often mediated by the relative dominance of the groups involved. There is evidence for a positive correlation between a group’s size (and the number of adult males) and its ability to displace other groups (though occasionally more subtle factors – such as the history of past relations between the groups – are involved). This results in a definite linear group dominance hierarchy revealed by approach-retreat encounters (e.g., Cheney, 1987; Kawanaka, 1973). Approach-retreat encounters (called Type C encounters by Deag [1973]) have, for example, been observed in most macaque species (Givens, 1975).

Little is known yet about bonobo intercommunity encounters. Smaller foraging parties normally avoid larger ones. When encounters occur they appear mildly antagonistic, ranging from peaceful mixing in the border area, nonlethal fighting (no observation has been made of participants killed in intergroup fights), to clashes sometimes leading to bloody wounds (Badrian & Badrian, 1984; Kano, 1984; Kano & Mulavwa, 1984; Knauf, 1991; Wrangham & Peterson, 1996). There appears to be intergroup dominance attenuating agonistic contacts (e.g., Kano, 1987).

8. Personal idiosyncrasies and ‘character structure’ of (mostly male) leaders strongly influence group integration, the movements of the group within its home range, and dominance-subordinate relationships with other groups. Careful control of trouble within the group and leading attacks on other groups was for instance characteristic of some leader males at Takasakiyama (Kawanaka, 1973). cf. also Russell & Russell’s (1968), and Carpenter’s (1974) story of Diablo, the ‘monkey warlord’ of Cayo Santiago.

Furthermore, concerted action and scouting behavior of group males seem to indicate a ‘consciousness of belonging’ (Kawanaka, 1973). Especially in relation to human ethnocentrism and xenophobia, which will be discussed in more detail in Ch. 6, it is
particularly interesting that in the nonhuman primates generally – as in humans – intragroup cohesion and intergroup hostility may be correlated (Cheney, 1992).

The Chimpanzee versus the Baboon IAB Pattern

Two distinct patterns of group antagonism in primates merit some closer scrutiny for reasons of later comparison with human primitive warfare. These are the baboon ‘pitched battle’ and the chimpanzee ‘ambush’. Let us briefly examine them in turn.

Van Hooff (1990) vividly portrays a massively escalated agonistic episode between two baboon (Papio anubis) groups of about 100 and 150 individuals respectively, at Gilgil, Kenya. He describes it as an impressive, sometimes earpiercing, spectacular and cacophonous event, lasting more than an hour. A great many animals from both groups formed two, more than 100 meters-long frontlines (or phalanxes), mutually threatening and making small sorties, meanwhile alternately ‘jerk-looking’ at their own neighbors (for reassurance) and at the adversaries, and making a hell of a noise (‘shriekbarking’). Suddenly, presumably when one or more adversaries shrank and retreated, a number of animals simultaneously rushed forward in a massive assault. Almost immediately the entire frontline dashed forward and drove the other party before it for some hundred meters, accompanied by a crescendo of shriekbarking by the entire chasing group. Gradually the chase lost impetus, slowed down, the frontlines coming to a standstill and again the parties confronted each other. After a while a similar surging attack would be repeated in the same or the reverse direction, the groups chasing each other to and fro. The end of the confrontation was less spectacular: it ended not in a decisive final chase, but petered out because gradually less and less individuals participated in the forays. This was especially true for the intruding group, which finally withdrew to its own home area. Most notable, according to Van Hooff’s account, was the small amount and short duration of physical contacts during the fight. There were no visible injuries. Furthermore, the females were just as active in the skirmishes as the males, if not more so.

Wrangham & Peterson (1996) describe these skirmishes as follows: “In some monkey species the fight escalates to where a group of females lines up as a tight phalanx, warriors moving shoulder to shoulder, snarling and lunging and screaming at the opposing phalanx only a few inches away. Battle lines form and re-form, isolated encounters occur at the edges of the main action, and the troops may fight for an hour or more until exhausted or until the weaker yields. Only terrestrial primates can fight with a coordination as tight as this... Fierce and frequent though it may be, however, this aggression is very different from the lethal raiding of chimpanzees. The goal in these fights over land or status is merely the opponent’s defeat. Dominate the other group. Remove them, perhaps. But once they give up, let them go. Don’t try to kill them. Most primates are satisfied with seeing the rear ends of their opponents”. Note that the battle line formation or phalanx, in primate as well as human warriors, probably results from each individual trying to have its vulnerable flanks protected.

See especially Smuts et al. (1987) for pictorial evidence of similar ‘pitched battles’ in a number of other primate species such as vervet monkeys, redtail monkeys, gray langurs, gelada baboons, and rhesus macaques (in all these cases the combatants are females).

Bygott (1974, 1979), Jane Goodall (1979 et seq) and Goodall et al. (1979) recently reported on the intercommunity relationships of the Gombe (Tanzania) population of chimpanzees,
especially episodes of what Goodall literally called ‘primitive warfare’. Parties of up to ten adult males, sometimes accompanied by females and subadults, quite regularly patrol the boundaries, keeping close together, silent and alert, often stopping to listen intently, apparently actively searching for signs of neighbors. Sometimes they climb a tree to scout the ‘hostile’ territory of the adjacent community, just like a human reconnaissance party might do (the original community had begun to divide into two separate communities about 1970). If no members of the neighboring community are detected, the patrol may stealthily intrude into the ‘enemy’ territory. When a fairly large ‘enemy’ party is encountered both parties may engage in vocal and gestural agonistic displays, or one of them may charge and chase the other away, or both give up and return to their core areas. At other times, a party, upon spotting ‘enemies’, may flee, thus avoiding encounter. When, however, small parties or single ‘enemy’ chimpanzees, particularly anestrous females, are encountered by the ‘warriors’, these may be severely and viciously attacked and killed. Goodall describes several such lethal episodes in some (gruesome) detail. “It seems”, she continues, “that we have been observing a phenomenon rarely recorded in field studies – the gradual extermination of one group of animals by another, stronger, group” (Goodall, 1979).

Subsequently, Goodall (1986) reported observations of five lethal attacks, and some 13 more that left the victims – including adults and infants of both sexes – severely wounded and bleeding profusely. Why, she wondered, would the aggressors attempt to kill, maim or injure their victims instead of merely chasing them away?

Bygott (1979) and Goodall et al. (1979) emphasize that the males actively seek out agonistic interactions with the adjacent community during their patrolling. Also Nishida (1979, 1980) and Itani (1982) have observed similar group antagonism in chimpanzees, which was described by Itani as a “skirmish in a war”. On the patrolling behavior of some ‘warrior groups’ Itani also reports: “they looked as if they were aiming for the best chance of encountering another group”, or as if they were looking for an opportunity to ‘hunt down’ conspecifics and inflict fatal injuries (Manson & Wrangham, 1991). Furthermore, the attacks were all characterized by “unusual brutality and persistence” (Bygott, 1979), and the observers could not escape feeling that the aggressors were ‘intentionally’ trying to kill their victims. All observed lethal attacks were unprovoked and lasted at least ten minutes. The victim was deliberately held down by some of the attackers, and subjected to a treatment more brutal than any found in intracommunity aggressive episodes. As Itani (1982) phrased it: “agonistic interactions of a group versus an individual, or a group versus another group, with the intent to kill, is peculiar to chimpanzee society” (cf. Ghiglieri, 1988; Goodall, 1986; Goodall et al., 1979; Manson & Wrangham, 1991).

Interestingly, intercommunity encounters involve mostly males. Females (usually while in estrous) sometimes accompany males on patrol, but they do not typically initiate ‘hostilities’ (Goodall et al., 1979; Wrangham, 1975). Another intriguing observation is that the intense excitement shown by the aggressors during and after the attacks rather easily ‘spills over’ into hunting and killing other primates (red colobus or baboons), which might suggest that at least in some instances similar motivational mechanisms may be involved in both intraspecific violence and interspecific predation (Bygott, 1979; Vogel, 1989). Possibly brief attacks on females encountered in overlap zones between neighboring communities attract rather than repel the females concerned (Goodall et al., 1979); some young unhabituated females not only remained within the home range but gradually moved into the core area despite occasional attacks (Pusey, 1979).
It appears that the violence of the chimpanzee ‘warriors’ is especially severe towards old, lactating, and anestrous females, and considerably less severe towards females in estrus, i.e., those with high reproductive value. “In particular, young nulliparous females are not attacked severely and instead may be escorted by or forced to travel with the aggressors (Wolf & Schulman, 1984; Goodall, 1986). This makes sense as part of a male reproductive strategy because such females are destined to transfer to a new group and are therefore potential mates. While lethal attacks were likely to be directed against solitary males and anestrous females, estrous females seem to be considered an attractive and alienable resource which can be transferred into the attackers’ group” (Manson & Wrangham, 1981).

Similarly, Ghiglieri (1984, 1987, 1988) recently reported on the Kibale Forest chimpanzee society in which cooperatively territorial and murderous males were observed to kill the adult males of a smaller group and then absorb their reproductive females (which also may have been a common strategy in hominid warfare). See also Nishida et al. (1985) for an account of the Mahale Mountains National Park chimpanzees.

Ghiglieri (1987) and Alexander (1989) speculate that this strategy may be a pattern common to the human-chimpanzee-bonobo clade: “Unlike gorillas and orangutans, males of the chimpanzee-bonobo-human clade retain their male offspring predominantly, live in closed social groups containing multiple females, mate polygynously, restrict their ranging to a communal territory, are cooperatively active in territorial defense, and, apparently, when a neighboring community weakens, the males of some communities make a concerted strategic effort to stalk, attack, and kill their rivals as do men” (Ghiglieri, 1987). Especially, the combination of male-male cooperation, ‘proto-ethnocentrism’, territoriality and female transfer has been singled out as the starting condition for lethal intergroup aggression (Goodall, 1986; Ghiglieri, 1987, 1988; Alexander, 1989; Manson & Wrangham, 1991; Wrangham & Peterson, 1996).

Perhaps ‘higher’ species (with a more elaborate cognitive make-up) need extra strong group demarcations, the strength of which must be somehow related to the species’ affective system. Maybe chimpanzees, like our own species, have very strong imaginations (schemata or mental representations) of we and they (‘proto-ethnocentrism’ or what Kawanaka [1973] called “a consciousness of belonging”).

Besides the general, more elaborate cognitive make-up, there may be highly (content-)specific cognitive mechanisms involved, which would also, at least partly, explain why ‘war-like’ intergroup conflict is actually so rare in mammals in general, and primates in particular. One should not lose sight of the fact that, despite the impressive list of species which do, thousands of other species do not have ‘group aggression’ in their behavioral repertoire.

In a similar vein, Tooby & Cosmides (1988) reasoned that the distribution of war in the animal kingdom is limited by the same factor that limits the emergence of the multi-individual cooperation on which war depends: specific cognitive preadaptations, and a distinctive coalitional psychology.

According to Manson & Wrangham (1991), the similarities between chimpanzee and human lethal male raiding seem to suggest a common evolutionary background.

In the primates’ group-antagonistic behavior, morphologically two more or less distinct patterns are discernible: (1) a pattern resembling the ‘pitched battle’ with parallel frontlines,
mutual threats, sorties and chases, resulting in none to few casualties, as described in baboons (the *baboon pattern*); and (2) a sneak-attack pattern, involving male patrolling, intentional and lethal attack on qualitatively and quantitatively weaker victims (often solitary and female), accompanied by unusual cruelty and frenzy, more resembling the human raid- and ambush-type of warfare, exemplified by the chimps of Gombe (the *chimpanzee pattern*). The latter is peculiarly unique and confined as far as is known, among nonhuman primates, to this species.

It seems that the particular social organization, cognitive capacities (and other psychological ‘preadaptations’), as well as, possibly, ecological circumstances of increased group competition, have facilitated development of a close parallel to human raiding in the Gombe chimpanzees. The human male, evidently, has both patterns at his disposal. All the other descriptions of IAB in the literature can be understood to be various mixtures or combinations of these two idiotypical patterns.

The pitched battle provides a striking parallel between primates and humans. In humans too, pitched battle is the *least* bloody and lethal form of primitive warfare (often boiling down to a few dyadic duels), and simultaneously the most clamorous, vociferous and emotional spectacle, abundant with magnificent display, showing-off of superb calisthenic skills, and torrents of verbal insults and obscenities; in short, an excellent *show of ferocity*, ending as soon as the first casualty has occurred. It also appears to be the most ritualized, regulated and conventionalized form of warfare. The main difference, of course, is that in baboons it is often the result of a chance encounter between groups, while in humans it is more often than not premeditated and prearranged (even the identity of the casualty-to-be may be preordained).

**Socio-ecology: Making Sense of It All**

Can we make sense of, and bring some order in, the apparent diversity of the intergroup behavioral patterns in the nonhuman primates and in the other species we have encountered? The most valiant attempt in that direction is the socio-ecological approach as developed by Wrangham (1977, 1980, 1987), Van Schaik (1983 et seq.), Van Schaik & Van Hooff (1983), Cheney (1987), Van Hooff (1988, 1990), and Van Hooff & Van Schaik (1992) a.o., on the ultimate causes of primate sociality. Though differing in detail and emphasis, these authors consider powerful ecological selection pressures to have shaped the social structure of primates (and by implication other species). Other factors, such as phylogenetic inertia, are also acknowledged, but the emphasis is clearly on the physical and social environment. The socio-ecological model underlying this reasoning is, highly simplified, the following:

1) Primates (organisms in general) are considered to behave as if they were maximizing their reproductive success (RS), and to compete for resources necessary to achieve this ‘aim’.

2) As scramble competition (also called ‘exploitation competition’) and contest competition (also called ‘exclusion competition’ or ‘interference competition’) can occur within social groups as well as between social groups, four main types of competition ought to be distinguished: Within-Group Scramble (WGS), Within-Group Contest (WGC), Between-Group Scramble (BGS), and Between-Group Contest (BGC). All four types of competition can be present simultaneously in one species, but my main focus here is
Between-Group Contest competition. The main conditions giving rise to contest competition within as well as between groups are: (a) resources in short supply, and (b) the defensibility of access to those resources. The factors limiting the reproductive success of males and females tend to be different, however, due to the strong asymmetry in parental investment. Consequently, males and females compete for different resources, and the competitive and cooperative (alliances, coalitions, bonding) isosexual interactions, as well as male-female bonds, are expected to reflect these different interests. For example, in situations where males are not able to provide significant services to females (such as protection against sexual harassment by other males), females are expected not to develop bonds with males, and in fact should actively attempt to keep them away or repel them from their groups.

3) Reproductive success of females is determined largely by the general factor ‘health’, good condition, or nutritional and energetic status, meaning the combined effects of access to vital (food) resources, safety from predators, absence of stress overload and infectious diseases, and absence of other factors which may adversely affect fecundity.

4) Reproductive success of males, on the other hand, is determined to a very large extent by access to fertile females (the only ‘resources’ who can convert the males’ fitness potential into reproductive success). These two considerations combined predict strikingly different reproductive strategies for the sexes. Females, in general, will maximize RS by maintaining a good condition for a long period of time. Males, on the other hand, maximize RS (a) by fertilizing many females and by investing in the maximization of the chances of fertilization (a polygamist strategy); or (b) by investing in long-term paternal care for a small number of consecutively raised offspring (a monogamist strategy). In the former case, male will have to face fierce competition by other males. In the latter, males will have to face possible ‘marital infidelity’ by their mates, and chronic challenges and threats to their paternity confidence.

5) Predation pressure largely determines sociality versus solitariness, while distribution and monopolizability of food resources largely determine the competition regime. Predictable and defendable resources are conducive to contest competition within and between groups, while abundant, non-clumped, undefendable food resources are conducive to scramble competition (i.e., competition in terms of efficiency of exploitation). When kin-based alliances of females increase access to food patches, females are expected to remain in their natal groups and cooperate with kin, and to form hierarchies of nepotistic ‘matriarchal clan systems’. They are also expected, as the resident sex, to be hostile toward (females of) other groups, in proportion to the economic defensibility of the home ranges, and to participate in intergroup conflicts as ferociously as males or even more so. Because males may aid females in dominating other groups, aggression toward extragroup males is expected to be less severe than toward extragroup females. Similarly, monogamous species are predicted to aggressively defend home ranges.

6) The competition regime largely determines the distribution and organization of females (e.g., female-bonded societies with matriline and complex hierarchies are common in frugivorous primates with within-group contest competition), and their attachment to the natal group, and, consequently, the migration of males. Males migrate (become the exogamous sex) when females are bonded in female kin-hierarchies and, therefore, discouraged from emigrating (because they will virtually always be worse off if they emigrate to another group). Once females emigrate as well, because they live in a situation of scramble competition and, therefore, are not forced into strong female bonds, males have the option to stay in their natal group and to develop long-lasting relationships based on familiarity and
kinship. In those species characterized by female dispersal, females are expected to avoid agonistic intergroup interactions and not to participate in home range defense. The intergroup behavior of males, on the other hand, should primarily involve defense of females against extragroup males.

7) The distribution, organization, and reproductive competition of males is determined largely by the distribution, organization, and monopolizability of females. When BGC competition is important, group members are expected to form a large alliance in order to improve their competitive ability as a group. This generally implies a more relaxed and egalitarian WGC regime, otherwise subordinates might either refrain from taking risks in intergroup conflicts, or even defect to another group.

In addition to food, males are expected to compete above all over access to females. Whether this competition takes the form of scramble or contest competition is determined principally by the distribution in space and time of estrous females. If females live in compact groups, access to them can be monopolized, which results in female defense polygyny (either one-male groups if the females can be guarded or herded effectively, or else multi-male groups). If the home ranges in which the females live, or the resources to which they are attracted, can be defended effectively, this gives rise to resource defense polygyny. In these situations intrasexual selection will favor contest vigor and dimorphism in males. If monopolization of females is impossible (females actively resist being monopolized or choose a diversity of mating partners), males may form either monogamous bonds with a single female (most often in the form of exclusive consort relationships with fertile females), or engage in scramble competition polygyny, in which case natural selection favors sperm competition.

The male reproductive competition regime largely determines the ‘politics’ of males, the genesis of (opportunistic) coalitions and support strategies, cooperation in hunting and intergroup conflict if present, the sharing of prey, and the functional analogon to human ‘fraternal interest groups’ in chimpanzees.

Male philopatry becomes an option when female contest competition is relaxed, and therefore the pressure on females to be philopatric is low. This situation is expected to facilitate the formation of preferably kin-based male alliances (‘fraternities’), which defend access to a territory and to the females attracted to it. Such a cooperative resource defense polygyny thus depends on restraint in within-group competition (especially sexual tolerance) in combination with cooperation in between-group competition. The ‘wars’ (lethal male raids) between chimpanzee communities may therefore be viewed as male reproductive strategies in which coalitions of males increase their territory and their access to females living on or lured to that territory.

The intricacies and complexities involved in polyadic coalitions within, and fierce, stealthy, raiding-type coalitional competition between groups may also have established a positive feedback loop with social and Machiavellian intelligence, and, possibly, ‘proto-ethnocentrism’.

If this analysis gives the impression that primate females are passive recipients of male aggressive and sexual strategies and power games, it should be corrected immediately. As we have seen, females are not only actively involved in agonistic intergroup encounters in many species, also in sexual matters females are the active solicitors in most species, and they exert
their privilege of Female Choice in mate selection – as well as their personal ‘erotic’ preferences and aversions – with gusto and bravado (see e.g., Hrdy, 1981; Smuts, 1987). Female choice must have been a potent selective force in the evolution of primate – including human – societies.

**Ultimate Explanations of Chimpanzee ‘Warfare’**

Chimpanzees, like humans, are ‘highly xenophobic’ (Schubert, 1983; Goodall, 1986; Diamond, 1992), and they sometimes engage in ‘armed fighting’ in defense against predators (Kortlandt, 1972), and, as we have seen, lethal raids with ‘intent to kill’ against conspecifics. Chimpanzees, like humans, are also conspicuous for their ‘hunting and predatory behavior’ (Kortlandt, 1972). Many authors have pointed to the developing tradition of cooperative hunting in male chimpanzees as a possible facilitating factor in IAB (as it is also hypothesized to be in the evolution of human warfare).

In contrast to the ‘matriotic’ primate societies structured around female coalitions and matrilines, primate communities organized around male interests tend to follow male strategies and, thanks to sexual selection, tend to seek power with an almost unbounded enthusiasm. “In a nutshell: Patriotism breeds aggression. Males have evolved to possess strong appetites for power because with extraordinary power males can achieve extraordinary reproduction” (Wrangham & Peterson, 1996).

As possible advantages of collective patrolling and IAB by male chimpanzees have been suggested the increased access to females (e.g., Bygott, 1979; Goodall et al., 1979; Low, 1990; Manson & Wrangham, 1991) and foraging for food resources (Nishida, 1979). Bygott (1979) and Nishida (1979) have drawn attention to the size and composition of the respective groups as determinants of arousing the males either to attack or flee.

The hypothesis that population pressure and drastic reduction of territorial space, due to increasing human encroachment on their habitat and deforestation, is responsible for the aggravation of chimpanzee ‘warfare’ (Goodall et al., 1979; Trudeau, Bergmann-Riss & Hamburg, 1981), has not been substantiated yet. Similarly, the hypothesis of abnormal pressures and unusual stresses introduced by artificial provisioning (e.g., Tanner, 1986; Power, 1991; Losco & Somit, 1995) has still to be confirmed.

From the individual-level-of-selection point of view, according to Bygott’s (1979) analysis, the chief advantage of collective territorial defense to a male chimpanzee is that he need be involved in very few potentially harmful confrontations with competitors from other communities. A group of males is a more powerful deterrent to intruders than a single one, since a group can inflict a severe or lethal attack with minimal risk to its members. Therefore “By merely accompanying other males on border patrols (which can be combined with foraging), an individual male can help to maintain his continued access to a large number of females. This model implies that there would be strong selection for males to be rapidly aroused to attack strangers, particularly males, on sight” (Bygott, 1979). Gang attacks on strange estrous females have not been recorded thus far. In contrast, Bygott continues, it might benefit males to attack strange females who were pregnant or had small infants, since by doing so they might destroy the offspring of competitor males and increase their own chances of genetic investment (which may also account for the infanticides observed). One major condition for the defense of a group territory, as well as collective hunting, is that...
males must cooperate to a certain extent. Cooperation depends on the strength of male bonding. Bonds should be strongest if males are incorporated into the male group at a relatively young age and if males are closely related (minimizing intermale competition for females). In chimpanzees, as we have seen, males indeed remain in their natal group, while the females transfer.

Goodall (1986) herself explains the chimpanzee proto-warfare in terms of the idiosyncratic pattern of chimpanzee territoriality and preadaptations common in chimpanzees and early humans. In three important ways, she contends, chimpanzee behavior does not comply with classical territoriality:

(a) Both at Gombe and Mahale it is the relative size and the composition of the two neighboring parties that determine the outcome of an encounter, rather than the geographic location;

(b) Chimpanzees have a large home range with considerable overlap between neighboring communities; and

(c) It is perhaps in the violence of their hostility towards neighbors that chimpanzees differ most from the traditional territory owners of the animal kingdom. Their victims are not simply chased out of the owners’ territory if they are found trespassing; they are assaulted and left, perhaps to die. Moreover, chimpanzees not only attack trespassers, but may make aggressive raids into the very heart of the core area of neighboring groups: “In the chimpanzee, territoriality functions not only to repel intruders from the home range, but sometimes to injure or eliminate them; not only to defend the existing home range and its resources, but to enlarge it opportunistically at the expense of weaker neighbors; not only to protect the female resources of a community, but to actively and aggressively recruit new sexual partners from neighboring social groups” (Goodall, 1986).

In order to maximize their mating opportunities, male coalitions do not attempt to monopolize females directly, but indirectly by means of the monopolization and ‘conquest’ of territory. A positive feedback loop of escalating intensity would then be established between successful conquest of territory, elimination of competitor groups by means of intimidation or violence, and the development of the male ‘gangs’ into true ‘warrior coalitions’. The amazing cognitive and affectional make-up of the chimpanzee might, then, partly be a spin-off of this ongoing evolution.

There is an amazing similarity to the situation among humans. The development of social structures, in which men join in discrete solidarity groups (fraternal interest groups) is regarded as a condition which favors the development of bellicose tendencies (Van Hooff, 1990; Boehm, 1992).

Otterbein & Otterbein (1965) have shown that in humans, feuding is most likely to develop among exogamous patrilineal groups with patrilocal postmarital residence. This arrangement ensures that closely-related males will remain coresident or live contiguously for life, while females are exchanged among various patrilineages or patriclans. They have characterized these groups as ‘fraternal interest groups’.

Granted that destructive warfare in its typical human form (organized, armed conflict between groups) is a cultural development, it nevertheless required preadaptations to permit its
emergence in the first place. The most crucial which Goodall identifies are cooperative group living, group territoriality, cooperative hunting skills, weapon use, and the intellectual ability to make cooperative plans. Another basic preadaptation was xenophobia: an inherent fear of, or aversion to, strangers, expressed by aggressive attack. Early hominid groups possessing these behavioral characteristics would theoretically have been capable of the kind of organized intergroup conflict that could have led to destructive warfare. Chimpanzees not only possess, to a greater or lesser extent, the above preadaptations, but they show other inherent characteristics that would have been helpful to the dawn warriors in their primitive battles:

(a) If the early hominid males were inherently disposed to find aggression attractive, particularly aggression directed against neighbors, as (at least some adolescent male) chimpanzees appear to do, this trait would have provided a biological basis for the cultural training of warriors.

(b) In humans cultural evolution permits pseudospeciation (Erikson, 1966). In its extreme form pseudospeciation leads to the ‘dehumanization’ of other groups, so that they may be regarded almost as members of a different species. This process, along with the ability to use weapons for hurting or killing at a distance, frees group members from the inhibitions and social sanctions that operate within the group and enables acts that would not be tolerated within the group. Thus it is of considerable interest to find that the chimpanzees show behaviors that bear strong resemblance to, and hence may be precursors to pseudospeciation in humans. First, their sense of group identity is strong; they clearly differentiate between ingroup and outgroup, between individuals who ‘belong to us’ and those who do not. This sense of group identity is, Goodall claims, far more sophisticated than mere xenophobia. The members of the Kahame chimpanzee community had, before they split, enjoyed close and friendly relations with their aggressors. By separating themselves, it is as though they forfeited their ‘right’ to be treated as group members – instead they were treated as strangers. Second, the patterns of attack strikingly differ from those utilized in typical intracommunity aggression: “The victims are treated more as though they were prey animals; they are ‘dechimpized’”.

Diamond (1992) wondered why these chimps are such inefficient killers compared to humans: “Chimps’ inefficiency as killers reflects their lack of weapons, but it remains surprising that they have not learned to kill by strangling, although that would be within their capabilities. Not only is each individual killing inefficient by our standards, but so is the whole course of chimp genocide. It took three years and ten months from the first killing of a Kahama chimp to the band’s end... “.

Two further aspects of chimpanzee behavior are of interest in relation to the evolution of behavior associated with human intergroup conflict: (a) In the chimpanzee, as in humans, cannibalism may follow intergroup conflict; and (b) Chimpanzees appear to possess the cognitive sophistication which is a prerequisite for the genesis of cruelty: they are capable to some extent of imputing desires and feelings to others, and they are almost certainly capable of feelings akin to (human) sympathy and empathy.

“...The chimpanzee, as a result of a unique combination of strong affiliative bonds between adult males on the one hand and an unusually hostile and violently aggressive attitude toward nongroup individuals on the other, has clearly reached a stage where he stands at the very threshold of human achievement in destruction, cruelty, and planned intergroup conflict. If
ever he develops the power of language – and, as we have seen, he stands close to that threshold, too – might he not push open the door and wage war with the best of us?” (Goodall, 1986).

Another category of explanations centers on a cost/benefit analysis of chimpanzee proto-warfare.

Emphasizing the principle that different behaviors may be adaptive under different circumstances, Manson & Wrangham (1987) note that chimpanzee intergroup raiding has been observed to occur only when the attackers belonged to a community substantially larger than the community containing the defenders.

“This suggests that chimpanzees conduct EIA [Exported Intergroup Aggression] in response to perceived intergroup strength differentials, although a complete model of this phenomenon is likely to be considerably more complex. Eventually, variation in the occurrence and intensity of human warfare may be explained rather completely via natural selection theory. This explanation will almost certainly refer, not to strength of selection for ‘aggression’ as a global trait, but rather to a cost-benefit model incorporating those features of the social and physical environments that cause individual contributions to varying levels of intergroup competition to be more or less effective means of increasing individual inclusive fitness”.

Manson & Wrangham (1991) base their explanation on the notions of ‘resource alienability’ and ‘(im)balance of power’, determining the cost/benefit ratio of the behavior: (intergroup) aggressive behavior has come to be viewed as a tactical option pursued when assessment indicates that it will be cost-effective, or, in other words, when the benefits sufficiently outweigh the inherent costs. The cost of severe aggression by chimpanzees appears to be unusually low, because, in contrast to the situation in aggression by other primates, chimpanzee victims are immobilized. This prompts the hypothesis that lethal attacks are promoted by an imbalance of power. Specifically, unrestrained attacks on opponents are favored merely because their cost is low. According to this hypothesis, long-term social bonds facilitate the formation of cooperatively attacking subgroups, and variation in subgroup size reduces the cost of damaging aggression to attackers with sufficient numerical superiority. The hypothesis predicts that (1) the cost to the aggressors will be low, (2) attacks will be restricted to occasions of overwhelming superiority, (3) potential victims will attempt to travel in large subgroups, and (4) attacks will occur whenever the opportunity arises.

In sum, evidence supports two influences on intergroup aggression by chimpanzees. First, attacks are lethal because where there is sufficient imbalance of power, their cost is negligible. Second, attacks are a male and not a female activity because males are the philopatric sex. This relationship conforms to Alexander’s (1989) proposal of the importance of male-male cooperation and female transfer, following earlier arguments by Bygott (1979), Goodall et al. (1979), Nishida (1979), and Wrangham (1979).

The relationship between male philopatry and predominantly male participation in intergroup aggression is explicable as follows (Ghiglieri, 1987): Across primate species male philopatry is closely associated with male-male cooperation (Pusey & Packer, 1987). Chimpanzee social organization probably evolved from a system in which both sexes were solitary because of the high cost of feeding competition. Males then became able to travel in pairs, although this was still inferior to solitary travel as a foraging strategy (Wrangham, 1987). But because singletons were then necessarily subordinate to pairs in mate competition, selection began to

Theoretically the ultimate benefit of intergroup aggression among chimpanzees is expected to be increased access by aggressive males to reproductively valuable females, via either incorporation of neighbors or encroachment on the territory of neighboring males.

Given the chimpanzee evidence, Manson & Wrangham (1991; cf. Wrangham & Peterson, 1996) propose that imbalance of power must have been an important factor favoring the evolution of damaging aggression in humans also and that, through variability in subgroup size alone, power imbalances may have favored lethal raiding even before the evolution of weapons.

Accordingly, Manson & Wrangham hypothesize that, among foraging humans, where crucial material resources are alienable, intergroup aggression will occur primarily over those resources, while where they are not it will occur over women.

Why does all this not apply to females? Why do not females raid for reproductive access to males? Why is coalitional aggression either absent or extremely rare in females? As we have seen, coalitions play an important role in male chimpanzee politics. To be sure, coalitions are not unknown to, or beyond the grasp of female chimpanzees, but females never seem to form coalitions for the purpose of communal violence. Why and whence this conspicuous difference between the sexes? Tooby & Cosmides (1988), whose approach predicts the striking asymmetry that exists between males and females in coalitional aggression, suggest some answers (elaborated in Ch. 4), which may be summarized as follows:

(1) Coalitional aggression evolved because it allowed participants in such coalitions to promote their fitness by gaining access to reproductive resources. For males, females are the limiting reproductive resource, and the ultimate benefit of multi-male coalitional aggression is increased access to females. Males can easily be induced to go to war, despite its lethal effects on many of them. Selection will favor participation in the coalitional aggression regardless of the mortality among the aggressors (within broad limits).

(2) Females, on the other hand, are rarely limited by access to males, so that the net reproduction of a coalition of females would drop in direct proportion to the number of females killed. In a curious fashion, males may be so ready to engage in coalitional aggression because it is reproductively ‘safer’ for them to do so. Females have more to lose, and less to gain, and such differences in consequences should be reflected in psychological sex differences in attitudes towards coalition formation and coalition-based aggression.

These considerations may be supplemented with the following:

In a cross-cultural study of female participation in warfare, Adams (1983) presents evidence that women are excluded from participation in warfare where there is patrilocal residence, internal warfare, and community exogamy. Adams argues that under these conditions a woman will likely have a conflict of interest – her husband may be fighting with her father and brothers. Husbands will have reason to fear their wives’ knowledge of war plans and therefore will prevent them from handling weapons and obtaining such knowledge. The obverse, of course, is that matrilocals societies (which tend to lack community exogamy and
tend to have external warfare; see Ember & Ember, 1971; Adams, 1983) are unlikely to
generate a conflict of interest in women and therefore are more likely to allow women to
participate in warfare. Adams’s explanation of female participation in intergroup aggression
is different from Manson & Wrangham’s, but the results for humans parallel the results for
nonhuman primates (Ember, 1991).

Irons (1991) ventured the thesis that human females participate in warfare by proxy in letting
the males do the fighting for them.

In anthropology textbooks one may find many variants of the so-called ‘relative
expendability’ argument as an explanation of why males have monopolized violence in
human societies. The ‘relative expendability’ argument goes something like this: “Because
fewer of them are needed to produce and maintain offspring, from a population maintenance
perspective, males are more expendable than females”.

But, as Rodseth et al. (1991) observe, this argument is vulnerable to all the criticisms of group
selection first articulated by G.C. Williams (1966). And even if a ‘relative expendability’
argument were evolutionarily sound, it could not account for the fact that males seem equally
expendable in savanna baboons and many other primate groups, yet females in these groups
regularly engage in violent competition with other females.

All these attempts to explain chimpanzee proto-warfare are, not surprisingly, far from being
mutually exclusive, rather they emphasize different aspects and facets of the same intriguing
puzzle. Virtually all theories converge in their final conclusion: the ultimate rationale of male
raiding is enhanced access to ‘nubile’ females. And ecological selection pressures, sexual
selection and kin selection have fueled this process.

Chimpanzee Hunting and ‘Warfare’

Of all the ‘higher’ primates, only human beings and chimpanzees hunt and eat meat on a
regular basis. Significantly, males do most or all of the hunting. For chimpanzees, meat is not
only another way to get nutrients like fat and protein, but a means to make political bonds and
gain access to sexually receptive females (Stanford, 1995). Kortlandt (1972) suggested that
hunting was a form of social display in which male chimpanzees revealed their prowess to
other members of the community.

Perhaps, Van Hooff (1990) speculates, the development of coordinated male between-group
aggression has paved the way for the development of such coordinated hunting, not only in
chimpanzees but also in the hominid/human evolutionary trajectory.

Eibl-Eibesfeldt (1975) already asserted that motivationally, hunting behavior in chimpanzees
has probably been derived from intraspecific aggression.

The usual argument is from hunting to warfare, using the social carnivore analogy.
Cooperation in a hunt, collaboration in rearing offspring, helping group-members, and
ingroup loyalty combined with merciless outgroup enmity – these are all characteristics
highly developed in the social carnivores. The suggestion is that by the human transition to a
more ‘wolf-ish’ and hunting lifestyle, these same characteristics have been strongly enhanced.
In this scenario, the development of hunting was at the roots of the development of warlike behaviors.

The recent observations of chimpanzee raiding suggest to Van Hooff that the development may well have gone the other way around. The cooperation in male between-group conflict may have brought about abilities and orientations which, subsequently, have allowed the development of systematic cooperation in hunting. Of course, a subsequent interaction between both processes might have occurred: hunting tools and stratagems might also prove useful in battle against conspecifics, and vice versa. A tactical refinement acquired in one functional context can be transferred to the other. If such an improvement increases the efficiency of this behavior pattern, then it might also shift the balance of costs and benefits. For example, a group which has developed a method of attack involving less personal risk, will come more easily to a decision to choose (pre-emptive) attack as a means of ‘conflict-resolution’ (Van Hooff, 1990).

In this context, it may be significant that in the pygmy chimpanzee or bonobo (Pan paniscus), who exhibits only mild intergroup antagonism, males do not develop strong bonds and are not habitually cooperative hunters (Badrian et al., 1981). Significantly, bonobos neither hunt monkeys cooperatively nor wage war (Wrangham & Peterson, 1996). Kano (1987) made the intriguing suggestion that in the pygmy chimpanzees the ‘in-group feeling’ among females is very strong, and therefore aggressive male expansion of territory is not connected with an increase in available females, and thus does not pay off. Wrangham & Peterson (1996) suggest that female power is the secret to male gentleness for intragroup interactions, while it is the food distribution that enabled this species to nonviolent intergroup interactions.

At this point some caveats are in order. First, nonhuman primate models applied to hominids are problematical for a number of reasons, not the least of which is the arbitrariness involved in the selection of the species to serve as the model. Suppose, for example, that we were to single out the bonobo as a model for early hominid social organization. Cooperative as well as competitive interactions among males would have been low-level, and would probably not include cooperative hunting, nor the Machiavellian and opportunistic coalitional maneuvering encountered in the other Pan species. Intergroup agonistic behavior would have consisted of visual and vocal displays and mild threats uttered from a safe distance, after which the bonobo-hominid braves would return to the home group and try out all coital positions described in the Kama Sutra for reassurance and pleasure.

There is, furthermore, no simple linear scale of complexity from prosimians, via monkeys and the great apes, leading to the human condition. The primates as a group have diverged widely, evolving in different directions. The nonhuman primates do not represent steps toward the evolution of humans, but rather, as Scott (1969), among many others, observed, diverging pathways from a common ancestor.

Finally, the landscape of hominid evolution is far richer and much complex than a simple linear view – many researchers view human evolution as “a long corridor where chimpanzees enter at one end and modern hunter-gatherers exit at the other” (Tooby & DeVore, 1987) – can accommodate. It is more likely to be a discrete series of branches, stages, and chronospecies. A feature, such as hunting or warfare, that seems to be an appropriate major adaptation for one chronospecies may have been completely inappropriate for others (for this line of argumentation see Tooby & DeVore, 1987).
With these considerations in mind, one should be able to appreciate the specific differences as well as the communalities in the behaviors discussed.

Boehm (1992) systematically enumerated the similarities as well as the differences between chimpanzee and human IAB. Among the similarities are: (a) Both species develop fraternal interest groups that are subject to divisive internal quarrels; (b) Effective management of internal conflicts helps to make possible the formation of community-wide macro-coalitions; (c) Acting as macro-coalitions both species go raiding for sustenance and breeding partners, and sometimes kill their enemies.

Among the differences Boehm notes: (a) Chimpanzees do not seem to have anything resembling the blood feud; nor do they engage in all-out warfare, in which the mobilized males of one group attack another group as a whole, or in which two groups deliberately meet on the battlefield; (b) Communities of humans often ‘manage’ such intensive external conflicts by making external alliances that balance power, and by ending their wars with peace treaties; and (c) Human warriors may be moved to engage in mass combat by a combination of patriotic ideology and negative sanctioning of cowards, two features of macro-coalitional competition that chimpanzees lack.

Some Conclusions

1. The main conclusion emerging from this chapter, namely that Intergroup Agonistic Behavior (IAB) is an adaptive behavior in a number of nonhuman (especially primate) species may sound disconcerting for many readers, yet this conclusion is inevitable given the evidence. The major implication of this conclusion is that a whole body of theories which regard IAB as erratic, or even pathological, behavior can be put quietly to rest.

2. The overwhelming majority of gregarious and social mammalian species does not have Intergroup Agonistic Behavior in its behavioral repertoire. For a good number of species the cost/benefit ratio of IAB precludes the evolution of such behavior anyway, but for an as yet unknown number of species it is less easy to explain why they lack this behavior, which would be highly profitable as a high-risk/high-gain strategy. It is likely that they lack the requisite social and cognitive (domain-specific) skills, such as a coalitional psychology, to cooperate for the sake of concerted competition.

3. In a number of the species reviewed, in which intergroup aggression is serious and concerted business, there seems to be an intricate relationship between intra- and intergroup processes. It even seems, particularly in the chimpanzee case, as if relatively ‘peaceful’ intragroup relations are conditioned by, and interdependent on, some level of xenophobia (or, rather, proto-ethnocentrism, a “tendency toward closure of the social networks” [Wrangham, 1987]) and hostility toward outgroups, as if it were an export-of-conflict mechanism. This interrelationship will be discussed more fully in Ch. 6 on kin selection and ethnocentrism. Note, however, that intergroup antagonism is no guarantee for suspending intragroup competition, and not necessarily alleviates tense and ambivalent male-male relationships.

4. The role of females in primate intergroup agonistic behavior as well as in human primitive warfare has been, until very recently, seriously underestimated. War, as ‘the great business of mankind’ has been mainly conducted by males – with females considered to be the active or
passive victims of this male preoccupation – but the (reproductive) interests of females in matters of war and peace are at least as great as those of males.

5. Having established at least the possibility of phylogenetic precursors in (or phylogenetic continuities between nonhuman and) hominid intergroup antagonism, I am quite aware that many questions on nonhuman IAB have been left unanswered (To mention only one: Is there any parallel between the selection pressures and ecological conditions underlying both sociality and warfare in the social insects and humans?) This is not because these problems are not vexing and intriguing in their own right, but simply because they would detract us too much from, or are less relevant to, the exploration of our main theme.