The origin of war
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3 Nonhuman Intergroup Agonistic Behavior and 'Warfare'

3.1 Intergroup Agonistic Behavior: Introduction

In this chapter 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. Such a circumscriptive definition includes the case of e.g., the single hyena of pack A who is chased and attacked by several members of pack B (Kruuk, 1972), but it obviously excludes e.g., the rape attacks of single male orang-utans on females with young (Galdikas, 1979; Mackinnon, 1971, 1979; Pitcairn, 1974).

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 (IAB). Furthermore, if it is stipulated that warfare involves armed conflict (in the sense of the use of artifactual weapons), there is no point in calling animal IAB 'warfare'. Such a distinction is considered trivial at the moment, for the sake of
argument, since I am interested in the 'why' of such behavior more than in the 'how'.
As will be seen, 'IAB' is a rather heterogeneous category in which one might distinguish such dimensions as unstructured vs. concerted, lethal vs. nonlethal, skirmish-like vs. ambush-like, spontaneous vs. premeditated, and possibly others.
I shall first epitomize the literature on animal IAB, and add a number of more or less tentative conclusions. Subsequently, I shall single out and analyze in some more detail two distinct patterns of IAB which I surmise to be basic in the sense that all other forms of IAB can be considered to be intermediate forms, and which are especially relevant to our main concern: hominid warfare. And lastly, I shall discuss the proximate and ultimate mechanisms involved in nonhuman IAB, and base some general conclusions on these observations. The occasional anthropomorphisms in the text are deliberately used and intended as such.

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). 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 - it is a convenient linguistic shorthand that bridges the gap between the level of the individual and the level of the gene. 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. E.O. Wilson (1978) adds the reduction of freedom to the reduction of genetic fitness in his definition, but some may consider the term ‘freedom’ in the context of animal behavior to be rather meaningless. Such a definition, centering on the reduction of fitness of the competitor or opponent, deviates prima facie from the usual, sometimes cumbersome, definitions of the social sciences (centering on harming, injuring, damaging, destruction, or ‘delivering noxious stimuli’; see van der Dennen [1980] and § 5.2.7 for an extensive review), but it is no less valid or operationally useful. According to Barash (1977), aggression takes place when individuals interact with each other such that one of them is induced to surrender access to some resource important to its fitness. The exact forms of aggression range from intimidating displays and threats to actual fights. Organisms are expected to exert themselves to acquire important resources or enlarge their supply, thereby enhancing their fitness. They are as much expected to resist the loss of important resources, thereby avoiding decrements to their fitness. "Accordingly, animals may respond to aggression by threatening back, fighting back, and, occasionally, signalling their submission and/or running away. All these encounter patterns are subsumed under the term ‘agonistic behavior’” (the term ‘agonistic behavior’ was introduced by Scott & Fredericson in 1951). 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, kronism 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. The evolutionary rationale has been elaborated by Hamilton (1971), Maynard Smith & Price (1973), Maynard Smith (1974, 1978), and Parker (1974), to mention only a few of the pioneers of the game-theoretical analysis of aggression: 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 or tactical option pursued when assessment indicates that it will be cost-effective in the competition for material and/or reproductive resources (E.O. Wilson, 1975; Dawkins, 1976; Durham, 1976; Geist, 1978; Schuster, 1978; Popp & DeVore, 1979; Borgia, 1980; Fry, 1980; Murray & Gerrard, 1984; Chagnon, 1988; Daly & Wilson, 1988; Alexander, 1989; Low, 1990; Manson & Wrangham, 1991; a.o.). (In order to avoid misunderstandings, it may be important to point out that the proximate model of aggression corresponding with the ultimate reasoning presented above is not a return to some 'instinct' or 'drive' conceptions of aggression: See Ch. 5).

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; see also Hausfater & Hrdy, 1984; 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 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 at any given point in time. 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 favorable strategy. 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 of 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 lose); 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. The fully complicated - yet, easy to understand once the underlying evolutionary rationale and logic are grasped - answer has been expressed most lucidly as follows by Low (1990):

Mammalian aggression is sexually dimorphic. An analysis of coalitions in non-humans makes clear that, compared to females, males tend to form coalitions that are riskier, more aggressive, and more often among non-relatives. 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. The return curve for reproductive success gained per unit of resources or status acquired differs for mating and parental effort. Mating effort, typical of mammalian males, has a large set-up cost; then the curve may rise steeply, for additional matings cost relatively little. For example, a red deer male, even to try for a first mating, must grow large (involving a cost of delayed maturation), grow antlers, and fight for dominance and control of good feeding grounds. The initial cost is great; the cost associated with each individual mating is small. For mammalian mothers, each offspring costs approximately as much parental effort as any other, and the maximum possible number of offspring is likely to be lower than for males. Males, while having the same average number of offspring as females, 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. This difference, of course, is what prompted Darwin (1872) to treat sexual selection differently from other selection, even though functionally it is identical. Ross’s (1983) observation that women’s politics and conflict over resources tend to be at the familial and neighborhood level, while men’s conflicts tend to have a broader scope, is therefore hardly surprising; similarly, the rarity of women warriors is predicted. Through evolutionary history, then, men have been able to gain reproductively by 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: rats, red deer stags, elephant seal bulls, mountain sheep males, baboons, and so on, fight over dominance, females and territory). Some other species, especially nonhuman primates and carnivores, also exhibit intergroup agonistic behavior, which may be more or less collective and more or less orchestrated.
3.2 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 especially E.O. Wilson [1975] for examples).

In primate species with multimale groups, organized defense is the rule. As E.O. Wilson (1975) observed: "The defensive maneuvers of a troop of large terrestrial primates is one of the natural world’s most impressive sights".

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 agoutis mobbing snakes (Smythe, 1970), and baboons and chimpanzees frenziedly attacking - and some daredevils even beating up - a leopard model (Kortlandt & Kooij, 1963; 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 (Altmann, 1956). 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. As Marler (1959) pointed out, the mobbing calls of different bird species are strongly convergent. Thus alerted birds are able to fly toward the predator being harassed, and sizeable mobs are quickly assembled. Furthermore, different species respond to each
other’s calls, since all make nearly the same sound, and mobbing becomes a cooperative venture. Detailed examples can be found in the monograph by Curio (1976) and in E.O. Wilson (1975), who states that the mobbing of some species has a vicious intent, and can result in severe injury or death to the predator. Gersdorf (1966), for example, described how starlings launched massive attacks against sparrow hawks in Germany, in which the hawks were sometimes killed.

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. Red squirrels are said to have engaged in a sanguinary conflict, emasculating and driving the gray squirrels out of New England in 1935 (Jackson, 1935).

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/belligerens*.

### 3.2.1 How Tiny Organisms Wage Huge Battles

Even among ants ‘war’ is mainly practiced by one taxonomic group, comprising only a few species among the tens of thousands known to myrmecologists. They are the harvester ants, inhabitants of arid regions where there is little to pick up during the dry months. Accordingly they collect the seeds of various grasses at the end of the growing season and store them in special underground granaries in their nests. It is these reserve supplies which are the object of ant warfare. The inhabitants of one nest set out deliberately to raid the supplies of another group (Huxley, 1944).

According to Huber (1861), Forel (1874), McCook (1879) 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 evolution.
civilization, when he began to accumulate stores of grain and other forms of
wealth (See § 5.2.3).

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. When similarly provoked conflicts occur between closely related
species, the term ‘war’ may perhaps be extended to them. 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 (E.O. Wilson, 1971, 1975). For further details one may consult

According to E.O. Wilson, territorial fighting among mature colonies of both
same and differing species is common but not universal in ants. It has been
recorded in very diverse genera of which the following form only a partial list:
Pseudomyrmex, Myrmica, Pogonomyrmex, Leptothorax, Solenopsis, Pheidole,
Tetramorium, Iridomyrmex, Azteca, Anoplolepis, Oecophylla, Formica,
Lasius, and Camponotus.

Huber’s (1861) observation of a great war originating in predation 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... In these curious wars the tactics of the ants is always free
and courageous. Without doubt they sometimes resort to ambushes
but only in skirmishing. In the great wars, they attack with open
force and without recourse to ruse. They struggle, moreover, with
extraordinary tenacity and it is more easy to tear them to pieces than
to make them prisoners. Indeed when a combatant ant has been

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sectioned in the middle of the body, the anterior part, the head and thorax separated from the abdomen still carry in their protection the menaced nymph. 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.

The most dramatic battles known within ant species are 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 $6\frac{1}{2}$ 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.

Territorial ‘wars’ between colonies of different ant species occur only occasionally in the cold temperate zones. Colonies of *Myrmica* and *Formica*, for example, sometimes overrun and capture nest sites belonging to other species of the same genus (Brian, 1952; Scherba, 1964). By contrast, intense interspecific violence is very common in the tropics and warm temperate zones. Certain pest species, particularly *Pheidole megacephala*, *Solenopsis invicta*, and *Iridomyrmex humilis*, are (in)famous for their belligerency and destructiveness. They attack native ant faunas wherever they have been introduced. They even go so far as to totally annihilate some of the species, especially those taxonomically and ecologically closest to them.

Some of the battles between ant species are epic in their proportions, and they may continue for several days or even weeks. E.S. Brown (1959), for example, has provided an account of a prolonged struggle between colonies of the introduced African ant *Anoplolepis longipes* and the defending phalanges of two native species, *Oecophylla smaragdina* and *Iridomyrmex myrmecodiae*, in the Solomon Islands.

Territorial competition for food, involving fighting between nests in red wood
ants belonging to the *Formica rufa* group has recently been much investigated (e.g., Mabelis, 1979, 1984). Le Moli & Parmigiani (1981) have demonstrated that *F. lugubris* is likely to attack 'alien' ants belonging to other species, e.g., *F. cunicularia*. Such combat generally ends in the death of the 'intruders'. Meetings of workers of wood ants (*F. polyctena*) also often result in an aggressive encounter. Locally, the number of fighting ants can increase rapidly due to storage and transfer of information about the battle: Ants can remember the location of the battlefield for a long time and can attract the attention of other workers by means of scent substances and excitable behavior (Mabelis, 1979; 1984). As a result, a 'war' can develop to the point at which thousands of ants are involved. The number of casualties may be very high; a great many of the workers of a particular nest may be killed and sometimes a whole population is exterminated. Casualties are dragged to the warring nests and they will be consumed there (Mabelis, 1979; 1984).

Le Moli & Parmigiani (1981; 1982) questioned whether (inter- and intraspecific) aggressive behavior in Red wood ants is an expression of predation or an expression of competition. According to Mabelis (1984) 'warfare' in this species has both aspects; there seem to be no essential differences between predatory and aggressive behavior.

There can be no question, E.O. Wilson (1975) 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. 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. Thus, if it is even of temporary selective advantage for individuals of a given species to be cannibals, at least a moderate probability exists that the entire species will evolve toward cannibalism" (E.O. Wilson, 1975).
3.3 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. Collective defense is exemplified by avian mobbing of raptors, as we have seen, and collective territorial defense in some other bird species. White-fronted bee-eaters (*Merops bullockoides*) (Hegner, Emlen & Demong, 1981), Florida scrub jays (*Aphelocoma c. coerulescens*) (Woelfenden & Fitzpatrick, 1984, Mumme, 1992) and green woodhoopoes (*Phoeniculus purpureus*) (Ligon & Ligon, 1982) concertedly defend breeding communities. Cooperative territorial defense has also been reported recently in the Australian magpie (*Gymnorhina tibicen*) (Farabaugh, Brown & Hughes, 1992), and the white-browed sparrow weaver (*Plocepasser mahali*) (Wingfield & Lewis, 1993). In the latter species, 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 3.1):

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<th>Table 3.1: Animal Intergroup Agonistic Behavior</th>
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<tbody>
<tr>
<td><strong>Turdoides squamiceps</strong> (Arabian babbler) Zahavi, 1987;</td>
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<td><strong>Gallinula mortierii</strong> (Tasmanian native hen) Putland &amp; Goldizen, 1998; Wrangham, 1999;</td>
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<tr>
<td><strong>Tursiops truncatus</strong> (dolphin) Connor, 1988; Connor, Smolker &amp; Richards, 1992;</td>
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<tr>
<td><strong>Helogale undulata</strong> (dwarf-mongoose) Low, 1993; Rasa, 1985, 1986; α♀</td>
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<tr>
<td><strong>Suricata suricatta</strong> (slender-tailed meerkat) No reference (TV-documentary);</td>
</tr>
<tr>
<td><strong>Otaria byronia</strong> (sea lion) Campagna, le Boeuf &amp; Cappozzo, 1988;</td>
</tr>
<tr>
<td><strong>Gazella gazella gazella</strong> (mountain gazelle) Geffen, Perevolotsky, Geffen &amp; Yom-Tov, 1999; α♀</td>
</tr>
<tr>
<td><strong>Canis lupus</strong> (wolf) Harrington, 1984, 1987; Mech, 1966 et seq.; Mech et al., 1998; Murie, 1944; Wrangham, 1999; Zimen, 1978; α♀</td>
</tr>
<tr>
<td><strong>Lycaon pictus lupinus</strong> (Cape hunting dog) von Kühme, 1965; van Lawick &amp; van Lawick-Goodall, 1971; α♀</td>
</tr>
<tr>
<td><strong>Acynonyx (Cynaelurus) jubatus</strong> (cheetah) Caro &amp; Collins, 1986; Frame &amp; Frame, 1981;</td>
</tr>
<tr>
<td><strong>Hapalemur griseus</strong> (gentle lemur) Nievergelt, Mutschler &amp; Feistner, 1998;</td>
</tr>
<tr>
<td><strong>Lemur catta</strong> (ring-tailed lemur) Budnitz &amp; Dainis, 1975; Hood &amp; Jolly, 1995; Jolly, 1966, 1972;</td>
</tr>
</tbody>
</table>
Klopfner & Jolly, 1970; Sussman & Richard, 1974; *

_Lemur [Eulemur] fulvus_ (brown lemur) Pollock, 1979; Sussman & Richard, 1974; *

_Propithecus verreauxi_ (white or Verreaux's sifaka) Jolly, 1966; Richard, 1977; Sussman & Richard, 1974; *

**Indri indri** (indri) Pollock, 1975, 1979; *

_Saguinus imperator_ (emperor tamarin) Terborgh, 1983; *

_Saguinus fuscicollis_ (saddleback tamarin) Terborgh, 1983; *

_Saguinus mystax_ (moustached tamarin) Garber, Pruetz & Isaacson, 1993; Heymann, 1996;

_Callicebus moloch_ (dusky titi) Mason, 1966, 1968; Robinson, 1979, 1981; Robinson, Wright & Kinzey, 1987; *

_Saimiri sciureus_ (squirrel monkey) Baldwin & Baldwin, 1976; Candland et al., 1978; Castell & Ploog, 1967; Ploog, 1998; Terborgh, 1983;


_Alopiatta senicus_ (red howler monkey) Richard, 1985; Rudran, 1979; Sekulic, 1982a,b,c; *

_Alopiatta fuscus_ (brown howler monkey) Chiarello, 1995;

_Cebus capucinus_ (white-faced capuchin) Klein, 1974; Oppenheimer, 1968;

_Cebus apella_ (brown, black-capped or tufted capuchin) Terborgh, 1983; *

_Cebus albifrons_ (white-fronted capuchin) Terborgh, 1983; *

_Cebus olivaceus_ (wedge-capped capuchin) Robinson, 1988; *

_Ateles belzebuth_ ([long-haired] spider monkey) Klein, 1974; Klein & Klein, 1975; Richard, 1985;

_Brachyteles arachnoides_ (muriqui or woolly spider monkey) Strier, 1992, 1994; Wrangham & Peterson, 1996;

_Lagothrix lagothricha_ ([Humboldt's] woolly monkey) Durham, 1975; Nishimura & Izawa, 1975; *


_Sugiyama et al., 1965; Vogel, 1975; Yoshida, 1968; *


_Presbytis pileata [Trachypithecus pileatus]_ (capped langur) Stanford, 1991;

_Presbytis cristata [Trachypithecus cristatus]_ (silvered leaf monkey or lutong) Bernstein, 1968;

_Presbytis senex [Trachypithecus retulus]_ (purple-faced langur) Rudran, 1973;

_Presbytis aygula_ (Sunda Island leaf monkey) Ruhiyat, 1983; *

_Presbytis potenziani_ (Mentawai langur) Tilson & Tenaza, 1976; *

_Presbytis thomasi_ (Thomas's [leaf] langur) Steenbeek, 1999;


_Cerocebus [Lophocebus] albigena_ (crested or gray-cheeked mangabey) Kinnaird, 1992;


_Cercopithecus ascanius_ (redtail monkey) Struhsaker, 1978, 1980; Struhsaker & Leland, 1979; *

_Cercopithecus mitis_ (guenon or blue monkey) Aldrich-Blake, 1970; Lawes & Henzi, 1995;

_Rudran, 1978; Struhsaker, 1969; Struhsaker & Leland, 1979; *

_Cercopithecus neglectus_ (De Brazza’s monkey) Gautier-Hion & Gautier, 1978; *

_Erythrocebus patas_ (patas monkey) Chism, Rowell & Olson, 1984; *


_Papio cynocephalus_ (yellow or savanna baboon) Altmann & Altmann, 1970; Byrne, Whiten &
Henzi, 1987; Cheney & Seyfarth, 1977; Richard, 1985; Shopland, 1982; σρ*.

*Papio anubis* (olive baboon) Hamilton, i.p.; van Hooff, 1990; Packer, 1979; Ransom, 1981; Rowell, 1966 et seq.; Strum, 1975 et seq.;


*Macaca radiata* (bonnet macaque) Rahaman & Parthasarathy, 1969; Simonds, 1965; Sugiyama, 1971; *

*Macaca sylvanus* (barbary macaque) Deag, 1973; Mehlan & Parkhill, 1988;

*Macaca fascicularis* (kra or long-tailed or crab-eating macaque) Angst, 1975; Davis, 1962; Furuya, 1965; Kurland, 1973; Shirek-Ellefson, 1968; σρ*

*Hylobates lar* (whitehanded gibbon) Carpenter, 1940, 1974; Chivers & Raemaekers, 1980; Ellefson, 1968, 1974; σρ*

*Hylobates klossii* (Kloss's gibbon) Tenaza, 1975; Tilson, 1981; σρ*

*Hylobates agilis* (agile or dark-handed gibbon) Gittins, 1980; σρ*

*Hylobates moloch* (moloch or silvery gibbon) Kappeler, 1984;

*Hylobates pileatus* (piledated or capped gibbon) Brockelman & Srikosamata, 1984; σρ*

*Hylobates (Symphalangus) syndactylus* (siamang) Chivers, 1974;


*Pan troglodytes* (chimpanzee) Boesch & Boesch, 1999; Brewer, 1978; Bygott, 1974, 1979;


Legend:

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

σρ* = Both sexes actively participate in the conflict *(vide infra).*

In brackets [*] the names according to the recent primate taxonomy by Groves (1993).

3.4 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) unhesitantly 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 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, 1973). 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 (Bertram, 1976, 1978; Packer, 1986; Packer & Pusey, 1982, 1983, 1984). Coalitions of male cheetahs driving smaller coalitions away from breeding females may inflict fatal injuries (Frame & Frame, 1981; Caro & Collins, 1986).

The following observations pertain specifically to the nonhuman primate species in Table 3.1.

1. As may be gathered from the Table, the majority of species in which IAB has been documented belong to the primate order (containing both prosimians and 'true' primates: the monkeys and apes). The intergroup behavior of primates is extremely variable - both inter- and intraspecifically - and ranges from very relaxed and 'peaceful' to lethal raiding.

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; McKenna, 1982; Cheney, 1983, 1987).

Among primates, exclusive use of space is generally maintained by (a) site attachment and avoidance of the ranges of neighboring groups (mutual proximity-dependent avoidance); (b) site-dependent aggression and regular definition of the conventional location of boundaries; 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 (Kinzey & Robinson, 1983). In contrast, Callicebus moloch has been described as 'territorial' (Mason, 1966, 1968) 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 (Robinson, 1979, 1981; Robinson, Wright & Kinzey, 1987).

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; King, 1980). 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 (e.g., bonnet macaques: Sugiyama, 1971; baboons: Hall, 1964; DeVore & Hall, 1965; Anderson, 1981). 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.

Also groups of squirrel monkeys, woolly monkeys, brown capuchins, rhesus macaques, and Barbary macaques are occasionally observed to mingle peacefully in the same feeding tree, water hole, or sleeping site, even though long-term associations are rare.

Some non-territorial species have evolved loud calls (‘duetting calls’) that aid in the regulation of intergroup spacing and mutual avoidance (Cheney, 1987).

In contrast, when groups defend all or part of their home ranges, most intergroup interactions are characterized by aggression rather than by mutual avoidance. Friendly interactions (play, grooming, copulation) between members of different intraspecific groups do, however, occur in both territorial and nonterritorial species (Cheney, 1987).

When two or more groups of primates meet, the resulting behavior may range from complete fusion of the groups (no agonism), via threats and displays, fights and chases, to outright killing. Typical outcomes of primate group encounters in escalating order of antagonism (Eberhart & Candland, 1981) are:

<table>
<thead>
<tr>
<th>Description</th>
<th>Characteristic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Complete Fusion</td>
<td>Groups coalesce permanently, with restructuring of social relations (e.g., rhesus monkeys: Bernstein, Gordon &amp; Rose, 1974).</td>
</tr>
<tr>
<td>Fission-Fusion</td>
<td>Groups aggregate and interact, but subsequently diverge (e.g., mountain gorilla: Schaller, 1963).</td>
</tr>
<tr>
<td>Indifference</td>
<td>Groups in proximity, but appear indifferent to, or ignore each other (e.g., Himalayan langurs: Sugiyama, 1976).</td>
</tr>
</tbody>
</table>
Mutual Avoidance Coordination of range use such that groups seem to avoid contact (e.g., prosimians: Sussman & Richard, 1974; Owl monkeys: Wright, 1978).

Unilateral Avoidance Avoidance or displacement of one group by another (e.g., baboons: Nash, 1976; rhesus: Gabow, 1973; Japanese macaques: Kawanaka, 1973).

Mild Threat Groups engage in gestural, locomotor, or vocal displays or threats (e.g., squirrel monkeys: Baldwin & Baldwin, 1976; bonobo: Nishida & Hiraiwa-Hasegawa, 1987).

Intensive Threat High intensity threats involving chases, physical contact between animals is rare (e.g., Kloss’s gibbon: Tenaza, 1975).

Ritualized Contact Aggressive physical contact between groups, but serious injury occurs rarely (e.g., black-and-white colobus: Schenkel & Schenkel-Hilliger, 1967).

Injurious Contact Severe aggressive contact, with injury or death in both groups (e.g., cercopithecines: Struhsaker, 1969).

Killing Death of one or more animals in one group (e.g., squirrel monkeys: Candland et al., 1978); chimpanzees (§ 3.8).

2. 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 in the sense of defended spatial exclusiveness (Crook, 1968; Rowell, 1972; Schuster, 1978; Scott, 1969; Vine, 1973). Rather, there is some overlapping of foraging ranges in most studied species of Cercopithecoidae and Ceboidea. Troops of rhesus (Southwick, 1962; Southwick et al., 1965), langurs (Sugiyama et al., 1965; Ripley, 1967), howlers (Southwick, 1962; Carpenter, 1965), and Japanese macaques (Kawanaka, 1973) avoid contact with each other when approaching the overlapping zones. Adjacent social groups in the majority of colobines generally interact aggressively (Struhsaker & Leland, 1987), with adult males usually the most aggressive and frequent participants. In most populations of *Presbytis entellus*, adult females (Ripley, 1967), as well as youngsters (Hrdy, 1977) may play prominent roles in intergroup fights. In at least one population of this species, however, neighboring groups were extremely tolerant of one another (Jay, 1965).

Little is known yet about bonobo intercommunity encounters. Encounters are mostly avoided, but when they occur they appear mildly antagonistic, ranging from nonlethal fighting (no observation has been made of participants killed in intergroup fights) to peaceful mixing in the border area, and mainly confined to adult males giving branch-dragging displays. There appears to be intergroup dominance attenuating agonistic contacts (Kano, 1987; Kitamura, 1983; Nishida & Hiraiwa-Hasegawa, 1987).

Home range size is influenced by both dietary requirements and the spatiotemporal distribution of food (Cheney, 1987; Clutton-Brock & Harvey, 1977). 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 (See § 1.3.8). 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.
Interspecific joint-territoriality sometimes occurs despite its costs. For
example, Peres (1992) described the joint-territorial behavior of saddleback
tamarins (*Saguinus fuscicollis*) and moustached tamarins (*S. mystax*).
Intergroup interactions imposed severe energetic costs on these monkeys,
resulting in greater proportions of time spent in energetically expensive or
negative activities, such as moving to boundaries, displaying to, and chasing
nongroup members, allowing less time for foraging.

3. The agonistic repertoire in these encounters ranges from vocal and gestural
displays, bluffing and intimidation, via threats, chases, ‘pitched battles’ to
‘deliberate’ killing (*vide infra*). The level of agonism in macaques depends on
the previous history of the troops, familiarity of the members, rank of the
troops, and location of the encounter (Chapais, 1983; Ciani, 1986; Hausfater,

4. Facilitating and/or aggravating conditions of IAB in primates include:
extreme crowding and population density due to e.g., areal reduction,
competition for food at artificial feeding sites and other rather ‘pathological’
conditions such as disruption caused by human interference (Ciani, 1986;
Kawanaka, 1973; Kummer, 1968; Mitani & Rodman, 1979; Nagel & Kummer,
1974; Ripley, 1967; Singh, 1969; Southwick, 1969; Southwick, Beg & Siddiqi,
1965; Southwick, Siddiqi, Farooqi & Pal, 1974, 1976; Sugiyama, 1967; Wilson
& Boelkins, 1970; Yoshiha, 1968), which is generally substantiated by reports
on zoo massacres (Hall, 1964; Kummer, 1957; Kummer & Kurt, 1965;
Reynolds, 1961; Russell & Russell, 1968; Zuckerman, 1932). In chimpanzees
agonistic intergroup encounters increase when the balance of dominance gets
out of order (Itani, 1982; de Waal, 1982 et seq.). These observations are in
general agreement with E.O. Wilson’s (1975) concept of ‘behavioral scaling’.

5. 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,
residents 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 moustached tamarins too (Garber, Pruett & Isaacson, 1993). These authors found no evidence that the tamarins patrolled range borders.

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) in 80% and physical fights in 50% of the cases (Harcourt, 1978; Stewart & Harcourt, 1987). Severe wounding (Harcourt, 1978) and probably death (Baumgartel, 1976) of adult males can result. Infanticides may occur during intergroup encounters (Fossey, 1979, 1981). In another population (that of Kahuzi) intergroup interactions with fierce displays but no physical violence were reported by Yamagiwa (1983).

6. For some primate species agonistic intertroop or intercommunity encounters may be highly attractive (at least for some individuals, mostly young males) (Bygott, 1979; Ellefson, 1968; Fossey, 1979; Goodall, 1986; Ripley, 1967; Morrison & Menzel, 1972;), and confrontations may be actively sought and provoked (which suggests intrinsic motivation: They seem to be 'spoiling for a fight') (vide infra). For the almost exclusive involvement of subadult and adult males in many Old World species, see: Cheney, 1987; Ciani, 1986; Deag, 1973; Goodall et al., 1979; Koford, 1963; Marsden, 1968; Neville, 1966; Rahaman & Parthasarathy, 1969; Southwick, 1962; Sugiyama, 1960; Vessey, 1968; A. Wilson, 1969.

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 (Smuts, p.c.). These represent extreme examples of female involvement in intergroup conflicts, but they serve to illustrate that such participation can greatly exceed that typically shown in chimpanzees and humans (Manson & Wrangham, 1991).

In many territorial primate species, females are frequently aggressive during intergroup interactions (e.g., ring-tailed lemurs, emperor and saddleback tamarins, vervets, redtail monkeys, blue monkeys, and Kloss' gibbons). Female aggression is more variable, however, in species that only infrequently defend ranges. In some of these, female aggression is common (e.g., macaque spp., red howlers, capuchins). In other species, however, males are the primary antagonists, perhaps because, as Cheney (1987) suggested, encounters more often concern mate, rather than food, defense (e.g., baboons, mountain gorillas).

In primate species 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. Gang attacks, involving mostly coalitions of females, have twice been reported to lead to deaths of males attempting to enter a group of red colobus (Manson & Wrangham, 1991; Starin, 1994; Wrangham, 1999). Cheney (1987) notes that the hostility of the females toward intruder males often escalates and affects the whole group. Female antagonism toward extragroup females also occurs in some of the social carnivores. Spotted hyena females returning to their natal group, after fissioning, were targets of severe aggression by adult female residents of the parent clan and by juveniles of both sexes. They fell, furthermore, to the bottom of the adult female hierarchy (Holekamp et al., 1993).

In monogamous primate species females may be as aggressively participating in cooperative range or territory defense and other intergroup interactions as males. In these situations the animals tend to be most aggressive toward individuals of their own sex, perhaps because they represent potential mate competition (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., in gorillas (Fossey, 1979; Harcourt, 1978), red colobus (Struhsaker & Leland, 1979), and hamadryas baboons (Abegglen, 1984). Among chimpanzee females attacks on females of other communities are rare, but not entirely absent (Goodall et al., 1979). The males in these species, in contrast, are generally hostile toward, especially male, members of other groups, which may be ultimately explained by male-male
Female involvement in intergroup aggression has been proposed to depend on whether resources that limit female reproduction are defensible through cooperative action. Where they are, females should form close bonds with allied females. Because of the effects of kin selection, such bonds are most effectively achieved through philopatry (i.e., breeding in their natal groups) (Wrangham, 1980, 1987; see van Schaik, 1989, for a contrasting view). Accordingly, species in which females cooperate may be expected to be those with female philopatry. This hypothesis was tested by Manson & Wrangham (1991).

The data of Table 3.3 indicate that female philopatry and female participation in intergroup aggression are indeed correlated ($\chi^2 = 8.26; \varphi = .76; p < 0.01$).

An alternative hypothesis appears not to be supported: there is no correlation between the degree of sexual dimorphism and the proportion of studies in which females are reported to participate regularly in intergroup aggression. 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).

Table 3.3: Female Participation in Primate Intergroup Aggression in Relation to Pattern of Intergroup Migration and Degree of Sexual Dimorphism

<table>
<thead>
<tr>
<th>Species</th>
<th>%</th>
<th>N</th>
<th>FT</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lemur catta</em></td>
<td>100</td>
<td>2</td>
<td>No</td>
<td>1.16</td>
</tr>
<tr>
<td><em>Propithecus verreauxi</em></td>
<td>100</td>
<td>2</td>
<td>No</td>
<td>1.06</td>
</tr>
<tr>
<td><em>Cebus olivaceus</em></td>
<td>100</td>
<td>1</td>
<td>No</td>
<td>1.26</td>
</tr>
<tr>
<td><em>Papio cynocephalus</em></td>
<td>28</td>
<td>5</td>
<td>No</td>
<td>1.33</td>
</tr>
<tr>
<td><em>Macaca mulatta</em></td>
<td>100</td>
<td>4</td>
<td>No</td>
<td>2.07</td>
</tr>
<tr>
<td><em>Macaca fuscata</em></td>
<td>100</td>
<td>1</td>
<td>No</td>
<td>1.29</td>
</tr>
<tr>
<td><em>Macaca fascicularis</em></td>
<td>100</td>
<td>1</td>
<td>No</td>
<td>1.44</td>
</tr>
<tr>
<td><em>Cercopithecus mitis</em></td>
<td>100</td>
<td>2</td>
<td>No</td>
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</tr>
<tr>
<td><em>Cercopithecus aethiops</em></td>
<td>57</td>
<td>7</td>
<td>No</td>
<td>1.33</td>
</tr>
<tr>
<td><em>Cercopithecus ascanius</em></td>
<td>100</td>
<td>2</td>
<td>No</td>
<td>1.45</td>
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<tr>
<td><em>Cercocebus albigena</em></td>
<td>100</td>
<td>1</td>
<td>No</td>
<td>1.41</td>
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<tr>
<td><em>Erythrocebus patas</em></td>
<td>100</td>
<td>1</td>
<td>No</td>
<td>1.79</td>
</tr>
<tr>
<td><em>Colobus guereza</em></td>
<td>100</td>
<td>2</td>
<td>No</td>
<td>1.28</td>
</tr>
<tr>
<td><em>Presbytis entellus</em></td>
<td>67</td>
<td>6</td>
<td>No</td>
<td>1.61</td>
</tr>
<tr>
<td><em>Alouatta seniculus</em></td>
<td>100</td>
<td>1</td>
<td>Yes</td>
<td>1.27</td>
</tr>
<tr>
<td><em>Macaca sylvanus</em></td>
<td>0</td>
<td>1</td>
<td>No</td>
<td>1.12</td>
</tr>
<tr>
<td><em>Ateles belzebuth</em></td>
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<td>1</td>
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<td>1.07</td>
</tr>
<tr>
<td><em>Papio hamadryas</em></td>
<td>0</td>
<td>1</td>
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</tr>
<tr>
<td><em>Colobus badius</em></td>
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<td>1.81</td>
</tr>
<tr>
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<td>Yes</td>
<td>1.34</td>
</tr>
<tr>
<td><em>Gorilla gorilla</em></td>
<td>0</td>
<td>1</td>
<td>Yes</td>
<td>1.72</td>
</tr>
</tbody>
</table>

% = Percent of studies reporting female participation
N = Number of such studies  
FT = Female Transfer (females typically transfer from natal group before breeding)  
SD = Sexual Dimorphism (male body weight divided by female body weight)  

Table from: Manson & Wrangham (1991)  

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 non-human primates generally - as in humans - intragroup cohesion and intergroup hostility may be correlated (Cheney, 1992).

7. In a number of primate and carnivore species IAB is accompanied by infanticide and, occasionally, cannibalism. Preferential gang-attacks on solitary females (with infants) are common in chimpanzees. 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 mates with the killer of her infant (See Wrangham & Peterson, 1996, for the evolutionary logic of this behavior).

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 (Itani et al., 1963; Kawai, 1964; Fossey, 1971 et seq; Kawanaka, 1973). Careful control of trouble within the group and leading attacks on other groups was for instance characteristic of some leader males at Takasakiyama. Furthermore, concerted action and scouting behavior of group males seem to indicate a ‘consciousness of belonging’ (Kawanaka, 1973) in this species. Cf. also Altmann’s (1962), Russell & Russell’s (1968) and Carpenter’s (1974) story of Diablo, the ‘monkey warlord’ of Cayo Santiago.

9. 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 (Altmann, 1962; Cheney, 1987; Deag, 1973; Givens, 1975; Imanishi, 1963; Kawanaka, 1973; Koford, 1963; Koyama, 1970; Lindburg, 1971; Loy, 1970; Neville, 1966; Nishida, 1963; Rahaman & Parthasarathy,
1969; Southwick, 1962; Southwick, Beg & Siddiqi, 1965; Sugiyama, 1960, 1968; Vandenbergh, 1967; Vessey, 1968, 1971; A. Wilson, 1969; Yoshi, 1968). Approach-retreat encounters (called Type C encounters by Deag [1973]) have, for example, been observed in most macaque species (Givens, 1975). Occasionally, groups expand their home ranges at the expense of their neighbors’, and in these cases the relative sizes of the groups - as well as the fighting ability of a particular individual - may determine success (Cheney, 1987).

10. With regard to the general function(s) of IAB in primates, Washburn & Hamburg (1972) succinctly epitomized: "Intergroup aggression either leads to one group’s having the resources of an area at its exclusive disposal, or at least creates a situation in which one is much more likely to obtain food in one area". Food is not the only resource nonhuman species fight over, however. Much more important - but only relatively recently acknowledged - is the struggle for differential reproduction. Nonhuman vertebrate males frequently come into open conflict over access to females, and/or control of resources useful in attracting females. Females, on the other hand, may cooperate in coalitions of kin to attack reproductive competitors, or the offspring of reproductive competitors (Wasser, 1983; Silk & Boyd, 1983); such situations typically involve harassment of subordinate females and infanticide, with little risk to the aggressors (Low, 1990; See review by van der Dennen, 1992).

The basic reasons for male-male intergroup aggression, rather than intergroup aggression by both sexes, probably include the different reproductive payoff curves for the two sexes in mammals generally. Male-male cooperation, and the benefits of risk-taking, may be enhanced by groups of related males living together (called 'male-bonded' or 'female transfer' in primates, and 'patrilocality' in humans), but this seems not to be an absolute requirement. In lions, males leave the natal group, while female relatives remain - yet, lions engage in male intergroup lethal conflict. In gorillas, both sexes may leave the natal group. In wild dogs, wolves, and mongooses, who have a monogamous, extended-family structure, both sexes are involved in lethal intergroup aggression (Low, 1990). See § 3.7 for an attempt to put the above observations on primate intergroup behavior in a more comprehensive socio-ecological perspective.
3.5 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 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, 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 shriek-barking 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, which was probably more due to the animals’ fear to be engulfed by the opponents, rather than to any magnanimous restraint or inhibition. Furthermore, there were no indications that the manifestly synchronized action could be ascribed to one or more coordinating leaders. "It was also striking that it were not primarily the males who stood in the front line. Contrary to what one would expect at first sight, the females were just as active in the skirmishes, if not more so. The same has also been observed in the defence of groups against predators. The classic picture of the adult male placing himself as a protective shield outside the group when it is threatened (Washburn & DeVore, 1961), does not seem to be a universal truth. Thus Rowell (1972) found that the long legs of the males in a threatened baboon group brought them soon to the head of the fleeing group. And Gouzoules et al. (1975) discovered, in one of the rare cases in which humans have witnessed a predator attacking a member of a primate group, that animals of all ages and both sexes took part in the defence when a lynx grabbed a young Japanese macaque" (van Hooff, 1990).
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. Why these brutal attacks? The northern males were not defending their own territory, since all the attacks except one were deep within the southern community home range. On the other hand, the aggressor males, before the community split, had access to the area that the southern community took over. If they were merely trying to reclaim territory they had lost, then they have certainly succeeded" (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: "antagonistic interactions of a group versus an individual, or a group versus another group, with the intent to kill, is peculiar to chimpanzee society" (Cf. Fossey, 1981; Ghiglieri, 1988; Goodall, 1986; Goodall et al., 1979; Schubert, 1983; Wrangham, 1975, 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). The male gang attacks on the old male Goliath are particularly puzzling, both in view of his extreme old age and his history of long and peaceful associations with the aggressor males. He could in no way be considered a reproductive competitor (Bygott, 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, 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; See also Ch. 8).

In these sections I have indicated the extent of IAB as it occurs in primates, and to a lesser extent in group-territorial carnivores; and presented some general observations on IAB as it occurs in these species. In the final sections, I shall briefly discuss the proximate and ultimate mechanisms proposed to account for the phenomena observed.

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 idio-typical 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).

It is very probable that the two behavioral patterns in their (hypothetical) pure and unadulterated form correspond with two discernible motivational systems and their neurophysiological and neuroendocrine substrata: the one tilting toward fight/flight motivation, the other toward predation. It is not hard to envisage the physiological differences between the silent and stealthy sneak-attack and the highly excited, clamorous and contagious 'pitched battles'. It is, indeed, remarkable how these primate battles and raids resemble those of human primitive societies, which brings us to the question whether any true homologies are involved. Any answer to this question must necessarily be speculative, but it would be a highly capricious and bizarre streak of nature if this would not turn out to be the case, at least for the chimpanzees, who are, after all, phylogenetically our very next-of-kin.

All in all, our data on infrahuman IAB seem *grosso modo* to confirm the observation by Itani (1982) that "the higher the species phylogenetically, the more frequent and varied is intra-specific killing". This is, in my opinion, only a more specific instance of the more generic proposition that the closer to *Homo s. sapiens* the species is phylogenetically, the more individual behavior is multi-determined (and the mind multi-modular). There is no 'instinct', in other words, to account for all the agonistic acts. But if there is no instinct or similar mechanism operating here, there must be something else: It may be a combination of 'male bonding' which is sort of a synergistic effect bringing about a strong demarcation against anybody outside (a kind of proto-ethnocentrism), and a more elaborate cognitive make-up.

I hypothesize, in other words, that 'higher' species need extra strong group delimitations, 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* (or what Kawanaka [1973] called "a consciousness of belonging"), which stress discreteness just like our symbols do. This discrimination may well be the price for 'de-instinctivation' in both humans and chimpanzees. 'De-instinctivation' is a very valuable asset: the individual is much less dependent on immediate external stimulus configurations. S/he 'knows' symbolically about relevant phenomena in the external cosmos. This may be less so in chimpanzees than in humans but to a certain extent there must be something similar at work here. 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 loose 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. Chimpanzees and humans appear to have the cognitive mechanisms it takes to observe, assess, and to regulate the appropriate pattern of response towards several different males structured into a coalition (e.g., de Waal 1982). They propose that these species have evolved specialized ‘Darwinian algorithms’, cognitive programs, that govern coalitional behavior, and constitute a distinctive coalitional psychology. These cognitive mechanisms cannot simply be either culturally ‘learned’ or be the product of ‘general intelligence’, but must be adaptively designed information processing systems specialized for these functions (See § 4.16.3).

Manson & Wrangham (1991; Wrangham, 1999; Wrangham & Peterson, 1996) referred to the chimpanzee ambush-like pattern of stealth, stalking and ‘stabbing in the back’ as ‘lethal male raiding’, and assert that it is similar to armed raiding in small-scale human societies in being conducted by small groups of adult males, being initiated to the surprise of the victim(s), and involving deliberate searching for opportunities to injure or kill members of a neighboring social group. These similarities between chimpanzees and humans seem to suggest a common evolutionary background.
Before I shall examine this proposition in more detail, a brief excursion to the proximate mechanisms involved in IAB may be in order.

3.6 Proximate Mechanisms

Obviously there are vast differences between species in the extent to which they show IAB. It is also obvious that the motivational-emotional and behavioral mechanisms which bring about such diversity in group behaviors are of different kinds.
Van Hooff (1990) discussed some of the behavioral and motivational mechanisms involved in IAB. In the simplest case the joint collective action is simply the summation of independent individual actions, each individual being affected by the same behavior-eliciting factors. Beyond this, several forms of individual interaction may lead to some structure and synchrony in collective action: ‘social sensitization’ and ‘mood-transfer’.
Social sensitization is the mechanism by which the intentionality or activity of one group member directs attention of other group members, perhaps inadvertently, toward the stimulus source (e.g., by alarm calls), and thus contributes to the synchronization of action, which may, in the case of a
predator threat or territorial intrusion, result in a more effective, simultaneous and more or less concerted defense. When the fitness of the individuals is thereby enhanced, a selection process is generated by means of which diverse structures that may contribute to such synchronization and coordination will spread in the population. In its simplest form this is the case when animals warn each other about a threat with special alarm signals. The evolution of breeding in colonies among birds such as gulls (e.g., Tinbergen, 1963; Gotmark & Anderson, 1984), and terns (Møller, 1982) must have been selectively promoted by the increased security resulting from the united call for defense.

A further stage in social influencing is the instigation or transfer of a particular attitude or mood. The receiver of an alarm call is then not merely made aware of a certain stimulus source, but the signal can also effectuate that initially neutral stimuli suddenly acquire an 'emotional color', for instance, that another animal is perceived as an 'enemy'. In many species aggressive displays have a contagious effect (cf. Russell & Russell, 1968).

A classical example of mood-transfer is the enticing behavior, described in ducks by Lorenz (1963), in which the female instigates aggression of the drake against strangers.

Analogously, in some species of Old-world monkeys 'side-directed' behavior can be observed: a form of polyadic agonistic interaction in which an animal can involve a third party in a dyadic conflict and incite the aggression of this third party against his adversary (van Hooft & de Waal, 1975; de Waal, 1976, 1977; de Waal & van Hooft, 1981). In an analysis of coalition formation and agonistic third-party intervention in a group of chimpanzees, de Waal (1978; cf. also 1982) distinguished a category of protective support, in favor of the weaker party in a conflict, and a category of opportunistic support, in favor of the stronger party. Opportunistic support concerns cases in which an animal helps another who is stronger than his opponent, and who would have had a large chance of winning the conflict on his own anyway. Such an exploitative and much less risky form of support is encountered, in chimpanzees, particularly among the males who seem to seek coalitions.

Coalitions have the character of transactions which continue as long as both participants derive net benefits and/or have more influence or freedom of movement than in other possible combinations. The choice which side to support appears to be less consistent over time (i.e., to be opportunistic) and to depend less on pre-existing relationships of interdependence. The support often seems to be mutual, or 'favors' may be given in compensation, as a kind of reward for the support (e.g., sexual permissiveness).

Opportunistic support may reflect the principles of 'reciprocal altruism' (Trivers, 1971), and seems to have a more calculated character than has protective support which seems to be more impulsive (and undoubtedly involves kinship considerations).

Indications about this kind of difference between the more altruistic form of
support, which depends on a relationship of attachment and affiliation, and the more opportunistic kind, where intervention depends on the possible advantage gained by the supporter, have also been found in other primate species (e.g., Netto & van Hooff, 1986; See Harcourt & de Waal, 1992).

Just as the giving of support can be facilitated by a relationship of attachment, so too can the reverse: Joining forces against a common enemy may enhance mutual attachment. A classic explanation of this phenomenon is the so-called redirection-of-aggression hypothesis. If an animal receives aggression-stimulating signals from a conspecific, but at the same time also receives signals which thwart the expression of that aggression (e.g., signals stimulating flight or sexual tendencies), the aggression may be redirected at an innocent third party. This redirection can be encouraged by one of the partners choosing a victim and 'picking on' him. A typical example has been described for monogamous species such as ducks and geese. When there is tension or uncertainty in the pair bond the weaker party, often the female, may set its mate on an outsider. The bond-strengthening effect of joint action against such an outsider can now become the main causal factor of such behavior, whereby the cementing of the relationship is the primary goal. A fine example is the 'triumph ceremony' of greylag geese, the origin of which can be traced back to the redirection incitation found in many duck species. When pairs meet again after some separation, they seem to be uncertain about the attitude of their partner. One of the two animals may now carry out an attack on an imaginary third party, in which he/she may be joined by his or her mate. After the attack both parties return to carry out synchronized, ecstatic pumping movements with their necks. Behavior which was originally intended as aggression redirection here has evolved into a declaration of attachment (Fischer, 1965).

There are indications that in cognitively highly developed species, such as primates, the redirection-victim is chosen not only because it is an enemy of the redirector, but also because the redirector 'knows' that it has a difficult relationship with its potential ally. This kind of strategy demands a high level of appraisal of the interaction possibilities among the other group members, and it has been postulated that the cognitive demands necessary for such a process must have formed the most important selective pressure in the development of primate intelligence (Humphrey, 1976, 1983), especially the kind of intelligence which has been labeled 'Machiavellian' (Byrne & Whiten, 1988; See also Ch. 8).

Concerted agonistic action or communal redirection of aggression against an enemy outsider may enhance durable emotional bonds (e.g., pair bonds). Some courting ceremonies may actually have evolved from such communal aggressive displays, as Lorenz (1963) has claimed. The process of regressive deritualization when such a bond occasionally breaks down then reveals its evolutionary origin.
In the case of the Gombe chimpanzees a kind of agonistic appetite seems to be involved, a real ‘spoiling for a fight’ with ‘intent to kill’ (counteracted by a healthy dose of ‘cowardice’), as may be derived from their active patrolling, searching for clues of the ‘enemy’, and the massive eruptions of intense and frenzied excitement during and after the rather vicious attacks (On primate agonistic intentionality, see Ellis [1986] who concludes: "behavior undertaken with some kind of neurological representation of the probable outcome of the behavior is intended behavior; many nonhuman primates appear to have these sorts of neurological representations just as humans do when they behave aggressively toward one another"). See also: Griffin, 1981 et seq.; Dawkins, 1993; de Waal, 1982, 1987).

The above observations seem to corroborate Rasa’s (1981) thesis that "self-defensive behavior is aversive, property-protective behavior appetitive", at least in (male) chimpanzees, and assuming that some kind of property-protective agonism is indeed operative.

The sound and the fury accompanying the baboon confrontations probably functions simultaneously as reassurance ritual (for the own side) and aversive, threatening and intimidating stimuli directed at the other party. The shriek-barking may indicate a high-intensity fight/flight ambivalence.

In most of the species reviewed here, gestures of submission elicit nonaggressive behavior by the attacker. In chimpanzees, attacks may continue in the face of submissive gestures (de Waal, 1982, 1989). Males form coalitions, fight single-handedly and in groups, and reconcile using vocal and behavioral signals of submission and alliance-seeking. Males have a formal dominance hierarchy, with far more aggression and reconciliation than females. De Waal (1989) suggests that the clear-cut dominance hierarchy provides a ritual format for reconciliation; reconciliations often follow a behavioral confirmation of formal status. Furthermore, "the unreliable, Machiavellian nature of the male power games implies that every friend is a potential foe, and vice versa. Males have good reason to restore disturbed relations; no male ever knows when he may need his strongest rival" (de Waal, 1989). Later, de Waal gives a striking and poignant example of how male-male power tensions, unresolved, can erupt with lethal consequences.

An important distinction between all nonhuman species and humans is the lack of any elaborate mechanism in other species for ending inter- (as opposed to intra-) group conflict. While the patterns of reassurance, even negotiation, are sometimes present, these occur in resolution of disputes within the group (in which participants already know each other, and will probably continue to live

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together). Low (1990) therefore argues that intragroup conflicts have been more frequent and selectively more important in these species’ evolutionary histories than intergroup conflicts.

### 3.7 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 (1980, 1987), van Schaik (1983, 1985, 1986, 1989), van Schaik & van Hooff (1983), Cheney (1987), and van Hooff (1988, 1990) 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\(^2\), are also acknowledged, but the emphasis is clearly on the physical and social environment.

The socio-ecological model underlying this reasoning is, highly simplified\(^3\), 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

\(^2\) Phylogenetic inertia refers to the (natural history of the) complex of traits a species has evolved which constrains the range of future evolutionary pathways. Natural selection has to work on, or tinker with, the material available. If there is no such material present, some options are simply closed. One cannot construct a Rolls Royce if there is no combustion engine, no brakes, no gear, etc. In a similar vein, we do not expect pigs to evolve wings – not overnight, not in ages to come – even if it would be highly advantageous for pigs to be ‘on the wing’. In more technical terms, constraints on social organization, relatively immune to ecological pressures, could be imposed by cognitive abilities limiting the development of polyadic coalitional (involving both complexly interacting cooperative and competitive) behaviors, by communicative constraints, by morphological constraints in relation to sexual dimorphism, etc. (See Wrangham, 1987).

\(^3\) Admittedly, the following model is a rough sketch only. For a more complete picture of (primate) social organization, we would also be obliged to consider the sex-, status-, and age-related alternative, conditional reproductive strategies (conditional strategies have the general form: “If dominant do X; if subordinate try Y”) of all individuals concerned, and always in relation to the strategies other conspecifics play (see Alcock, 1979; Smuts, 1987; van der Dennen, 1992; for reviews of such strategies); the powerful mechanisms of conflict resolution, reconciliation strategies and ‘peace-keeping’ politics (e.g., de Waal, 1987, 1988); specific selection pressures; population dynamics; the specific history and quality of past intergroup relations; etc. Please keep this in mind when the model seems occasionally to be too oversimplified, undetailed, sweeping, and ignoring exceptions to the general rules.
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 conducive to a poor physical condition, and 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 matrilines 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’ 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’ (See Ch. 7 and 8).

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4 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 was seen, females are not only actively involved in agonistic intergroup encounters in many species, also in matters sexual 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 Hrdy, 1981; Smuts, 1987). Female choice must have been a potent selective force in the evolution of primate — including human — societies.
3.8 Ultimate Explanations of Chimpanzee ’Warfare’

Chimpanzee social organization is relatively complex and differs from most other primate species. It has been speculated that it might be similar in many important ways to the societies of early Man (e.g., Hamburg, 1978; Itani, 1980; McGrew, 1981; Trudeau et al., 1981; de Waal, 1982; Nishida & Hiraiwa-Hasegawa, 1987). Chimpanzees, like humans, are ‘highly xenophobic’ (Schubert, 1983), and they sometimes engage in ‘armed fighting’ (Kortlandt, 1972) in defense against predators, and, as we saw, lethal raids with ‘intent to kill’ (Itani, 1982) 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; see § 3.9).

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, due to increasing human encroachment on their habitat, is responsible for the aggravation of chimpanzee ‘warfare’ (Goodall et al., 1979), has not been substantiated yet (Trudeau et al., 1981).

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,

\[5\] Chimpanzees are also in other ways extraordinary creatures. Young chimps may throw temper tantrums like spoiled human children do. The joyful games chimpanzee youngsters play resemble in considerable detail the games human children play all over the world, including teasing behaviors and quasi-aggression (Hebb & Thompson, 1968; Adang, 1985). And whole communities occasionally engage in 'festivals' or 'carnivals' (also called 'booming' or 'rain dances') with drumming and other clamorous fun going on for many hours (Nissen, 1931; Goodall, 1965; Reynolds & Reynolds, 1965; Sugiyama, 1969), and 'social feasting' when the spoils of a successful hunt are to be shared (Teleki, 1973; Goodall, 1986).
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 saw, males indeed remain in their natal group, while the females transfer (Goodall, 1986; Nishida, 1979; Pusey, 1979; Wrangham, 1979).

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 explains, 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, like hyenas and lions, 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 a subchapter 'The Precursors of Warfare', Goodall highlights the common preadaptations as follows: 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 of these were probably 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, nongroup members may not only be violently attacked, but the patterns of attack may actually differ from those utilized in typical intracommunity aggression. The victims are treated more as though they were prey animals; they are 'dechimpized'.

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)

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6 The behavioral patterns in intergroup aggression are strikingly different from those in intragroup aggression as Goodall in an interview on the West German Radio (1986, as cited in Vogel, 1989) relates: "The most severe fighting is fighting between chimps of different communities. And these fights are different from intra-community fights in two ways. First of all they last much longer, and all of those that we have seen have been gang attacks, that is two or more males, up to five males, attacking a single victim jointly, and they have been very much longer than the fights that we have seen between members of the same community. Fights between members of the same community last at the most three minutes, usually they are less than one minute. Fights on members of another community last up to twenty minutes. And secondly the patterns of aggression in inter-community fighting are sometimes different and we have seen patterns otherwise only observed in meat eating contexts, such as tearing off strips of skin from the victim, twisting limbs as so trying to dismember the victim, and even drinking his or her blood. Those we see in killing and hunting of large prey animals. Never ever have we seen them in fights between community members".
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).

An alternative explanation is offered by Bailey’s (1987) phylogenetic progression/regression model, which presupposes a high degree of phylogenetic continuity in the primate - including Homo - order. If we assume, he says, a more or less constant, innate killing potential in baboons, chimpanzees, and humans, then the baboon → chimpanzee → human phylogenetic ‘progression’ from less to more killing could be parsimoniously explained by the elaborationist hypothesis: That is, the primitive motive forces to kill and their associated behavior patterns may be homologous up to monkeys, apes, and humans, whereas the greater actual killing at ‘higher’ levels is a product of greater intelligence and response elaboration within and across situations.

A third explanation can be derived from the socio-ecological theorizing presented in § 3.7 on the ultimate causes of primate sociality. In this model, as we saw, ecological factors such as distribution properties of preferred foods largely determine the nature of social organization and structure (which is itself the outcome of multiple interactions of individual adaptive strategies) of a primate species with respect to e.g., social hierarchies, coalition systems such as female kin bonds, and migration patterns. Now, in chimpanzees the females disperse (female exogamy), while the males remain in their natal groups. This state of affairs has a profound impact on the proximal mechanisms of chimpanzee social structure. It facilitates, for instance, the development of male bonding and coalition formation. 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. Hamadryas baboons with their ‘brother-clans’, red colobus, and the South-American spider monkeys (Ateles and Brachyteles) are each more or less
evolving in an analogous direction (van Hooff, p.c.).

In baboons, macaques, and most other primate species the male competitive mating strategies of monopolization of females in harems, or of scramble promiscuity and sperm competition, do not give rise to male bonding beyond temporary and opportunistic (and mostly dyadic) coalitions, which, in turn, accounts to a large extent for the differences in the intergroup agonistic behavior patterns.

Besides being more reliable, there is another reason why coalitions among male kin may be favored by natural selection. Van Hooff (1990) explained it as follows:

Cooperation between males to monopolize access to a female or a group of females, or to monopolize certain consorts within a group, is not often seen among primates. This is probably hampered in most species by the males being strangers to each other. There is then no easy solution to the question of how the profits of the cooperation are to be shared: 'who gets the consort, of whom the coalition took possession?' A recent study of baboons, where such coalitions do nevertheless occur, shows that this can lead to complex 'negotiating' situations (Packer, 1977: Noë, 1986, 1989). Coalitions for mates occur between males who have been in the same group for a long time, and have got to know each other so well that cooperation on a basis of mutual advantage becomes possible. A situation of male cooperation can occur more easily if the males are closely related. Even if there is no fair distribution of the profit, such cooperation can bring gain to all those involved in the form of an inclusive 'fitness' advantage by means of 'kin selection'. This situation exists where brothers migrate together, as they do in lions (Bertram, 1976) and turkeys (Watts & Stokes, 1971), or where males are the resident sex, and their family relations thus stay intact. This last situation has been discovered among a few populations of chimpanzees (Pusey, 1979; Tutin, 1979). These fruit-eaters can only form groups at times when the food supply is superabundant. In order to avoid competition for food, female chimpanzees usually travel alone or at most with a few relatives (offspring). On the whole the situation is characterized by scramble competition. Chimpanzee females are, therefore, hardly competitive amongst each other, and appear to migrate easily. Under these circumstances groups of related males can stay together and defend an area against other 'brotherhoods'. The larger and richer this area is, the more females will be able to live in it. The willingness of chimpanzee males to engage in intergroup 'warfare' now becomes understandable. We know from studies carried out in the wild (e.g., Goodall, 1986), and in captivity (de Waal, 1982), that dominant male chimpanzees can be tolerant, even if not always with heartfelt sincerity, of the sexual behavior
of their coalition partners. There is reason to assume that this tolerance of promiscuity makes it worthwhile for non-dominant males to keep lending their support to the coalition. Bearing this in mind, it is possible to comprehend the exceptional, 'purposeful' cooperation which male chimpanzees give in intragroup conflicts.

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).

Also Boehm (1992) noted that the human groups most similar to chimpanzees are the feuding nonliterate societies, that is, those in which closely related males stay in their natal groups for life and develop very close bonding. Otterbein & Otterbein (1965) have shown that in humans, feuding (with its limited, reciprocating homicidal retaliation between groups) 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', and have argued that a group of coresident males who are closely related (e.g., a clan) may be prone to act politically as a single unit. Societies based on fraternal interest groups readily develop a politically competitive warrior mentality, and kin groups may compete as coalitions at many different levels. Such a segmentary lineage also can become an 'instrument of predatory expansion', particularly when it shares frontiers with societies that lack their own segmentary organization.

Note that in this socio-ecological model there is no scala naturae of 'higher' or 'lower' phylogeny as implied by Itani’s statement.

The last 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, hinted at by King (1976) and implied by Goodall (1986), 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 (and spider monkey) 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 favor male gregariousness. Bonded males compete more effectively than solitaires, so males form bonds wherever the ecological costs of bonding are not prohibitive (Rodman, 1984). 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) 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.

To determine whether human intermale intergroup resource competition actually represents reproductive competition (i.e., whether material resources attract women), they also test the hypothesis that where crucial material resources are alienable the accumulation of wealth will be associated with hunting success, political skill, ability to defend women, or other characteristics (Table 3.6). In societies in which resources were coded as not alienable, the cause of warfare tended to be conflict over women, whereas the presence of alienable resources was significantly associated with conflict over resources. Polygyny and wealth should accordingly be associated in societies where resources are alienable, whereas there is no expectation that they will be in others. This expectation is also strongly supported.

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? Why are the Amazons mythical rather than historical reality? As we saw, 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.

<table>
<thead>
<tr>
<th>Society</th>
<th>Cause of Intergroup Aggression</th>
<th>Resources Alienable?</th>
<th>Polygyny and Wealth Related?</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
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<td>Women</td>
<td>Yes</td>
<td>No</td>
<td>Davydov (1977 [1812])</td>
</tr>
<tr>
<td>Tribe</td>
<td>Gender</td>
<td>War</td>
<td>Peace</td>
<td>Author</td>
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</tr>
<tr>
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<td>Yes</td>
<td>No</td>
<td>No</td>
<td>Man</td>
</tr>
<tr>
<td>Aranda</td>
<td>Women</td>
<td>No</td>
<td>No</td>
<td>Spencer &amp; Gillen</td>
</tr>
<tr>
<td>Aweikoma</td>
<td>Women</td>
<td>No</td>
<td>No</td>
<td>Henry</td>
</tr>
<tr>
<td>Bellacoola</td>
<td>Resources</td>
<td>Yes</td>
<td>Yes</td>
<td>McIlwraith</td>
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<tr>
<td>Botocudo</td>
<td>Women</td>
<td>No</td>
<td>Yes</td>
<td>Métraux</td>
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<tr>
<td>Cahuilla</td>
<td>Resources</td>
<td>Yes</td>
<td>?</td>
<td>Bean</td>
</tr>
<tr>
<td>Chiric. Apache</td>
<td>Resources</td>
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<td>Yes</td>
<td>Spencer &amp; Gillen</td>
</tr>
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<td>No</td>
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<td>Opler</td>
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<td>Women</td>
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<td>Yes</td>
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<td>Resources</td>
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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 matrilocal 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. The fact that males who reside uxorilocally (matrilocally) maintain ties with their natal groups through visiting, ritual, and important exchanges of benefits means that they can easily maintain kin-based male coalitions for purposes of intergroup aggression even though their residences are somewhat scattered. Thus which sex is philopatric may be of less consequence for human intergroup aggression than it is for other species.

Given the fact that male kin coalitions are always available regardless of residence pattern and the fact that human females maintain extensive reciprocal exchanges of benefits with male kin, mates or both (Irons, 1983), the cost/benefit ratio may be more favorable for females’ indirect participation in intergroup aggression. That is, they may find it least risky and most beneficial to goad male allies (mates, kin, or both) into fighting their battles for them (Irons, 1991).

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" (Mukhopadhyay & Higgins, 1988).

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.

There is still one more relationship, only hinted at in the previous discussion, to be explored: Cooperative hunting and its relation to warfare in chimpanzees - leading to a novel and fascinating hypothesis concerning the evolution of human war. This hypothesis has been developed by van Hooff (1990) and van Hooff & van Schaik (1991) in the context of the socio-ecological model presented above.

3.9 Chimpanzee Hunting and 'Warfare'

Deliberate coordination of male actions as observed in chimpanzee intercommunity raiding is also obvious in another form of cooperation, namely hunting. From the Gombe study area came the first observations that male chimpanzees regularly hunt baboons, colobus monkeys and a number of smaller animals. The chimps surrounded their victim by keeping a close watch on each other, and blocking the prey’s possible escape routes from the trees. Such hunting forays have been reported now in a number of populations (Teleki, 1973; McGrew, 1979; Nishida & Uehara, 1983; Hasegawa et al., 1983; Boesch & Boesch, 1989, 1994).

Perhaps, van Hooff speculates, the development of coordinated male between-group aggression has paved the way for the development of such coordinated hunting. Structured between-group aggression and the relaxation of within-group male competition is certainly not a necessary condition for the development of cooperative hunting. This behavior has also been reported in some populations of baboons (Harding, 1975; Strum, 1981). However, there it never took on the deliberate, coordinated character seen in chimpanzees, nor was it associated with the 'social feasting', the sharing of the spoils (Teleki, 1973).

The development of cooperative hunting and the transition to a hunter-gatherer culture by early hominids has often been proposed as a major pacemaker for the development of human characteristics such as sex-linked task differentiation, food sharing, male-female bonding and paternal care, the refinement of communication in cooperation (in particular the development of verbal communication), the manufacture and use of tools and weapons, the development of cooperative tactical skills, etc.
For some of these aspects there is a striking analogy with the social carnivores. It has often been claimed (e.g., Schaller & Lowther, 1969; Peters & Mech, 1975), that in order to appreciate the conditions which determined the evolution of mankind, we could learn a great deal by looking at analogous developments in other social-cooperative hunters such as the wolf (Mech, 1966, 1970; Fox, 1971; Zimen, 1978) and the Cape hunting dog (von Kühme, 1965; van Lawick & van Lawick-Goodall, 1971). These animals not only hunt cooperatively, often for game which is far larger than the hunters are themselves, but also share in a far-reaching responsibility for the rearing of the young. They bring back food for the nurses and the pups. Cape hunting dogs, which have developed this communality even further than wolves, will take care of sick and injured animals for long periods of time. Contrasting with this ingroup loyalty is a bloody and merciless enmity toward non-pack-members (Murie, 1944; Zimen, 1978).

Cooperation in a hunt, and, possibly stimulated by this, collaboration in rearing offspring and in helping group-members, and the dedication to one's own group and its leader(s) - these are all characteristics highly developed in these carnivores. The suggestion is that by our transition to a more 'wolf-ish' lifestyle, these characteristics have been strongly enhanced.

This, in turn, may have strengthened the assumption that the development of hunting was at the roots of the development of warlike behaviors, possibly via intraspecific predation (cannibalism), rather than vice versa (See Ch. 4: Carnivorous Psychology Theory)."
In this conception, motivational mechanisms and the derived satisfactions involved in the capturing and the killing of prey are assumed also to reward the warrior who slays an enemy; a process facilitated by the dehumanization of the outgroup conspecific.

The recent observations of chimpanzee raiding suggest to van Hooff that the development may well have gone the other way around. Male philopatry has permitted the development of male-bonded defence polygyny. The concomitant cooperative tolerance has become manifest, among other things, in a more egalitarian distribution of resources, mates included, and a certain ‘respect’ for the intersex bonds of group members, in a hamadryas-like manner. 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. In view of the comparative evidence it is more parsimonious to assume that hominid/human development has followed this course.

Of course, a subsequent interaction between both processes might have occurred which could have facilitated the further development of each of the behaviors in its own context. Thus, certain actions which are useful as an instrument in hunting might also prove useful in battle against conspecifics, and vice versa. Tactical skills and the use of weapons can be applied in both contexts. 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). 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.

Van Hooff and van Schaik assume, as do many other scholars, that armed warfare is as old as mankind itself; and that human societies, in which violent confrontations between groups are reported never to occur, are remarkable but nevertheless marginal exceptions. The latter notion will be discussed more fully in Ch. 7. After a critical examination of the warfare-hunting hypothesis, I shall discuss the evidence on which the assumption that war is as old as mankind is allegedly based.

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has probably been derived from intraspecific aggression].
3.10 Criticism of the 'Chimp-Model' of the Evolution of Warfare

Is, as van Hooff suggests, the 'chimp-model' of the evolution of warfare - that is, that cooperation in 'tribal warfare' subsequently set the scene for cooperative hunting - a valid model in hominid evolution? Despite the very different evolutionary trajectories of the two species, the suggested priority of intergroup conflict may have been the same for both of them. There is, however, some (circumstantial) evidence to throw doubt on such a scenario.

(1) There is no compelling reason to assume that the early hominids had sociocultural patterns similar to those of contemporary chimpanzees (Panidae). The evolution of concealed ovulation, female orgasm, and similar adaptations in hominids make sense in a context of early hominid monogamy and pair-bonding, or 'limited' polygyny, and very little sense in a context of cooperative resource-defence polygyny. Or, as Rodseth et al. (1991) formulated a similar idea: "If protohominids, then, like chimpanzees, formed only temporary sexual consortships, a critical step toward human society would have been not out-marriage, as the exogamy theorists believed, but marriage itself. The problem, in other words, would be not how early hominids came to avoid incest or how one sex came to breed in other groups but how exclusive sexual bonds evolved from a chimpanzee-like pattern of promiscuity".

It is, furthermore, a distinct possibility that the chimpanzee proto-warfare is one of those rare instances of observing evolution 'in action', i.e., that it represents a truly novel evolutionary 'invention', an emergent feature in statu nascendi, the birthpangs of which we have the privilege to witness. In that case, it is not very likely to be an exact duplicate of the processes among hominids some million years ago.

(2) If the hypothesis were true, one would expect tools for hunting to have developed from tools for war (i.e., weapons). Archaeological evidence does not point to that direction. The oldest archaeological stone and bone artifacts known to us from all over the Old World (scrapers, burins, blades, denticulates, bone points, bone spatulates, beads and pendants) are clearly tools and items of personal adornment (Klein, 1992), and cannot possibly be construed as weapons. There are many archaeological artifacts which make perfect sense in a hunting context, but not in a context of war. Furthermore, there seem to be no peoples with tools specialized for war but not for hunting, many peoples with tools for both hunting and warfare, and many peoples with tools specialized for hunting and tools specialized for warfare (Among the Amazonian Indians, for example,
long arrows and blowpipes are used exclusively for hunting). This indicates that tools for warfare developed from tools for hunting, and not the other way around.

(3) There is a growing body of evidence that the proto- and early hominids were gatherer-scavengers rather than hunters, and only relatively late developed (anatomical) adaptations for hunting. Regarding the anatomical-morphological evidence, Trinkaus (1987) concludes:

This consideration of the Pliocene and Pleistocene paleoanthropological record and its implications for the evolution of human predation reveals a complex process, one in which predation played an increasingly important role during the course of human evolution. Yet, it appears that human predation as known ethnographically and ethnohistorically is a recent phenomenon in human evolution, associated with anatomically modern humans.

It also appears that relatively few of the anatomical characteristics of recent humans can be seen solely as the results of selective pressures generated by a predatory existence. Although the introduction of animal products into the human diet permitted expansion into increasingly seasonal environments, most of the distinguishing human characteristics, such as bipedality, manual dexterity and elaborate technology, and marked encephalization can be viewed as having been promoted by the demands of an opportunistic foraging system in which hominids fit themselves around more specialized mammalian groups (Trinkaus, 1987).

It is hard to imagine how such an inadequate, not to say inept, hominid hunter could have been a competent warrior.

On the other hand, it should be pointed out that the scavenger hypothesis (e.g., Shipman, 1983, 1986) is itself not without problems. As Tooby & DeVore (1987) have noted, the ecology of predation and scavenging makes it unlikely that scavenging is an adequate characterization of our ancestors’ major subsistence patterns, for the following reasons:

(1) In the first place, due to their position in the food chain, large ranges are required to support predators, and consequently, in any specific area kills by large predators are rare. Scavenging as a form of subsistence is dependent on what is left over (often, very little) from such rare kills after the predator has finished. Add to this intense competition with micro-organisms, insects, avians, and mammalian carnivores and scavengers (not to mention the returning predator or its kin).

Moreover, hominid competition for such remains would be actively dangerous: most mammalian scavengers are themselves predators. Active scavenging would continuously lead hominids to converge on the same resources as those...
dangerous animals.

(2) Scavenging as a niche is a specialized and competitive one. Observed primate behavior testifies to this: primates very rarely avail themselves of dead carcasses. Even modern humans do not seem to scavenge much.

(3) If hominids were formidable enough to scavenge, hunting itself was open to them as an option. Hunting only opposes the hunter to game animals, which are far less dangerous than predators. Instead of the opposed concepts of the timid scavenger and the fearless hunter, a fairer characterization would be the timid hunter and the fearless scavenger.

Tooby & DeVore do not deny that some opportunistic scavenging of meat occurred (e.g., scavenging of bones for their marrow content). What remains at issue, however, is the frequency and the importance of scavenging behavior at the various stages of hominid evolution.

If hunting were a major part of hominid foraging, it would, according to Tooby & DeVore, elegantly and economically explain a large number of the unusual aspects of hominid evolution: male parental investment; sexual dimorphism; male coalitions; reciprocity, sharing, and social exchange; sexual division of labor; home bases; stone tool use; brain size; geographical distribution; and, finally, the pongid-hominid divergence.

At this point some caveats are in order. Firstly, 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.

All the remarkable similarities should not, in other words, blind us to the real differences that exist. Warfare *sensu stricto* remains a uniquely human phenomenon (Carpenter, 1968; Fox, 1968; Goodall, 1986; Jolly, 1972; Kennedy, 1971; Scott, 1969), which cannot be reduced to a mere summation of 'individual aggressions' (see van der Dennen [1986] for the arguments against the aggression-warfare linkage).

If a battle is defined as a violent encounter between two groups, then battles may be said to occur in nonhuman primate species. But, as Passingham (1982) observed, a battle is not a war: "To conduct a war over several days requires an intellectual, social and economic sophistication to which animals do not aspire. The reason why man is the only primate that conducts wars is that only man is ABLE to do so. There is no cause to suspect the monstrous presence of a 'beast within'. Our trouble is that we are too clever for our own good" (Passingham, 1982). In what way are we too clever for our own good? Many high-strung propositions have been advanced but, in the final analysis, these all collapse into the statement that man has embarked upon a new, autonomous (or so it is claimed) level of sociocultural evolution, and thereby created symbolic universes and moral cosmologies, or 'entered into the cognitive niche'. What this entails for the explanation and understanding of primitive warfare will be the subject matter of the next chapters. In the remainder of this chapter the claim that war is as old as mankind will be examined.
3.11 The Evidence of Human Warfare

Explicit claims that warfare is as old as mankind itself have been made by a great number of authors, and is implied in many theories (Ch. 4). Together with the claim that human warfare was/is universal (and often completed by a third claim: that 'man is aggressive/violent/warlike by nature'), these belong to the standard cocktail party wisdom of the average intellectual. Birdsell (1972) is often referred to as the authority to substantiate these claims.

What evidence do we actually have? Birdsell’s book is a very competent and encompassing summary of the paleoanthropological and archeological state of the art anno 1972, but the subject of violence and warfare is limited to a few references to ‘murder’ and alleged headhunting in relation to the practice of cerebrophagy (eating the brains of the deceased or alleged victims), a practice connected, in contemporary humans, with ritual-ceremonial cannibalism or anthropophagy\(^8\). These claims will be examined below. The only time Birdsell explicitly refers to 'population contest' and 'powerful fighting bands', it is in the context of explaining the ultimate extinction of European Neandertals and their - no doubt violent in his view - displacement by the more modern Cro-Magnon type.

Placed on the evolutionary time scale, the human being appears as a mere afterthought. Placental mammals evolved around 100 million years ago, towards the end of the Cretaceous period. The primates diverged from the ancestral mammalian stock roughly 75 million years ago. The hominids, the ancestral stock from which humans are derived, split off from the remainder of the ape family (the pongids) some 8 million years ago, towards the end of the Miocene epoch, in Africa east of the Great Rift (Wood, 1992; Coppens, 1994; See Ch. 8). Archaic *Homo sapiens* appeared on the scene by about 400,000

\(^8\) The word 'cannibal' is derived from the Latinized name of the Carib Indians of the West Indies, who were depicted by the Spaniards as notorious human meat eaters. Already Herodotus described tribes which practiced cannibalism. In 1559 Hans Staden published his account of Tupinamba cannibalism, and the first essay on the subject was written by Michel Eyquem de Montaigne in 1580. Helmhuth (1968, 1973) proposed the following typology of anthropophagy (the more neutral term) in descending order from endo- to exocannibalism: (1) Endocannibalism motivated by love and affection (also called patrophy); (2) Juridicial cannibalism; (3) Cannibalism motivated by the idea of continuity; (4) Magical-ceremonial cannibalism; (5) Funerary (or mortuary) cannibalism; (6) Exocannibalism for the purpose of transmittance of power; (7) Exocannibalism motivated by hate, scorn and contempt (also called revenge cannibalism). To this typology may be added (8) Consumptive (or gustatory) cannibalism motivated by the relishing of human flesh; and (9) Survival or emergency cannibalism in cases of extreme starvation. For the sake of convenience, types (1) to and including (5) may be collapsed into one generic category of Ritual Anthropophagy. Note that only the types (6) to and including (8) imply some degree of violence toward the victim and may be taken as valid indicators of the possible existence of intergroup violence and war.
years ago; and our subspecies *Homo sapiens sapiens* has been in existence for a mere 35 to 50,000 years or so (Passingham, 1982; Tooby & DeVore, 1987; Jones, Martin & Pilbeam, 1992; Stringer, 1992).

The ancestors of the hominids were probably the ape-like creatures referred to as the dryopithecines, for which there is fossil evidence in Africa, Europe and Asia. The earliest dates for these apes are around 20 million years ago. The dryopithecine stock gave rise to several genera known collectively as the ramapithecids, deposits of which date from 14 to 8 or so million years ago. But there is then a gap of over 4 million years before good evidence is found of undisputed hominids in East Africa around 3.5 million years ago.

It is not until less than 2 million years ago that we find fully convincing evidence of the presence of Homo. Most authorities agree that *Homo erectus* lies on the direct line to modern man. The earliest skull comes from the Lake Turkana region in East Africa, and it is estimated to be 1.5 million years old. Later skulls have been found at Trinil in Java, and in caves at Zhoukoudian (Chou Kou Tien) near Peking; the Trinil skulls are probably around 700,000 years old, the Peking skulls as recent as 400,000 years old.

Modern man (*Homo sapiens sapiens*) is first found in Europe around 35,000 years ago. The skeletons of the slightly more rugged and robust Neandertal (also spelled Neanderthal) man (*Homo [sapiens] neandert[al]ensis*) are found in Europe from around 230,000 years on until they are rather suddenly (in geological terms) replaced by the more gracile *Homo s. sapiens* (Passingham, 1982; Klein, 1989; Bilsborough, 1992; Stringer & Gamble, 1993; a.o.). By just before 30,000 BP (Before Present) *H. [s.] neandert[al]ensis* has disappeared altogether. The possibility of interbreeding between the two Homo subspecies is often canvassed, but the majority opinion is that, if it occurred at all, it was to a very limited extent, and unlikely to have happened in Europe. It is more likely that the Neandertals were ousted by *Homo s. sapiens*. According to a still popular hypothesis, they were simply exterminated by the Cro-Magnons (e.g., Bigelow, 1969; Birdsell, 1972; Claiborne, 1974; Bailey, 1987; a.o.). "At one time dramatic genocidal massacres were envisaged, but no evidence exists for this, no caches of dozens of bones of Neanderthals slain in battle", and on balance the studies of sites like Arcy-sur-Cure goes against it.

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9 The sinister picture of the anatomically more modern Cro-Magnons — arriving in Europe during the fluctuating climates of 45,000-30,000 years ago — massacring and wiping out the Neandertals they encountered there does not only lack fossil evidence. It is also an unlikely scenario. Stringer & Gamble (1993) sketch a simple Gaussian displacement scenario as follows: "If the Cro-Magnons became more skilled at coping with and exploiting the European environments than the Neanderthals, the Cro-Magnon populations and ranges would have increased. With only finite resources, the Neanderthals would have suffered from economic competition unless they withdrew to more marginal areas... [and] attrition would probably have caused Neanderthal populations gradually to decline towards extinction. In fact, using a computer-simulated model, archaeologist Ezra Zubrow (1989) has shown how rapidly the Neanderthals could have become extinct. Assuming interaction between stable populations of Neanderthals and Moderns, a Neanderthal mortality rate only 2 percent higher than
The demise was likely to have been a more long-drawn out affair, piecemeal, mosaic, in character, with attitudes towards the Neanderthals among Moderns varying across the spectrum as widely as they do on most subjects today, and perhaps vice versa" (Richards, 1987).

The archeological and paleoanthropological evidence of human violence consists of skeletal material, artefacts and weapons, pictorial evidence such as petroglyphs (rock carvings), and fortifications. Let us first examine the skeletal evidence.

3.11.1 Skeletal Evidence

Birdsell (1972) presents the case of the australopithecines (Australopithecus africanus) - Lower Pleistocene bipedal 'apemen' who hunted and killed baboons apparently by clubbing them on the head - dis- and uncovered in the 1920s by Dart in southern Africa, in the following words:

The bones of the australopithecines themselves show evidences of violence. Sometimes the top of the skull contains depressed fractures not unlike those found on the baboons. Another time, the injury seems to have been inflicted with a round, pointed weapon. Some years ago when talking about the problem with Professor Dart, I asked him what proportion of the australopithecines he thought had been murdered. "Why, all of them, of course," he replied. The fragmentary nature of their remains, combined with the visible variety of fatal injuries, suggests that his estimate is not unduly exaggerated... The available evidence suggests that in addition to some scavenging and big game hunting, these early direct ancestors of ours also indulged in murder and gustatory cannibalism.

The sanguinary fantasies ventilated by Dart (e.g., 1957) and popularized in the writings of Ardrey regarding these allegedly cannibalistic 'killer-apes' (See Ch. 4) have in the mean time more or less quietly passed away.

The earliest discovered forms of Homo erectus (± 400,000 to 600,000 years ago) come from Java and North China. Originally labeled by their discoverers with the genus names Pithecanthropus and Sinanthropus, they are now included in the Homo category and regarded as subspecies of Homo erectus. On Java, the Trinil beds, dating from the Middle Pleistocene, have yielded a number of incomplete crania (von Koenigswald, 1943, 1958; Helmuth, 1968, 1973). According to Birdsell (1972) "All of the cranial remains of these

that of the Moderns could have resulted in Neanderthal extinction within about 1,000 years". See also Graves (1991).
Javanese men, women and children have been mutilated in such a fashion as to suggest that after they were murdered, their brains were eaten". And he notes that this treatment is very similar to that practiced in historical times by headhunters in both Indonesia and New Guinea. Opening the base of the skull by breaking away the bone around the foramen magnum in order to extract the brain may seem repulsive table manners by 20th-century Western standards, but it does not necessarily imply headhunting (not even murder, for that matter).

Regarding the finds of *Homo erectus pekinensis*, known colloquially as Peking Man, at Zhoukoudian (Weidenreich, 1928 et seq.), Birdsell (1972) reports that they included 14 skullcaps in generally incomplete condition, six separate skull bones, portions of 10 jaws, and a total of 147 teeth. The distribution of skeletal parts in the deposit is biased, for from these nearly four dozen individuals were found only a few fragments of the postcranial skeleton. These included seven fragmentary thigh bones, portions of the shafts of two humeri, one damaged clavicle and a single hand bone. "There was no evidence of intentional burial and, ominously enough, all of the skulls had had their bases prised open, and some showed head injuries which had occurred in life". Helmuth (1968, 1973) considers this excavation to be the "first incontroversial claim of anthropophagy" because the "firesites contained human bones which had been broken and split by other humans". Lorenz (1966) described Peking Man as "the Prometheus who learned to preserve fire [and] used it to roast his brothers: beside the first traces of the regular use of fire lie the mutilated and roasted bones of *Sinanthropus pekinensis* himself".

This view is an established one, although it is expressed less graphically in many textbooks, but in fact of all the human bones and bone fragments found at Zhoukoudian only one fragment showed evidence of burning, and even that one is doubtful (Weidenreich, 1939, 1943; Oakley, 1961; Montagu, 1976; Ferrill, 1985).

Weidenreich, the excavator himself, had examined the depressed fractures on some of the skull fragments, and reported in 1943:

My early suggestion still stands, namely: that the strange selection of human bones we are facing in Chou Kou Tien has been made by *Sinanthropus* himself. He hunted his own kind as he hunted other animals and treated all his victims in the same way. Whether he opened the human skulls for ritual or culinary purposes cannot be decided on the basis of the present evidence of his cultural life; but the breaking of the long bones of animals and man alike, apparently for the purpose of removing the marrow, indicates that the latter alternative is the more likely (Weidenreich, 1943).

This conclusion went too far even for Birdsell (1972) to witness from his comment: "All the evidence points to cannibalism’s being consistently
practiced in Pleistocene times. But Weidenreich’s statement that the men of Chou Kou Tien consistently hunted neighboring men is probably an overstatement of the case. No carnivores earn their living by hunting their own kind, for this way of life would lead to extinction". Nevertheless, Birdsell, as well as the authors mentioned above, clearly believed that the evidence of cannibalism was there for anyone to see:

When it is considered that the deposits at Chou Kou Tien may extend over a period of fifty thousand or more years, then the cannibalized relics of some forty individuals need not represent this vice’s going on at a very active rate. But the appetites of these pithecanthropines were not selective, as was indicated by the fact that both males and females are represented as adults in these grisly relics, and, even worse, 40 percent of the total were children of various ages. Those were not pleasant times in which to live (Birdsell, 1972).

Yet, the whole issue of Zhoukoudian cannibalism may simply rest on a tragic misunderstanding. Richards (1987) tells the following sobering story about these and other allegedly cannibalistic cave dwellers:

The earliest writers on Zhoukoudian, Breuil, Weidenreich and Chardin being the foremost, conjured up a fairly detailed picture of life in the cave which was almost ritually recited from then on. In this picture H. erectus is depicted as (a) a cave dweller (since the finds were made in a cave), (b) a hunter of deer (since deerbones were particularly numerous, (c) a fire user (since there appeared to be layers of ash, interpreted as hearth-sites), (d) a cannibal (on the basis of the nature of the damage to the base of the skull and face, combined with lack of post-cranial remains) and (e) a user of bone tools (on the basis of some features of the damage present in the animal bones). Binford (1981) raised some initial doubts about these interpretations and in a more recent paper, co-authored with a Chinese researcher (Binford and Ho, 1985) an attack is mounted on every single one of these conclusions, though fire-use is not entirely ruled out... Of particular interest is the belief that the Peking Man fossils showed evidence of cannibalism. This is still routinely mentioned in textbooks and popular summaries. Yet the matter rests on a dubious interpretation of two features of the fossils: firstly, the lack of a cranial base and facial area: secondly, the absence of other parts of the anatomy other than the skull. The former was thought to indicate that the skulls had been broken in such a fashion that the brains could be extracted, while the latter suggested that they had been brought into the cave separately from the rest of the skeleton. Ritual cerebrophagy by the camp-fire seemed the logical conclusion. But these kinds of damage are now known to be commonplace and 'understandable in terms of a number of taphonomic
alternatives’ (Binford and Ho, 1985, p. 8), hominid skulls recovered from secondary deposits... typically lack faces and parts of the skull base’ (ibid, p. 9).

Having reviewed the ‘evidence’ we are convinced that there is no support for the cannibalism interpretation. All such interpretations of the facts appear dependent upon a poor understanding of taphonomy and the modifications that bones can suffer after an animal’s death and during the inclusion of bones in geological deposits. (ibid., p. 11, italics in original)”

The upshot is, as Richards concludes, that the evidence for H. erectus cannibalism in China seems, for the time being at any rate, to have evaporated (Cf. also Rowley-Conwy, 1993).

Attempts at assessing the frequency of warfare among hunters and gatherers during the Paleolithic on the basis of archeological evidence have led to inconclusive results. Mutilated skulls found in Paleolithic caves, dating back some two million years, have been interpreted by Howell (1965), Lorenz (1966), Birdsell (1972), and many other influential scholars, as indicating prehistoric headhunting and cannibalism.

Such evidence is equivocal, however, because it is not known how the individuals died; nor is it necessarily true, even if cannibalism was practiced, that the individuals were enemies, because, as Bigelow (1975) among others, argued, processing and eating of the skulls and brains of deceased kin as part of ritual mortuary practices (so-called funerary anthropophagy) is an ethnographically well-known custom (See also Harris, 1980). Furthermore, Steinmetz (1896), Behm-Blancke (1958, 1959), Becher (1967), Helmuth (1968, 1973) and others have gathered impressive evidence that the bases of human anthropophagy are most probably of a religious and ritual nature, and that exocannibalism developed out of ritual endocannibalism rather than the other way around.

It is, however, equally unjustified to conclude, as did Eckhardt (1982), on the basis of this archeological evidence that "humans are basically cooperative rather than aggressive among themselves”.

Let us proceed now to the Neandertals who inhabited Europe and the Middle East before the Middle Pleistocene. From the first phases of the Würm ice advance (until about forty thousand years ago), all of the skeletal remains are those of Neandertal Man. Unlike the cartoons in which they are typically depicted with coarse and brutal features, and even more brutal habits, the Neandertals were a "people of some sensitivity and perceptiveness" (Birdsell, 1972). Even in their record of violence they may have resembled modern man more than any other hominid. There is ample, and less equivocal, evidence of
(gustatory?) cannibalism in the archeological finds. Very late in the Third interglacial period, or early in the first advance of the Würm, are placed a series of remains from Krapina (in former Yugoslavia). The exact number of individuals represented is difficult to estimate, for they are assumed to have been victims of intensive cannibalization (Gorganovic-Kramberger, 1906; Helmuth, 1968, 1973; Birdsell, 1972). Fragments of human skulls and long bones were discovered hacked and burned beside remnants of animal bones in and around a firesite. Similar remains of alleged cannibalism have been located in Weimar-Ehringsdorf (Virchow, 1920; Weidenreich, 1928; Behm-Blancke, 1959; Helmuth, 1968, 1973), and La Quina (Weinert, 1951; Gieseler, 1952; Helmuth, 1968, 1973).

There is no conclusive evidence that cannibalism was practiced at other paleoanthropological finds such as La Chapelle, Le Moustier, La Ferrassie, Mount Carmel, Teshik-Tash, and Monte Circeo (Helmuth, 1968, 1973). For the latter site, Monte Circeo, there was, however, supposed to be evidence of another 'modern' practice: human sacrifice. Birdsell (1972) relates:

In the inner chambers of Guattari cave some sixty miles south of Rome was discovered the skull of a classic Neanderthal man under what are certainly unusual circumstances. The find, known as Circeo I, was almost complete except for two significant mutilations. The right side of the skull and face had been badly damaged by violent blows. The base of the skull has further been mutilated so as to get at the brain in a way that is exactly similar to that practiced by living headhunters in Melanesia. The skull was found in an inner chamber which had not been used as a living site. It lay surrounded by a circle of stones with its base pointed upward. Three bundles of bones of wild cattle, red deer, and pigs were placed in the chamber in calculated clusters. From this evidence, Professor Blanc (1961) hypothesized that this skull represented a sacrificial victim who had been killed by a heavy blow on the temporal area of the skull as is done among present-day headhunters. The victim was beheaded and the skull mutilated outside of the cave, since there is no trace of either the rest of the skeleton or the fragments of the skull inside. The skull was then brought into the inner chamber and placed in an honored position within the circle of stones. This position suggests that it may have been used as a cup (Birdsell, 1972).

There is little doubt that violence existed, Bailey (1987) asserts: "Ample evidence of killing, body mutilation, and cannibalism exist at many Neanderthal sites. Much of this violence was probably associated with ceremonies, rituals, and religious practices".

Indeed, the cannibalism referred to here may still have been ritual and funerary, which does not, in any way, imply violence (unless the concept is stretched beyond credibility). The 'ample evidence of killing' is confined to a couple of
skeletons which exhibit wounds that seem to have resulted from weapons. This claim has, for example, been made regarding the pelvis of a skeleton from esSkhûl (Mt. Carmel caves, Israel) (the individual had incurred a spear wound in the leg, but is not usually considered a Neandertal: Richards, 1987), the ribs of one of the Shanidar Neandertals and the elbow of a skeleton found in Wadi Kubbuaniya (Egypt) (Clark & Piggott, 1965; Starr, 1974; Larsen, Matter & Gebo, 1992; Slurink, 1993). From the fact that many of the Neandertal fossils show signs of, sometimes severe, injuries from which the sufferer subsequently recovered, as well as other disabilities such as an atrophied arm in one of the Shanidar skeletons, one may conclude that Neandertal life was dangerous - as well as social and caring for the sick and disabled - but whether the danger emerged from predators and other exigencies of life, or from other Neandertals is hard to establish. For collective violence on the scale of warfare among them there is hardly any evidence.

Some 40,000 years ago Neandertal populations began to disappear from Europe. Their disappearance remains a mystery, for while cave deposits show that Europe continued to be inhabited, there were no further human skeletons recovered during an interval of about 15,000 years, that is, until 25,000 years ago (Birdsell, 1972). Then a totally different, modern, kind of human being is found who produced stone tool making cultures such as the Perigordian, Aurignacian, Solutrean, and Magdalenian. (Today, the consensus seems to be that Neandertal Man was not an ancestor of anatomically modern humans, and consequently is no longer considered a subspecies of *Homo sapiens*).

Proceeding now to this *Homo sapiens sapiens* level, the evidence of cannibalism among these 'modern' humans is solid, though the nature (gustatory cannibalism?, revenge cannibalism?) remains obscure in many cases, as well as the question whether the mutilations to the corpses were applied before or after death. According to Helmuth (1968, 1973), traces of cuts on the cervical vertebrae, suggesting decapitation; openings in the base of the skull; openings of the skull; and mutilation of the corpse in the case of a sapient skeleton from Döbritz are clearly ascertained (Mollison, 1936; Gieseler, 1952; Behm-Blancke, 1956; Grimm & Ullrich, 1965). Circumstances in the case of numerous finds from Bad Frankenhausen also seem to attest to cannibalistic practices (Behm-Blancke, 1956, 1958). The skeletal finds from Neuessing (Gieseler, 1953) revealed evidence of injuries and mutilations chiefly of the extremities in the area of the joints, while the effects of fire were also obvious. Finally, remains of human bones found in the kitchen-middens of North America among the Hopi Indians (Turner & Morris, 1970) and the Iroquois (Tuck, 1971) sites, on the coast of Cayenne, Brazil (Boehm, 1932) and Sumatra (Wastl, 1939) testify to the wide distribution of anthropophagy (Helmuth, 1968, 1973).
In a recent review of the evidence, Slurink (1993) notes: "Many presumed traces of cannibalistic practices in *Homo erectus* and *Homo sapiens* do not meet the criteria of scientific scrutiny. Yet the finds in Krapina and Hortus are difficult to explain otherwise. Research on the skull from Bodo, an archaic *Homo sapiens* of between 0.5 and 0.2 million years, shows that this has been deliberately defleshed (White, 1986). As cannibalism in the contemporary peoples who practice it is associated with the hope of acquiring the strength and courage of the enemy, clear traces of cannibalism *could* indicate also higher levels of intergroup competition".

The kind of cannibalism that Slurink seems to envisage - based on the notion that by consuming enemy flesh one assimilates the animus of another group’s hostile power into one’s own (Sanday, 1986) or that one extracts regenerative or corroborative properties from the consumed flesh, while at the same time reducing and degrading the enemy to food and excrement as the ultimate act of revenge and domination - cannot be excluded as a possibility within the grasp of these hominids, but, once again, the ‘deliberately defleshed skull’ and the other evidence cited do not exclude funerary endocannibalism - that symbolically ties the living to the ancestral dead in perpetuity - either.

The issue whether warfare existed at this time is also highly controversial. Roper (1969), surveying the evidence for intra-human killing in the Pleistocene, concludes that some intra-hominid, perhaps intra-specific killing probably took place among *Homo sapiens* in the Upper Paleolithic. Claims rest primarily on certain damage to skulls, the so-called depressed fractures which occurred before or shortly after death when the bones still possessed some plasticity. On the basis of this, however, we can and may not conclude that there were wars. It is even impossible to tell whether the fractures "were the result of accidents, of attack by predators or intraspecies fighting" (Huntingford & Turner, 1987)¹⁰.

Probably the most proper conclusion on the fossil evidence has been presented by Bailey (1987). He notes that the fossil evidence regarding man’s predecessors is very fragmented and incomplete. "Because all of man’s forbears are extinct, it is not possible to resolve any issue of man’s nature short of controversy, and what are cited as facts are, in reality, personal deductions based on scraps of evidence. Thus, the rightness or wrongness of evolutionary reconstructions reflects the theorist’s reputation, his or her skill in argument,

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¹⁰ Eibl-Eibesfeldt (1984) refers to an article by Mohr (1971) "die 158 Knochenverletzungen aus der Alt- und Jungsteinezeit untersuchte. Von diesen waren 63 Prozent verheilt. Die Verletzungen betrafen den Schädel (47 Fälle), die oberen (16) und unteren (14) Extremitäten, die Wirbelsäule (16), das Brustbein (3) und das Becken (1). An Wirbelknochen und an den Knochen der unteren Extremitäten fand sie Pfeilverletzungen zum Teil mit eingehielten Steinspitzen. Die Mehrzahl der Schädelverletzungen rührte von Steinaxten her". I have been unable to obtain a copy of this article, and thus to check the validity of these claims.
and reader’s receptivity to a great degree”.
In a thoughtful contribution to *The Cambridge Encyclopaedia of Human Evolution* (1992), Bahn discusses the prehistorical evidence of cannibalism (particularly in relation to the defleshing of bones) in the following words:

Where prehistory is concerned, cannibalism has long been a favourite and dramatic theory, from the Palaeolithic to Minoan Crete and the Anasazi of the American Pueblo culture. All these interpretations depend on indirect cues and on assumptions, as nobody has yet found definite evidence of the practice, such as human remains inside preserved human faeces (coprolites).

What appears at first sight to be overwhelming evidence for cannibalism was uncovered at the Neolithic cave of Fontbrégoua, southeastern France, where the bones of over a dozen people of the second millennium BC were found in three disposal pits, next to 10 pits containing animal bones. The human bones bore cut marks and breakage patterns identical to those on the animal remains, and were claimed to result from cannibalistic defleshing of fresh bones. However, the mortuary rituals of some Australian Aborigines can produce similar kinds of remains, from bodies left exposed to decompose, then defleshed and broken up for secondary disposal. Several individuals may be deposited together. So the onus of proof is still on those hoping for cannibalism at Fontbrégoua...

Two principal sites were heralded as providing evidence of Neanderthal cannibalism: Krapina and Monte Circeo. Krapina, a cave in Yugoslavia, was first dug in 1899 and has yielded over 650 fragments of bones from dozens of individuals, dating to between 100 000 and 50 000 years ago. These were interpreted as a cannibal feast, in which bodies had been smashed open to get at marrow and brains, and flesh cut off.

This gruesome image does not stand up to scrutiny. The bones display no evidence of the impact fractures characteristic of marrow extraction by humans. Instead, the extensive fragmentation can be explained by roof-falls, crushing by sediments, and the use of dynamite during excavation. There are linear grooves and striations on some bones that seem to be cut marks; but a detailed comparison of these with butchery traces on reindeer bones at the Mousterian (Neanderthal) site of Combe Grenal, France, showed a great difference in the location, orientation and length of the marks.

On the other hand, the Krapina marks resemble in appearance, location and frequency cut marks on human bones from secondary burials in a Michigan ossuary of the Late Woodland period (fourteenth century AD). It is therefore probable that the Krapina bones, like those at Fontbrégoua, were defleshed with stone tools after partial decomposition as a stage in a mortuary practice.

At Monte Circeo, Italy, two Neanderthal bones where found in Guattari
Cave in 1939: a skull and a jawbone, probably from the same individual. The context of the find was extraordinary: the skull lay in a 'ring of stones' on the cave floor, the hole at its base was enlarged, and there were fractures around the right temple. Inevitably, it was assumed that the Neanderthal, a man of about 45, had been killed by a blow to the head and his brains extracted through the basal hole for consumption. These factors - together with the position in a stone circle - all pointed to ritual cannibalism. Many popular works on prehistory have accepted this view unquestioningly.

However, more careful analysis suggests that the 'ring of stones' was not artificial but caused by a landslide; and the animal bones lying all over the cave floor, some of them bearing gnaw marks, and the presence of hyena bones and coprolites indicates that Monte Circeo was a hyena den around 50 000 years ago when the bones were deposited there. No cut marks have been seen on bones from the cave, and there are few stone tools on the floor.

The skull itself displays no modification by humans, and it is known that hyenas sometimes carry human skulls into their lairs. The fractures on the skull are consistent with hyena tooth marks; the enlarged hole at the fragile base has gnawed edges without a trace of stone tools, and the jawbone was also gnawed by hyenas. Since the cave was used by Neanderthals before hyenas took possession, it is possible that the carnivores took the head from a burial in or near the site, but the skull's preservation suggests that it was never interred.

One cannot deny the possibility that cannibalism occasionally existed in prehistory, but concrete evidence is hard to find. Research is underway into marks on other human bones from early periods, but as yet they can all be interpreted as the result of mortuary practices (as at Krapina) or carnivore activity (as at Monte Circeo). In view of the extreme scarcity of cannibalism in historic times, its very existence in prehistory is becoming hard to swallow (Bahn, 1992; Cf. also Trinkaus, 1985; Russell, 1987; Bahn, 1991; White & Toth, 1991).

It has been argued that indiscriminate massacres of enemy populations date back to the Paleolithic: the rock-shelter at Alfalou Ben Rhummel in North Africa contains remains of men, women and children who appear the victims of such misfortune (Arambourg et al., 1934). Clear cases of prehistoric genocide are very scarce. Klein (1989) mentions "an extraordinary terminal Pleistocene (ca. 14,000 - 12,000 years-old) cemetery near Jebel Sahaba in Sudanese Nubia where nearly half of the fifty-nine individuals exhumed had either unhealed antemortem skeletal injuries or had stone artefacts lodged in or near their bones".

Ferrill (1985) paints a frightening picture of this burial site along the Nile in ancient Nubia. The prehistorians of ancient Egypt refer to the site as 'Cemetery
117. Discovered in the 1960s, it belongs to the Qadan culture (12,000 to 4500 BC), possibly Proto-Neolithic, at least in its extensive use of microliths and its experimentation with agriculture. There were fifty-nine excavated burials at Site 117, and the skeletal remains are generally in a good state of preservation.

Signs of staggering human savagery greeted the excavators. Included in the graves of about forty per cent of the skeletons were small flake points (microliths), probably arrowheads since they seem too small for spears or darts. Points were actually embedded in the bones of four of the dead men and women (some of whom suffered several wounds). In two of these cases the points were found in the sphenoid bones in the skull, and they must have entered from under the lower jaw. That probably means that the individuals were wounded and disabled, lying on their backs, in agony, heads thrown backwards, when they were shot through the throat with the bow and arrow.

Although these remains may reflect a simple execution rather than war, some of the multiple wounds are frightening to imagine. Burial no. 44, a young adult female, had twenty-one chipped-stone artifacts in her body. Three of them found in front of, inside, and behind the mandible, must have been attached as points and barbs on an arrowshaft that was shot into her mouth. Essentially she has been hit over her entire body. Overkill may be a modern concept, but it was an ancient practice. Burials 20 and 21, two adult males, showed six and nineteen wounds respectively, including for no. 21 two stone artifacts in the skull.

It is possible that many of the remaining sixty percent of Cemetery 117 died from wounds also. Presumably arrows could sometimes be extracted from the dead with points intact, and in that case there would be no archaeological evidence of death by violence. Seven of the skeletons show fractures of the arms that are characteristically produced when the arm is used to parry a blow. These fractures had healed before death, but they illustrate the dangers of life for the people of Cemetery 117. Altogether at the site there were skeletons of eleven children, twenty adult males, twenty-one adult females, and seven adults, sex unknown. Roughly the same percentage (about forty-five per cent) of men and women were clearly killed by microliths, and four of the eleven children (just over thirty-six per cent). We may have in this site the first extensive skeletal evidence for warfare in prehistoric times. It is possible that the dead with multiple wounds were simply executed, but it is far more likely, since the percentage of executions in the group would be incredibly high, that they died from an act of war. Whether it was organized war or simply a primitive ambush or skirmish, we cannot know, and the victims cannot now care (Ferrill, 1985).

Also a recent excavation in the Netherlands is not conducive to the picture of
prehistoric man as a peaceful hunter-gatherer (Louwe-Kooijmans, 1990). "[T]he species concerned is, however, Homo sapiens sapiens. This suggests that only in this species the levels of intergroup conflict increased significantly as a result of ecological dominance" (Slurink, 1993; see Ch. 8).

Also Ferrill (1985) presents the general conclusion: "In fact there is little evidence from all but Late Palaeolithic sites of anything that can be called organized warfare. Feuds and quarrels undoubtedly led occasionally to violence and killing. A few hominid and early human skeletons reflect violent death, but whether as a result of war or warlike action cannot be determined" (Cf. Childe, 1941; Eisler, 1987; Gabriel, 1990; Gowlett, 1984; Lindman, 1985, 1987; Keeley & Cahen, 1989; Milner et al., 1991; Roper, 1969; Vencl, 1984; World Archaeol., 1986; Sponsel, 1994; although it must be admitted that absence of evidence is not necessarily evidence of absence).

3.11.2  Pictorial Evidence

The next group of material to have bearings on the presence of war among prehistoric humans are the rock paintings and carvings or petroglyphs. Most of the Paleolithic petroglyphs do not depict any violent motif (such as the theme of the 'wounded man' [Dams, 1984]), but examples of such motifs date from the Neolithic (beginning some 10,000 years ago in S.E. Europe) until the Bronze Age Period (e.g., Pidal, 1947; Maringer & Bandi, 1953; Kühn, 1955, 1958; Sandars, 1968; Hasselrot, 1984).

Cave paintings in southern France and Spain depict scenes of people shooting at each other with arrows. Kühn (1958), who studied these cave paintings, was quite touched by those scenes. At the sight of the cave paintings in the Valltorta Cannon he wrote: "In another niche I can see the painting of a hunter hit by arrows and sinking to the ground. He has put one leg in front and his hand is resting on his knee. A head-dress like a crown is falling from his head. With his right hand he still clings to his bow, but the arrows of the enemies have pierced his body, his life is coming to an end. Consequently man killed his kind already in prehistoric times. The paradise - a fading dream of man? Is war - is fighting the essence? Is it as eternal as life? Here we are faced with pictures
dating from ancient times, older than our legends and fairy tales, and already the killing of man by his fellow-man, already fighting, already war" (quoted and translated by Eibl-Eibesfeldt, 1977).

Also Donahue (1985) has noted that "in the Saltadora Cave in Castile, Spain, there's a crude painting of a man that [presumably] dates from the Mesolithic era. He has been shot with an arrow. He drops to the ground, clutching his own bow as he goes down: the first recorded victim of our own species' thirst for its own blood" (depicted in Bandi et al., 1961; Prideaux, 1973; and Huntingford & Turner, 1987).

But, as Kroeber & Fontana (1986) comment, it is a large step from what may well be an instance of individual aggression to socially sanctioned, organized warfare. For that matter, the Saltadora cave figure may be history's first recorded hunting accident, a tragedy, rather than a thirst for blood.

Several scenes in Spanish Levantine art show bands of archers attacking each other in what seems to be more or less disciplined combat. This early warfare involved simple forms of military ranking, military dress, and honor codes (Bandi et al., 1961; Prideaux, 1973; Beltran, 1982; Ferrill, 1985; Bailey, 1987; Huntington & Turner, 1987).

Ferrill (1985) concludes that the cave paintings of Cougnac, Niaux, etc., "reflect very little evidence of warfare or of advances in weapons technology. There are several thousand scenes of animals, and, on the whole, they are idyllically peaceful. Only about 130 depictions altogether may be of men - the figures are too crudely drawn to permit certainty - and a few of the men (sometimes referred to as 'anthropomorphs', meaning that they might possibly be men) seem to be dead or dying from wounds. Still, most of the 130 anthropomorphs are shown in peaceful scenes" (e.g., Leroi-Gourhan, 1967, 1968; Ucko & Rosenfeld, 1967; Hadingham, 1979; Moorey, 1979; Dams, 1984; Bahn & Vertut, 1988; Leakey & Lewin, 1992; For South Africa see Lewis-Williams, 1983; For North America see: Keyser, 1977, 1979; and Barry, 1991).

It is not until in much later periods that unequivocal evidence of war can be observed in human pictorial art. Bleek (1930), Samachson & Samachson (1970), Eibl-Eibesfeldt (1975, 1977), Woodhouse (1979 et seq.), and Huntingford & Turner (1987) depict a North African rockpainting dating from ca. 4000 BC, in which a group of archers is involved in a cattle raid. The fresco called 'The Archers of Tassili' (ca. 3500 BC), found at the Tassili Plateau of the Sahara Desert, depicts a combat between warriors using two different types of bow - one the ordinary semi-circular bow, the other a bow with a triple curve (UNESCO, 1963).

The so-called 'palette of Narmer', emblematically depicting the unification of lower and upper Egypt, and the subjection of the 'enemies' (depicted with ignoble features), dates from ca. 3100 BC. The obverse side shows the king examining the headless bodies of his enemies under the standards of his army.
What may well be the oldest pictorial evidence of warfare was only recently discovered, and consists of battle scenes painted by northern Australian Aboriginals (in Arnhem Land) on rocks, dating from 6000 to as many as 10,000 years BP (Taçon, 1993; Taçon & Chippindale, 1994). In the earliest works male 'dynamic' figures are shown in combat, carrying large spears, hurling boomerangs, dodging spears and chasing one another with raised weapons. Some figures have spears sticking out of their bodies while others are bending down to help fallen comrades. Scenes produced some 6000 years ago show more 'modern' weapons such as spear-throwers and three-pronged spears. They also portray more numerous and larger battles involving leaders with special headdresses and dozens of warriors. Most earlier works depict small skirmishes or one-to-one contests.

3.11.3 Evidence from Weapons

An important part of the archaeological material indicating prehistoric war consists of weapons. Weapons are better (less equivocally) suited to this purpose than skeletal injuries. Weapons have received considerable attention in archeological studies and there is a vast literature on details of their typology and chronology (Lindman, 1987).

According to Mansfield (1982; see also Zur, 1987), for the last 200,000 years hominids have had the technical and physical capability to create and use weapons against each other, but only since the Neolithic period have humans begun to design and use weapons to defend and attack against other human beings: "Thus for 187,000 years humans had the knowledge and ability to create warfare-type weaponry but did not" (Zur, 1987).

In the Mesolithic Age, 12,000 to 8000 BC, there was a revolution in arms technology. Four staggeringly powerful new weapons make their first appearance, weapons (along with the Paleolithic spear) that would dominate warfare down to the present millennium: the bow, the sling, the dagger (or short sword), and the mace. This new, revolutionary technology was combined with the invention of military tactics and, by historical standards, enabled true warfare (Ferrill, 1985).

Where the bow and arrow were invented nobody knows, but probably around 10,000 BC they appeared and spread rapidly around the Mediterranean. Neolithic cave painting clearly reveal their use against humans as well as animals (See e.g., Maringer & Bandi, 1953; Lommel, 1966; Prideaux, 1973; Brentjes, 1969; Brooks & Wakankar, 1976; Säve-Söderbergh, 1970; Uyanik, 1974). Bow, dagger, sling and mace have all been found at Çatal Hüyük in Anatolia dating from about 7000 BC.
3.11.4 Other Evidence

Roper (1975) investigated the evidence of warfare in the Near East from 10,000 to 4300 BC. Her main conclusions are the following. The earliest evidences of warfare in the Near East (and the world) are the massive fortification walls at Jericho dated to ca. 7500 BC. The sixth millennium exhibits three sites where conflict might have occurred: Ras Shamra Va, Tel es-Sawwan (in Iraq), and Hacilar on the Anatolian Plateau. About 5200 BC there was a fortress at Hacilar, thought to be the seat of a local ruler, which was destroyed.

With the westward influence of the Halafians at the opening of the fifth millennium comes evidence of site destruction and fortifications on the ancient east-west trade route from central Mesopotamia to the Anatolian plateau and beyond. At Mersin XVI, a garrison with soldiers’ quarters provides evidence of centralized social control and a soldier or warrior class - two main characteristics exhibited by warring societies in succeeding millennia in the Near East.

Trade, fortifications, and site destruction seem to be related factors with regard to early evidences of warfare in the Near East. Accumulations of negotiable wealth and control of strategic sites for exploitation of trade seem paramount as the instigators of hostilities. The social organization developed to handle trade relations may have been a prerequisite for the centralized control necessary to direct the building of fortifications.

The old notion that hostilities developed between agriculturalists, pastoralists, and hunter-gatherers is not confirmed by the findings of Roper’s study. Indeed, events in the Israeli/Jordanian area in the 5th and 6th millennia and elsewhere indicate that diverse lifestyles existing near each other did not produce conflict. Rather, trade was the catalyst from which hostilities arose. Warfare became a popular method of getting what was wanted - which in the Near East appears to be materials attainable only from afar, negotiable wealth, and control of popular trade-related sites (Roper, 1975).

According to Leakey (1981), the wall of Jericho may have been built for military defense, but, he submits, it is just as likely that the wall was erected to keep out silt, rather than people. Situated as it is near the slopes of mountains, large quantities of silt were probably washed down the valley during floods and could have buried the town’s buildings.
3.12 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. Hominid/human warfare 'from the dawn of history onward' is a distinct possibility, but it is not and can not be based on the fossil or pictorial evidence, in spite of vigorous claims to the contrary. Certainly, this conclusion is not meant to support the view that intergroup violence of any significance was launched only during the phase of agricultural settlement, and that (therefore)
intergroup competition has not played a central role in early hominid/human evolution (e.g., Montagu, 1976; Leakey & Lewin, 1977; Reynolds, 1980; and implied in evolutionary models such as those presented by Lovejoy, 1981; McGrew, 1981; and Tanner, 1981). By the same token, this conclusion is not meant to support the opposite point of view, most strongly articulated by Alexander (1979 et seq.). Alexander admits that the fossil and other archeological evidence is not unambiguous when one wants to prove the existence of violent intergroup competition as a regular (proto)human behavior pattern. Instead, he demands the evidence of no cut-throat intergroup competition to be unequivocal. Such a reversal of the burden of proof is scientifically inadmissible. By extrapolating and retrojecting contemporary intergroup behavior back into the evolutionary past, he seems to envisage some kind of unilinear trend which does neither do justice to the caleidoscopic picture of radiations, branches, chronospecies and populations in hominid/human evolution, nor allows for profound changes in the functions of this behavior over time and in varying ecological niches.

In an attempt to reconstruct the social behavior of the common ancestor of both humans and the three living species of African apes by means of phylogenetic comparison, Wrangham (1987) presents the following conclusions: The common ancestor is implied to have commonly had closed social networks, hostile and male-dominated intergroup relationships with stalk-and-attack interactions, female exogamy and no alliance bonds between females, and males having sexual relationships with more than one female.

This reconstruction of the 'ancestral suite', Wrangham points out, does not imply an evolutionary history of inevitable territorial aggression (contra e.g., Ardrey, 1970; Lorenz, 1967) because there is no implication that territoriality occurred at all. And, more importantly, intergroup aggression was not necessarily universal (though it might have been). Instead, its distribution may have depended on ecological conditions, as it is probably true of chimpanzees and certainly is of humans (See Ch. 8).

6. 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.