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Evolution of Coalitionary Killing

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ABSTRACT Warfare has traditionally been considered unique to humans. It has, therefore, often been explained as deriving from features that are unique to humans, such as the possession of weapons or the adoption of a patriarchal ideology. Mounting evidence suggests, however, that coalitional killing of adults in neighboring groups also occurs regularly in other species, including wolves and chimpanzees. This implies that selection can favor components of intergroup aggression important to human warfare, including lethal raiding. Here I present the principal adaptive hypothesis for explaining the species distribution of intergroup coalitional killing. This is the "imbalance-of-power hypothesis," which suggests that coalitional killing is the expression of a drive for dominance over neighbors. Two conditions are proposed to be both necessary and sufficient to account for coalitional killing of neighbors: (1) a state of intergroup hostility; (2) sufficient imbalances of power between parties that one party can attack the other with impunity. Under these conditions, it is suggested, selection favors the tendency to hunt and kill rivals when the costs are sufficiently low. The imbalance-of-power hypothesis has been criticized on a variety of empirical and theoretical grounds which are discussed. To be further tested, studies of the proximate determinants of aggression are needed. However, current evidence supports the hypothesis that selection has favored a hunt-and-kill propensity in chimpanzees and humans, and that coalitional killing has a long history in the evolution of both species. Yrbk Phys Anthropol 42:1–30, 1999.

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Two related but distinct hypotheses have proposed that warfare has its origins in pre-human violence. The first is no longer supported. This was the so-called "killer ape" hypothesis, which stated that warfare springs from an aggressive instinct that began among australopithecines and continued into humans (Dart 1953; Ardrey, 1961, 1966; Lorenz, 1966; Tiger, 1969). Raymond Dart based this idea on South African hominid fossils, which he interpreted with increasing pessimism after the Second World War until eventually concluding that *Australopithecus africanus* not only hunted other mammals but also killed adult conspecifics (Dart, 1953; Dart and Craig, 1959; Cartmill, 1993). At the time of these ideas, intraspecific killing was considered to be absent in other wild mammals (including chimpanzees *Pan troglodytes*) (Lorenz, 1966). Therefore, killing by australopithecines was considered part of a uniquely hominid suite of characteristics. Lorenz (1966) lent ethological authority to Dart's ideas by suggesting how killing could evolve. He proposed, for example, that the use of weapons, such as pebble tools, could overcome natural inhibitions against killing conspecifics. Lorenz (1966) thus followed Dart in arguing that human warfare had evolved from australopithecine aggressive instincts.

The killer ape hypothesis provoked vigorous attacks (e.g., Ashley Montagu, 1968). Much criticism was directed at theoretical components, such as the claim that humans have an innate aggressive drive that needs periodic expression. It was empirical evidence that felled it, however. Most importantly, the fossils suggestive of intraspecific violence were convincingly reinterpreted in terms of predation by carnivores and taphonomic processes, and the supposed bone and horn weapons were better explained as fragments produced by carnivores chewing bone (Brain, 1981; Cartmill, 1993). The killer ape hypothesis fell into general disrepute in the 1970s, even though the notion that warfare evolved out of complex hunting patterns has not completely died (Morris, 1977; Ferrill, 1985).

In the 1980's a second, unrelated, set of ideas arose, which I collectively call the chimpanzee violence hypothesis (CVH). Like the killer ape hypothesis, the CVH proposes that human warfare is built on pre-human tendencies. In contrast to the killer ape hypothesis, however, the CVH does not posit a prior history of hunting, nor an aggressive instinct. These and other differences make the killer ape hypothesis irrelevant to the CVH (Table 1). The remainder of this paper is concerned with the CVH, and not with the killer ape hypothesis with which it has sometimes been confused (Sussman, 1997).

The CVH proposes that selection has favored a tendency among adult males to assess the costs and benefits of violence, and to attack rivals when the probable net benefits are sufficiently high. It suggests that this tendency occurs as a result of similar conditions in the lives of chimpanzee and human ancestors, including a fission-fusion system of grouping, and intergroup hostility. It also raises the question of whether lethal raiding had a common origin in the ancestor of chimpanzees and humans around 5–6 mya, or whether it evolved later and independently in each line.

The CVH was stimulated by observations of male chimpanzees collaborating to kill or

TABLE 1. Comparison of the killer ape and chimpanzee violence hypotheses

	Killer ape hypothesis	Chimpanzee violence hypothesis
Lethal violence	Important in human evolutionary history	Important in human evolutionary history
Significance of hunting	Critical precursor to intraspecific violence	Possible consequence of intraspecific violence; not a necessary precursor
Mechanism of aggression	Instinct	Strategic assessment
Putative reason for intraspecific violence	Inadvertent breakdown of natural inhibitions	Assessment that costs of eliminating rival are low
Chimpanzees considered to be	Nonviolent	Strategically violent
Killing among animals other than hominids	Assumed to be absent	Known to occur
Reliance on fossil evidence	Critical	Relevant, not critical
First ancestor of humans supposed to have coalitionary violence	Australopithecines	Unknown
Evolutionary mechanisms favoring violence	Include group selection	Group selection appears unnecessary

brutally wound other adults (Goodall et al., 1979). Most such attacks were directed toward members of neighboring communities, in patterns reminiscent of human war raids (Goodall, 1986). As a result, various authors raised the possibility of functional parallels and/or evolutionary continuities linking chimpanzee violence and human warfare (Trudeau et al., 1981; Otterbein, 1985, 1997; Goodall, 1986; Alexander, 1987, 1989; Wrangham, 1987, 1999b; Ghiglieri, 1988; van Hooff, 1990; Hamburg, 1991; Knauft, 1991; Manson and Wrangham, 1991; Boehm, 1992; van der Dennen, 1995; Wrangham and Peterson, 1996; Boesch and Boesch, 1999). For example, Otterbein (1997, p 253) noted that similarities between chimpanzee communities and human bands suggest that "early man . . . is likely to have been organized into localized groups of related males, groups that engaged in intergroup conflict." If so, Otterbein concluded, warfare has been continuous in human and pre-human ancestry for at least 5 million years. This idea of an ancient origin of warfare is supported by the rarity of coalitionary lethal violence toward adult conspecifics in other primates, and by evidence that subsequent to the split with gorillas *Gorilla gorilla* (Pilbeam, 1996), chimpanzees and humans share a common ancestor around 5–6 mya.

In the first part of this paper, the evidence for coalitionary killing by chimpanzees and the nature of their intergroup aggression are examined. The principal adaptive explanation linking chimpanzee and human violence is then reviewed. This is the imbalance-of-power hypothesis, which states that coalitionary kills occur because of two factors: intergroup hostility, and large power asymmetries between rival parties. After considering separately the costs and benefits of lethal raiding among chimpanzees, how the imbalance-of-power hypothesis also applies to bonobos (*Pan paniscus*) and to humans is assessed.

In the third part, objections and problems are considered. Arguments are discussed that deny the relevance of biological arguments for understanding human warfare, including the following claims: warfare is wholly cultural (e.g., Keeley, 1996); modern war is too complex for individual aggression to be important (Hinde, 1993); and, nothing useful can be learned by studying species other than humans, because humans are already known to be violent (Leach, 1968; Gould, 1996).

Criticisms directed specifically at the imbalance-of-power hypothesis are also discussed. These include concerns about the validity of the chimpanzee data (e.g., Power, 1991; Sussman, 1997) or about the interpretation of human data (e.g., Knauft, 1991; Sponsel, 1996), and claims that data on bonobos undermine the use of chimpanzees as a reference species for early hominid ancestry (Zihlman, 1997; Stanford, 1998a). They also include accusations of genetic determinism (e.g., Regal, 1998; Sussman, 1997) or societal bias (e.g., Sussman, 1997).

These are important considerations, but they do not invalidate the comparative approach. Therefore this article ends with a brief discussion of the implications of the imbalance-of-power hypothesis for human psychology, warfare, and morality.

COALITIONARY KILLING AMONG CHIMPANZEES AND OTHER SPECIES

Species distribution of coalitionary killing

Contrary to initial assumptions (Lorenz, 1966), research in recent decades has revealed that intraspecific killing occurs in a variety of species, commonly following patterns explicable by natural selection theory. For example, among primates infanticide is widely reported, typically committed by nonrelatives (Hausfater and Hrdy, 1984; Palombit, 1999). Among spiders, killing of adults occurs predictably when resources of high value are at stake (Austad, 1983). Among ants, large imbalances of power increase the probability of lethal intercolony aggression (Hölldobler, 1981; Adams, 1990). Obvious parallels can be found among humans (Daly and Wilson, 1988; Bueno de Mesquita, 1981, 1985; Bueno de Mesquita and Lalman, 1992). To some extent, therefore, patterns of human killing appear to follow the ordinary patterns of lethal aggression found in other species.

Not so ordinary, however, is the way that human killing occurs. Among humans most killing occurs in warfare, where the predominant style of violence is coalitionary. In most animals, by contrast, even where aggression occurs at high rates, lethal violence is dyadic (one versus one) rather than coalitionary (many vs. one, or many vs. many). During rut-fighting among male pronghorn antelope (*Antilocapra americana*), for example, 12% of 82 fights over mating rights to estrous females led to the death of one or both males (Byers, 1997). Likewise, in different populations of red deer *Cervus elaphus,* 13–29% of adult male mortality came from rut-fighting (Clutton-Brock et al., 1982). Many similar examples occur. Deaths tend to occur in intensely escalated contests in which both opponents expose themselves to high risk of injury, typically because "a major part of a contestant's lifetime reproductive success is at stake" (Enquist and Leimar, 1990). But killing is never coalitionary in these species.

The explanation for the widespread absence of coalitionary violence is trivial. Most species never form coalitionary alliances in any context. But coalitions are not a sufficient condition for coalitionary killing. Thus many primates form coalitions without any evidence of adult-killing [e.g., *Cercopithecus aethiops* (Cheney et al., 1988)] or with fatal fighting known only from dyadic interactions [e.g., *Cebus capucinus*] (Miller, 1998).

Indeed, the only nonprimate mammal for which coalitionary violence is known to be commonly responsible for adult deaths is the wolf *Canis lupus.* In at least three sites, adults are known to kill other adults at high rates [Denali (Alaska), Isle Royale (Michigan), and Minnesota] (Mech et al., 1998). For example in Denali, 39–65% of adult mortality was due to intraspecific killing, based on 22 intraspecific killings recorded from 17–20 packs (Mech et al., 1998). This is the least disturbed study site of wolves. In northeastern Minnesota, 43% of wolves not killed by humans were killed by other wolves. Killings tended to occur in buffer zones (where territories met), which wolves mostly avoided (Mech, 1994). These data suggested to Mech et al. (1998) that intraspecific killing is a normal consequence of wolf territoriality.

Occasional coalitional killing of adult conspecifics in neighboring groups has also been recorded among other social carnivores [lions *Panthera leo,* spotted hyenas *Crocuta crocuta,* cheetahs *Acinonyx jubatus* (Kruuk, 1972; Caro and Collins, 1986; Goodall, 1986; Packer et al., 1988; Grinnell et al., 1995)] and at least one group-territorial bird [Tasmanian native hen *Gallinula mortierii* (Putland and Goldizen, 1998; A. Goldizen personal communication)]. However, the frequency of killing has not been reported for these species. Outside of mammals, only social insects are known to kill conspecifics regularly with coalitional aggression (van der Dennen, 1995).

These data suggest that animals can be divided into three major categories. First are species in which intraspecific killing of adults is rare (e.g., less than 1% of all adult deaths). Most species fall into this category. Second are those where killing occurs more frequently [often 10% of more of deaths (Enquist and Leimar 1990)], but entirely in dyadic interactions. In these species, fatal fighting is dangerous. In the third category, killing is also frequent, but differs by being polyadic (coalitionary). Furthermore, as argued below, fatal fighting need not be dangerous for the killers.

Ants dominate this last category, which contains probably less than 10 mammalian species and perhaps no other vertebrates. Chimpanzees and humans (or at least, certain populations of these species) are the only primates known to be frequent coalitionary killers. A possible additional candidate is the western red colobus monkey (*Colobus badius*), for which at least two and possibly four coalitionary kills were recorded by Starin (1994). In these cases, coalitions of females attacked and killed males attempting to enter their groups.

The lethal-raiding problem

In chimpanzees, humans, and some other animals, coalitionary killing can occur in the context of lethal raiding. Lethal raids are an unusual form of aggression because they do not escalate from a conflict. Instead, parties of allied males collectively invade a neighboring territory, seek one or more vulnerable neighbors, apparently assess the probability of making a successful attack, conduct a “surprise” attack that leaves one or more victims dead or dying, then return to their own territory. “Surprise” refers to the attack occurring without any initial conflict, without escalation from a lower level, and without the victim interacting with the opponents until the attack starts.

Thus, lethal raids indicate an appetite for hunting and killing rivals that is akin to predation. By contrast, most animal conflicts escalate in a stepwise manner that allows both opponents to assess each other and to withdraw when the risks of losing appear too high (Archer and Huntingford, 1994). The “appetite for lethal raiding” therefore requires explanation in different terms from escalated conflicts.

Among humans, lethal raids are widespread in all forms of warfare. For example, Keeley (1996) regards small raids and ambushes as “the commonest form of combat employed in primitive warfare” (see also Turney-High, 1949; van der Dennen, 1995; Maschner and Reedy-Maschner, 1998). Abundant evidence routinely attests to the blood-lust of the participants.

Against the notion that men have a ready appetite to attack their enemies, combatants in modern warfare are often reluctant to fight (Hinde, 1993; Ehrenreich, 1997; Grossman, 1999). This front-line lack of aggressiveness is understandable because in modern warfare, unlike intergroup aggression in primates, soldiers are organized hierarchically and are ordered into battle by their superiors, regardless of their personal motivation. Participation in raids among pre-state societies, however, is normally voluntary (Keeley, 1996). Thus, reluctance of soldiers under orders does not undermine the more widespread phenomenon of male eagerness for fighting.

It is likely that lethal raids also occur in some of the carnivore species that engage in intraspecific killing of adults. For example, lethal raiding is suggested by the report of Mech et al. (1998) that neighbors killed three members of a wolf pack, two others disappeared unseen, and the defeated pack’s territory was taken over by the killers. There are also reports of spotted hyenas making incursions into neighboring territories to attack neighbors (Goodall, 1986). Among invertebrates, patterns similar to lethal raiding occur in a variety of ants (Hölldobler, 1981; van der Dennen, 1995).

Among species other than humans, however, lethal raids have been most clearly reported in chimpanzees. Evidence of chimpanzee raiding has been fundamental for the development of the CVH. I therefore review the chimpanzee data in detail.

Lethal raiding by chimpanzees

Although lethal raiding among chimpanzees has been described more clearly than for any other mammal, few cases have been completely observed. Furthermore, all the detailed observations come from a single site, Gombe National Park in Tanzania (Goodall, 1986). Of course, lethal raids are expected to be rare, as they must be in any long-lived, slowly reproducing species. Nevertheless, the concentration of observational evidence at Gombe has suggested to critics of the CVH that lethal raiding may have been induced in Gombe by unnatural condi-

TABLE 2. Territorial behavior in chimpanzees and bonobos[1]

	P. t. schweinfurthii				*P. t. verus*	*P. paniscus*	
	Gombe	Mahale	Kibale	Budongo	Taï	Wamba	Lomako
Territorial defense	+	+	+	+	+	+	+
Border patrols	+	+	+	?	+	−	−
Deep incursions	+	+	+	?	+	−	−
Coalitionary attacks	+	+	?	?	+	−	−
Coalitionary kills	+	+	+	+	−	−	−
Border avoidance	+	?	+	?	+	−	−
Peaceful intercommunity association	−	−	−	−	−	+	+

[1] All long-term studies are included except for Bossou, where the community is isolated by agricultural land from its nearest chimpanzee neighbors. "Coalitionary kills" refers to adult victims only. "Coalitionary attacks" means non-lethal attacks by several males on a single victim. Data are from: Gombe (Goodall, 1986); Mahale (Nishida, 1979, 1986; Nishida et al. 1985); Kibale (Chapman and Wrangham, 1993); Budongo (V. Reynolds, personal communication); Taï (Boesch and Boesch, 1999); Wamba (Kano, 1992; Hashimoto et al., 1998); Lomako (White, 1996).

TABLE 3. Chimpanzees and bonobos: lethal violence by site[1]

Site	Subspecies	Adult deaths	Infanticides	Years of study
Gombe	*P. t. schweinfurthii*	6 (3)	6 (3)	38
Mahale	*P. t. schweinfurthii*	1 (6)	4 (6)	33
Kibale	*P. t. schweinfurthii*	2 (0)	1 (0)	11
Budongo	*P. t. schweinfurthii*	1 (1)	1 (1)	8
Bossou	*P. t. verus*	0 (0)	0 (0)	22
Taï	*P. t. verus*	0 (0)	0 (0)	19
Wamba	*P. paniscus*	0 (0)	0 (0)	24
Lomako	*P. paniscus*	0 (0)	0 (0)	15
Total		10–20	12–22	170

[1] Numbers include (for adult deaths) kills recorded on the basis of direct observation and/or fresh bodies as well as (in parentheses) those from suspicious disappearances (see Table 5), or (for infanticides) kills observed directly or (in parentheses) inferred from context (Arcadi and Wrangham 1999, updated for Mahale by Nishida (personal communication). "Years of study" is number of years from beginning of continuous study until 1998. Bonobo studies have been intermittent.

tions such as reduced habitat, or provisioning, and therefore that lethal raiding is uncharacteristic of chimpanzees more generally (Power, 1991).

There are six study sites in which habituation of chimpanzees is sufficiently good to allow multi-hour observations of known individuals traveling throughout the home range (Tables 2 and 3). These include four studies of the eastern subspecies (*P. t. schweinfurthii*), none of the two central subspecies (*P. t. troglodytes* and *P. t. vellerosus*), and two of the western chimpanzee (*P. t. verus*). In one of the *P. t. verus* studies, at Bossou, the study community is "semi-isolated" by loss of habitat, separated by several kilometers from the home ranges of its closest neighbors (Sugiyama, 1989; Sugiyama et al., 1993). Consequently there is no possibility of territorial behavior or intercommunity interaction from Bossou. This leaves five studies of chimpanzees, varying in duration from 8 to 38 years, that permit observation of intergroup interactions (Table 3).

Six components of chimpanzee intergroup aggression are especially relevant to lethal raiding: territorial defense (showing evidence of hostile intergroup relationships), border patrols, deep incursions, coalitionary attacks, coalitionary kills, and border avoidance (Table 2).

Territorial defense. This has been reported in all studies in which intercommunity relationships have been described, based on some combination of: counter-calling between parties of neighboring males; rapid travel toward a site where an opposing party has been detected; avoidance of opposing parties that were obviously larger; charging displays directed toward an opposing party of males; or one party chasing another (Nishida, 1979; Goodall, 1986; Boesch and Boesch, 1999; V. Reynolds personal communication; Wrangham et al., in preparation). For example on nine occasions chimpanzees in Taï have been seen in "back-and-forth attacks" with neighbors, in which all males rush toward the opponents, giving loud attack calls, and opponents may flee up to 400 m. In a further nine cases, males in the front line of attack were supported by loud calls from females in a rear line (Boesch and Boesch, 1999).

Border patrols. These are an intrinsic component of lethal raiding, because they put a party of individuals in a position to stalk and to hunt a neighboring victim. Border patrols are visits to a peripheral sector of a home range by a party of males that monitors the area. They are initiated without any immediate contact with members of the neighboring community, and are often undertaken with little or no feeding. According to Goodall (1986) and Boesch and Boesch (1999), they include some or all of the following features: (1) cautious and slow travel around or across the border, including long periods of gazing toward the neighboring home range; (2) nervousness shown toward unexpected sounds; and (3) inspection of signs of other chimpanzees, such as discarded food wadges, feces, nests, or abandoned termite-fishing tools.

Border patrols were first reported at Gombe in 1971 by JD Bygott, who was the first researcher to conduct regular all-day observations of individual males (Bygott, 1979). Most patrols at Gombe were by males of the principal study group, the Kasekela community, but the Kahama males patrolled also (Bygott, 1979; Wrangham, 1975). Border patrols do not occur every time a party reaches the boundary area. In Gombe, for example, patrols occurred during 28% of 134 boundary visits made by parties from the Kasekela community from 1977 to 1982 (calculated from Goodall, 1986, Table 17.1). Their frequency appears to vary as a function of relations between particular communities. Thus, during and after the 1974–1977 period, during which the Kasekela community killed the males of the neighboring Kahama community, Kasekela border patrols were disproportionately directed towards the Kahama territory (Goodall, 1986). The recorded frequency of border patrols by Kasekela males was highest in 1972–1973, when 13 border patrols occurred in 58 days of observation, i.e., a rate of 82 per year (Wrangham, 1975, Table 5.9). By contrast, in the 5 years following the extinction of the Kahama community (1978–1982), border patrols continued at a rate of 18 per individual per year (range 9–27; calculated from Goodall, 1986, Table 17.1).

Table 2 shows that border patrols have been reported also from Mahale, Kibale, and Taï. Border patrols have not been described in detail from Mahale, but key elements of border patrols have been reported—including scouting, and silent and cautious travel, mainly by males, in border areas (Nishida, 1979, 1990; Nishida et al., 1985). The Kibale evidence comes from border patrols seen at Kanyawara, involving parties of males intermittently checking their territorial boundaries (Wrangham et al., in preparation). In Taï, border patrols occurred in 29% of 129 territorial actions, normally involving at least four males, and included all of the elements listed above (Boesch and Boesch, 1999).

Deep incursions. These were included as part of border patrols by Goodall (1986), but I distinguish them because they involve deliberate travel into the neighboring territory rather than merely checking of the border area. Deep incursions are characterized by (1) substantial penetration into the neighboring territory, e.g., for one kilometer or more; (2) silent and cautious travel during periods of moving outwards from own territory; and (3) noisy and vigorous displays on return to their own territory. Deep incursions have been well described at Gombe and Taï. Boesch and Boesch (1999) found that "many patrols were probably aimed at finding and attacking strangers. . . . . . (they) were impressive by the intensity with which the males searched for strangers, not only entering deep (into) their territory, but once even heading backwards to find the neighbors." Deep incursions lasted up to 6 hours, and on 5 of 129 territorial interactions in Taï, led to attacks. All incursions were led by males.

Coalitionary attacks. These are interactions in which observers assess that the intent of those in the aggressive party is to hurt or to kill one or more victims. They can occur within the territory of either the aggressors or the victims, or in the boundary area. In Gombe, coalitionary attacks have included both interactions between the well-habituated Kasekela and Kahama communities, as well as other communities. In late 1974, for example, a party of three Kahama males encountered a male and female found to the south of their territory (the "Kalande" community). Two of the Kahama males grabbed and attacked the Kalande male, but he escaped without serious injury (Goodall, 1986).

In Mahale, cases included both attacks by M-group toward K-group males, and vice versa. For example, Nishida (1979) recorded three K-group males chasing an M-group male for 200 m. Two of the pursuers gave up, but the third caught the victim, forced him to the ground, bit his thigh, stamped on him, chased him as he tried to escape, but then suddenly gave up.

In Taï, Boesch and Boesch (1999) reported a category of attack which they called "commando," in which a party of males (with or without females) penetrated into the neighboring range and attacked one or more neighbors, i.e., a combination of a "deep incursion" with a coalitionary attack. The Taï males sometimes "waited and listened silently for hours before they attacked. We twice saw the study community being victim of a commando attack, in one of which Macho (an adult male) escaped with 19 wounds" (Boesch and Boesch, 1999). A second form of coalitionary attack was the "lateral attack" (seen six times), in which a party moved laterally while looking in the direction of strangers, then approached, chased, and on at least one occasion caught and attacked one of the opponents. This appeared to be a tactic for increasing the imbalance of power by isolating a victim from the rest of the party (Boesch and Boesch, 1999).

In Kibale, no complete coalitionary attacks have been seen, but twice parties of neighbors have silently charged toward isolated males of the Kanyawara study community, then veered off on seeing observers, suggesting that coalitionary attacks were averted by the presence of humans. In a third case, five Kanyawara males attacked an adolescent male and nulliparous female near the territorial border, but later retreated when confronted by four adult males from the neighboring community, who chased the aggressors for 700 m (M. Muller, personal communication).

Coalitionary attacks also occur within communities. For example, a bullying and insubordinate young adult male (Jilba) in Mahale's M-group was attacked so severely by six males and two females that it took him 3 months of traveling alone before he recovered sufficiently to rejoin the community (Nishida, 1994).

Coalitionary kills. No cases have been reported of dyadic violence leading to the death of an adult chimpanzee. However, lethal coalitionary attacks on adults have been reported from all four study sites of the eastern subspecies (Table 4). Table 4 lists known and inferred cases. The largest sample comes from Gombe and includes five observed brutal attacks followed by the disappearance of the victim (four male, one female), and one case of a fresh corpse of an unidentified female, considered to have been killed by the Kahama males. Goodall (1986) summarizes the observations as follows: the attacks lasted at least 10 min each; the victim was always held to the ground by one or more of the assailants while others attacked; the victim was dragged in at least two directions, eventually gave up resisting, and was essentially immobilized by the end of the attack.

In Mahale, Nishida et al. (1985) recorded the deaths of all six adult males of K-group community between 1969 and 1980. In Nishida's words, the observers "speculate that at least some adult males, particularly Sobongo and Kamemanfu, were killed by M-group's chimpanzees. Severe fighting was occasionally witnessed between males of K-group and M-group in (their area of overlap). . . . M-group's males were sometimes seen to penetrate into the core area of K-group's range from 1974 onwards" (Nishida et al., 1985, p 288). The males who disappeared were all healthy, not senile. In one case, M-group males were known to be very near to K-group males; there were many outbursts of calls; and the next day another

TABLE 4. All reported intraspecific kills of adult chimpanzees[1]

			Aggressor's		Victim's			
Result	Site	Date	Community	Party	Community	Party	Victim's ID	Ref.
Death	Gombe	1974	Kasekela	7M, 1F	Kahama	1**M**	Godi	Goodall (1986, p. 50)
Death	Gombe	1974	Kasekela	3M, 1F	Kahama	3**M**, 1F	Dé	Goodall (1986, p. 50)
Death	Gombe	1975	Kasekela	5M	Kahama	1**M**	Goliath	Goodall (1986, p. 50)
Death	Gombe	1977	Kasekela	6M	Kahama	1**M**	Sniff	Goodall (1986, p. 51)
Death	Gombe	1975	Kasekela	4M	Kahama	1**F**	Madam Bee	Goodall (1986, p. 51)
Death	Mahale	1995	M-gp	gang	M-gp	1**M**	Ntologi	Nishida (1996)
Death	Budongo	1998	Sonso	gang	Sonso	1**M**	Zesta (+2 injured)	K. Fawcett (personal communication)
Death	Kibale	1992	Rurama	gang	Kanyawara	≤1**M**	Ruwenzori	KCP
Death	Kibale	1998	Kanyawara	gang	Sebitole	≥1**M**	Unknown	KCP
Death	Gombe	1972	Kahama	?	Kalande?	≥1**F**	1F	Wrangham (1975)
Death	Gombe	1977	Kasekela	5M	Kahama	≥1**M**	Charlie	Goodall (1986, p. 50)
Death?	Mahale	1996	M-gp	?	M-gp	1**M**	Jilba	M. Huffman (personal communication), Hofer et al. (1998)
Death?	Mahale	1970-83	M-gp	?	K-gp	?	Some males?	Nishida et al. (1985)
Death?	Gombe	1981	Kalande	?	Kasekela	?	Humphrey killed?	Goodall (1986, p. 51)
Attack	Gombe	1974	Kahama	3 M	Kalande	1**M**, 1F	M attacked, caught by 2, escaped	Goodall (1986, p. 49)
Attack	Gombe	1980	Kalande	?	Kasekela	1**F**	Passion (inferred)	Goodall (1986, p. 51)
Attack	Mahale	1974	K-group	3M	M-group	1**M**	1 on 1 fight	Goodall (1986, p. 51)

[1] Parties for aggressors and victims show the number of adult males (M) and females (F). Letters in bold show the victim's sex. KCP (citation for Kibale deaths) is records of the Kibale Chimpanzee Project.

K-group male was missing (Kasonta) (T Nishida, personal communication).

In Kibale, after 3 days during which males from the Kanyawara and Rurama communities had been counter-calling at each other in a hostile manner, a Kanyawara male (Ruwenzori) was found freshly dead in the border area. His body, huddled face down at the bottom of a slope around which the vegetation had been beaten down, showed clear evidence of a violent attack by chimpanzees. In an unrelated incident, the Kanyawara males were followed by observers to the fresh corpse of an individual from a neighboring community (Sebitole) who had apparently been killed by chimpanzees the previous evening. There were numerous wounds on the front of his body, his trachea had been ripped through, and both testicles had been removed. Nine Kanyawara males had been patrolling the border on the previous evening, all of whom were present the next morning (17 hours later), and several of whom beat on the victim's body and dragged it about (M. Muller, personal communication).

Like coalitionary attacks, coalitionary kills also occur within communities. At Budongo in 1998, an adult male was killed by other males of his own community (K. Fawcett, personal communication). Intracommunity killing is also thought to have occurred in Mahale, where adult male Ntologi was found dead in the center of M-group's territory with numerous wounds on his body. His death followed several coalitionary attacks on him by his former subordinates—after his defeat as alpha-male of M-group

TABLE 5. Chimpanzee coalitionary kills of adults[1]

Site	Aggressor community	Victim's community	Kill seen, or fresh corpse	Suspicious disappearance	Reference
Gombe	Kasekela	Kahama	5	2	Goodall (1986)
Gombe	Kahama	Kalande	1		Goodall (1986)
Gombe	Kalande	Kahama		1	Goodall (1986)
Kibale	Rurama	Kanyawara	1		KCP
Kibale	Kanyawara	Sebitole	1		KCP
Mahale	M-group	K-group		6?	Nishida et al. (1985)
Mahale	M-group	M-group	1	1	T. Nishida (personal communication)
Budongo	Sonso	Sonso	1		K. Fawcett (personal communication)
Total			10	10?	

[1] Intra-community aggression is indicated by the victim and aggressors being in the same community. KCP, records of the Kibale Chimpanzee Project.

(Nishida, 1996; T. Nishida, personal communication).

The chimpanzee data are summarized in Table 5. Tables 4 and 5 also list suspicious disappearances. These are cases where observers believed the most likely explanation for disappearances was that they were killed by neighbors, because: (1) those who disappeared were healthy and not senescent; (2) other causes of death appeared improbable; and (3) the disappearances occurred at a time and place where there were patently hostile relationships with a neighboring community.

Although the reported episodes of lethal coalitionary violence are still few, the killings are noteworthy because they have been reported from four sites and, in relation to total observed adult deaths, they appear to be demographically significant. In Gombe, data reported by Goodall (1986) indicate that for adult males in Kasekela and Kahama, the proportion of adult male mortality from intraspecific coalitionary aggression was 30–40%. Although fewer kills have been seen elsewhere, it seems likely that this variation is partly a function of observation time. Thus, Figure 1 shows that in relation to observation time, the number of observed and suspected kills appears similar in the four *schweinfurthii* study sites. The idea that as observation years accumulate, more killing will be seen, is supported by the data on infanticides, which show a similar trend (Fig. 1). In summary although the evidence needs to be substantiated by continuing observation, current evidence is that in all four populations of the eastern subspecies, adults kill each other occasionally through coalitionary violence. Figure 1 suggests a rate of approximately 0.25 adults killed per year.

On the other hand, there is no evidence of lethal intraspecific aggression toward either adults or infants from either of the studies of the western subspecies, i.e., from Taï or Bossou. Because the Bossou community has no neighbors and few males, low rates of aggression are not surprising. However, as demonstrated by Figure 1, lethal coalitionary aggression would be expected to have been seen at Taï: the study is now 21 years old and should therefore have produced evidence of about five killings each of adults

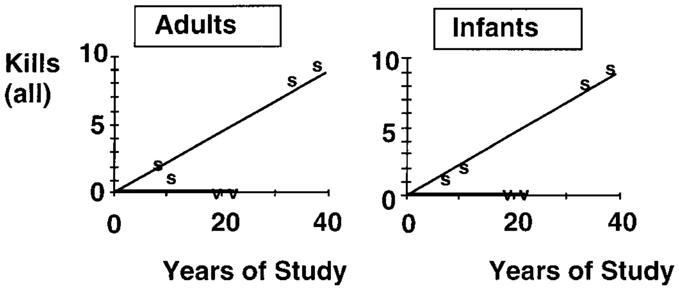

Fig. 1. Chimpanzee intraspecific killings by study site. S, *P. t. schweinfurthii;* v, *P. t. verus.* See Tables 3 and 4 for data and sources.

and infants if this population conformed to the *schweinfurthii* pattern. Although the sample sizes are small, the fact that Taï chimpanzees show all components of lethal raiding but no coalitionary kills suggest that the nature of aggressive relationships differs between Taï and the eastern populations (below).

Finally, *border avoidance* is expected if individuals are aware that the border is physically dangerous. Low frequency of use of border areas has been documented by Boesch and Boesch (1999), who found that in Taï 75% of time was spent in the central 35% of the range. When Gombe or Kibale (Kanyawara) chimpanzees do visit border areas, they tend to do so in parties that are relatively large (Gombe) and contain a higher proportion of males than normal (Kanyawara) (Bauer, 1980; Chapman and Wrangham, 1993). Finally, high prey densities in border areas have been reported for the main prey species of chimpanzees, red colobus (*Colobus badius*), both in Gombe (Stanford, 1998b) and Kibale [Ngogo (D. Watts, personal communication)]. Similarly among wolves, prey densities are higher in border areas between territories, a result of avoidance of those areas by wolves (Mech et al., 1998). Border avoidance by territory holders has not been reported in other nonhuman species, but is presumably widespread in humans.

In summary, there are five study sites (Gombe, Mahale, Taï, Kibale, Budongo) in which chimpanzees have neighbors and where intercommunity interactions have been at least partly described or observed (Table 2). At the three best-documented sites (Gombe, Mahale, Taï) patterns of territorial interaction appear similar: all of them show territorial defense and border patrols by adult males, with violent coalitionary attacks on neighbors. All these patterns are similar to the data on wolves, which is the only other nonhuman mammal with fission-fusion grouping and group territories in which intergroup interactions have been well described. These points suggest that all the major elements of lethal raiding are routinely present in populations of chimpanzees.

The known kills at Gombe occurred between 1973 and 1977, during a period of intense hostility between two communities that had recently split from a single community, and which were each dominated by two alpha-males with mutually hostile relations (Goodall, 1986). Border patrols by Kasekela males were directed mostly toward the Kahama community during this period, which ended with the extinction of the Kahama community (Goodall, 1986). Thus, unusual demographic and social conditions applied to elicit this particular bout of lethal raiding.

Therefore, nonlethal raiding is a routine component of the chimpanzee behavioral repertoire. Coalitionary killing is less common. However it has been recorded in four out of five sites. This raises the question of why chimpanzees have an appetite for agonistic interactions with members of neighboring communities, and why they sometimes kill opponents.

THE IMBALANCE-OF-POWER HYPOTHESIS

Explaining chimpanzee violence

Many reasons have been advanced to account for chimpanzee lethal raiding, including: male–male bonds, hostility toward outsiders, cooperative group living, cooperative hunting skills, power imbalances when parties from neighboring communities meet, large and overlapping home ranges, high cognitive ability, and innate killing potential (reviewed by van der Dennen, 1995). The only attempt at a cost-benefit analysis that explains the species distribution of lethal raiding, however, is the imbalance-of-power hypothesis. This hypothesis was implied by Goodall (1986), then elaborated by Manson and Wrangham (1991), Wrangham and Peterson (1996), and Wrangham (1999b). The imbalance-of-power hypothesis proposes that the function of unprovoked intercommunity aggression (i.e., deep incursions and coalitionary attacks) is intercommunity dominance. By wounding or killing members of the neighboring community, males from one community increase their relative dominance over the neighbors. According to the imbalance-of-power hypothesis, the proximate benefit is an increased probability of winning intercommunity dominance contests (nonlethal battles); this tends to lead to increased fitness of the killers through improved access to resources such as food, females, or safety.

The imbalance-of-power hypothesis contrasts with proposals that chimpanzees are exceptionally capable of conducting attacks, or win particularly large rewards from intergroup competition.

The significance of power imbalances

Both within and between primate groups, contests tend to be won by the larger of two coalitions, though variables such as dominance rank and geographic location are also important (Cheney, 1986; Chapais, 1995). Coalition size appears even more important for interactions among chimpanzees from different communities. In the four longest studies of chimpanzees, the principal determinant of the nature of intercommunity interactions is not the geographic location but the relative size and composition of parties when they encounter each other. This conclusion is based on direct observations at Gombe, Kibale, Mahale, and Taï (Bygott, 1979; Nishida, 1979; Goodall, 1986; Boesch and Boesch, 1999; Wrangham et al., in preparation), as well as playback experiments at Kibale (M Wilson et al., personal communication). For example, Boesch and Boesch (1999) found that small parties of males (1–3) mainly checked for the presence of strangers by drumming and listening to the response (67% of 18 occasions). Middle-sized parties (4–6 males) tended to make incursions into the neighboring territory more often (37% of 76 observations). Large parties (7–9 males) tended to attack the strangers (63% of 30 observations). More generally, at all sites, the probability that a party will advance, exchange displays, or retreat appears to be well predicted by whether it is larger than, equal to, or smaller than the opposing party (Boesch and Boesch, 1999). Relative party size is also a critical variable among lions (McComb et al., 1994; Grinnell et al., 1995).

The evidence therefore suggests that chimpanzee parties are bolder when they contain relatively more males. In addition, playback experiments at Kibale support the hypothesis that males are more likely to attack when a party of three or more males encounters a lone victim (M Wilson et al., personal communication), supporting the observational data from Gombe. These observations make sense because to date, there appear to be no records of any aggressors receiving serious wounds.

In light of such data, several authors have proposed that it is the ability of a gang of three or more males to overwhelm a lone victim, at low risk of injury to themselves, which at least partly explains why chimpanzees are so ready to attack (Goodall, 1986; Manson and Wrangham, 1991; Wrangham and Peterson, 1996; Boesch and Boesch, 1999). The logic is that a victim can be held down or otherwise disabled by two or more, while another aggressor can impose damage at will. This idea that the low cost of lethal aggression elicits lethal raiding is central to the imbalance-of-power hypothesis (Manson and Wrangham, 1991; Wrangham and Peterson, 1996).

Origins of power imbalances

All chimpanzee populations have fission-fusion grouping patterns, with individuals sometimes alone and sometimes in parties (Fig. 2), and adult males more gregarious than mothers (Wrangham, 1999a). Demographic, social and ecological variables influence party size (Boesch, 1996). For example, party size increases both with the number of females having sexual swellings, and with the amount of fruit in the habitat (Nishida, 1979; Goodall, 1986; Boesch, 1996; Wrangham, 1999a). Parties appear to be constrained by fruit availability as a result of scramble competition, with larger parties formed more when fruit is sufficiently abundant to allow gregariousness (Chapman et al., 1995).

Neighboring communities can experience markedly different levels of fruit supply, a result of differences in fruit-tree density, or in fruiting success (Chapman et al., 1997). This means that, on occasion, neighboring communities may contain parties of different mean size. The community in which parties are able to be larger can then make low-risk raids to attack neighbors. This socioecological connection has been observed in Mahale, when the M-group community

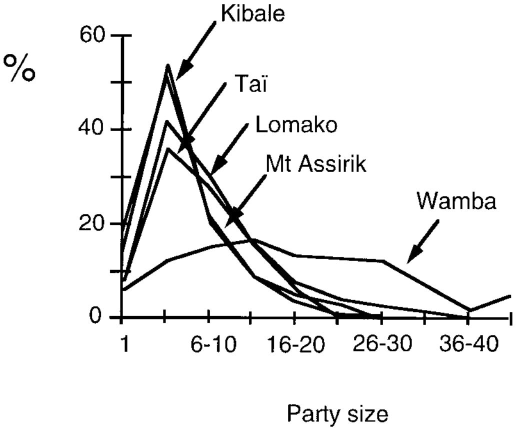

Fig. 2. Party size distribution among chimpanzees and bonobos. Data sources: eastern chimpanzee *P. t. schweinfurthii:* Kibale, Kanyawara community 1994–1996. Western chimpanzee *P. t. verus:* Taï (Boesch, 1996); Mt. Assirir (Tutin et al., 1983). Bonobo *P. paniscus;* Wamba (Kuroda, 1979); Lomako (White, 1988). All populations show substantial variation in party size over time and between communities. Comparable data for Gombe and Mahale were not found.

would make seasonal forays into the territory of the K-group community, supplanting K-group parties and sometimes attacking them (Nishida, 1979).

Why are chimpanzees (compared to other species) particularly vulnerable to the pressures of scramble competition that lead to a fission-fusion, rather than a stable-troop system of grouping? Wrangham et al. (1996) argued that the important characteristic of chimpanzees is that even when fruits are scarce, individuals continue to search for them. Consistent with this hypothesis, chimpanzees (unlike gorillas) are restricted to areas that contain year round fruits, and spend significantly greater proportion of their feeding time eating ripe fruits than do sympatric frugivorous monkeys (Wrangham et al., 1998). This strategy of constant fruit search is presumably forced on chimpanzees by species-specific digestive adaptations, such as the rate of food passage through the gut and the ability to ferment long-chain carbohydrates (Milton, 1987). Whatever its origins, it exposes them to relatively intense scramble competition.

The imbalance-of-power hypothesis states that violence is facilitated by vulnerability, because lone individuals can be vigorously attacked by a coalition at low risk to the aggressors. This means that populations (or seasons) with fewer encounters between solitaries and large groups should have fewer violent interactions. Data on wolves at Denali (Alaska) offer a test of this prediction. The ratio of the number of parties containing three or more wolves to the number of solitary individuals was higher during winter (5.2) than summer (0.1). This means that solitaries were much more likely to encounter a large party during winter than summer. As expected, winter was also the season when intraspecific kills were more likely (a sevenfold increase in probability, from 22 dated kills) (data calculated from Figs 5.4 and 5.7, Mech et al., 1998).

If a similar effect applies to chimpanzee populations, and if the fact that Taï has had a low kill rate is meaningful (rather than stochastic), Taï should have larger, less fissioned parties than at Gombe, Mahale, or Kibale. Preliminary data suggest this prediction is qualitatively correct, because Boesch (1996) found that among six chimpanzee populations, the mean party size was highest at Taï (8.3, compared to a mean of 5.2 ± 0.8 at the other five sites, including Gombe, Mahale, and Kibale). The percentage of lone individuals was also lowest in Taï (4%, compared to 14% ± 3% for the three populations with data, Boesch, 1996, Table 8.2). These data thus indicate consistently larger parties in Taï than elsewhere, compatible with evidence that Taï is a relatively productive habitat (Boesch and Boesch, 1999).

Further data will test whether party size and the frequency of high-intensity aggression do indeed co-vary among sites, and how often chimpanzee populations tend to have small parties and high rates of aggression. Two points suggest that the high frequency of intense aggression seen at Gombe and suggested by the other eastern chimpanzee populations may be unusual for the species as a whole. First, skeletal trauma indicative of intraspecific aggression has been found at higher rates in a sample of chimpanzee crania from Gombe than from elsewhere (Jurmain, 1997). Second, the four *P. t. schweinfurthii* study sites (Gombe, Mahale, Kibale, and Budongo) are all located at the extreme east of the species geographical range, where dry seasons are relatively long. These eastern populations may therefore be living under relatively harsh conditions of food availability compared to more western sites.

In summary, chimpanzees are vulnerable to particularly intense scramble competition, apparently because of their digestive adaptations to ripe fruit. This competition forces them to travel alone or in small parties when fruits are scarce. Patchy fruit distribution can mean that one community has abundant supplies, while its neighbors have few. Demographic differences between communities (i.e., differences in the number of adult males) may also mean that parties in one community can be dominant over those in the neighboring territory. Such factors can account for differences between populations or communities in the number of males in parties, and hence for differences in their vulnerability to attack by coalitions of neighbors.

Group territoriality and the benefits of lethal raiding

Understanding the selective advantage of aggression is more complicated for intercommunity than interindividual relationships, because any fitness benefits gained by a rise in intercommunity dominance are shared among individuals within the community. This might be expected to favor free-riders (individuals who would benefit from lethal raiding without taking part), which would lead to a suboptimal level of collective action (van Schaik, 1996; Nunn, 1999). In fact, however, there is no evidence of defection among raiding chimpanzees (Goodall, 1986; Wilson et al., personal communication) [(or, for that matter, among lions in similar intercommunity contexts (Grinnell et al., 1985)].

How lethal raiding escapes the free-rider problem is not understood. One possibility is that intercommunity conflict has been so intense that selection has occurred at the between-group level (Boehm, 1999). However, this is unlikely because it would require very frequent group extinctions with few survivors. Another is that free-riders are policed by others in the community (Boehm, 1999), but no evidence suggests that this occurs in chimpanzees. Others are (1) that the benefits of raiding rise so steeply with increased party size that it pays individuals to participate for selfish reasons or (2) that chimpanzees have evolved exceptional cooperative abilities in contexts other than lethal raiding (C. van Schaik, personal communication). This remains an important problem, as it does for much of human behavior (Boehm, 1999).

On the other hand, the occurrence of territoriality among chimpanzee communities, and of occasional imbalances of power between parties from neighboring communities, are easily explained. First, current theory suggests that home ranges are economically defensible if individuals can easily cross their home range in a day. Chimpanzees can do so (Lowen and Dunbar, 1994; see also van Schaik, 1996). Second, a system of fission-fusion grouping can explain why lone individuals occasionally encounter larger coalitions, and are therefore vulnerable to attack.

But neither long day ranges nor fission-fusion grouping can explain lethal raiding, in which individuals seek opportunities to attack (as opposed to responding to invasion, escalated contest for resources, etc.). As Goodall noted, for example, there have been three major invasions at Gombe and Mahale. "Kasekela males took over Kahama range, Kalande males pushed deep into Kasakela range, and M-group moved into K-group range. During all these invasions adult males (and some females) were killed or disappeared. Even if it is argued that the Kasekela males were merely trying to reclaim an area to which they previously had free access, the assertion does not explain the northward thrust of the Kalande community or the takeover by the M-group at Mahale" (Goodall, 1986, p. 528).

Two kinds of hypothesis have been presented to account for such incursions, proximate competition and dominance drive. First, aggression may be proximately elicited by resource competition, such as for mates, food, or land (Manson and Wrangham, 1991). This hypothesis is strongly supported by some observations, such as the incursions by Mahale's M-group into the K-group range. These occurred in a seasonal rhythm coincident with fruit shortages in M-group's range and abundant fruits in K-group's range (Nishida, 1979). Again, in certain circumstances raiding might help males to recruit young females: this possibility is suggested by evidence at Gombe that severe attacks on the mothers of nulliparous females in neighboring communities are sometimes followed by the young females joining the aggressor's community (Goodall, 1986).

Alternatively, aggression may be elicited merely by the opportunity to reduce the coalitionary power of the neighbors (Manson and Wrangham, 1991; Wrangham and Peterson, 1996). According to this "dominance drive" hypothesis, no resources need be in short supply at the time of the raid. Instead, unprovoked aggression is favored by the opportunity to attack "economically," that is, at low personal risk. If raiding leads to the wounding or death of a neighboring male, the neighboring community's competitive ability is substantially reduced. For example, if the neighboring community has 10 males, its fighting power is reduced by 10%. This reduction lasts for a considerable time, because the system of male philopatry means that a dead male can be replaced only via births within the community, which is a slow process. The aggressors' probability of winning future intercommunity contests (battles, not raids) will therefore be significantly increased by killing a neighboring male. The increase in relative fighting power can be expected to enable a community to enlarge its territory, as suggested by preliminary evidence of a correlation between the number of males and territory size at Gombe (Stanford, 1998b). Over the long term, therefore, if fitness is correlated with territory size, successful raiding is expected to increase the raiders' fitness.

This "between-community dominance drive" hypothesis for explaining aggression between groups is therefore similar to the "within-community dominance drive" hypothesis, which contributes to explaining patterns of aggression between individuals within dominance hierarchies (Popp and DeVore, 1979; Chapais, 1995). Within chimpanzee communities, for example, male aggression occurs predictably over status; weakness of a dominant due to aging, wounding, loss of allies or loss of confidence increases the rate of attack by a subordinate (Bygott, 1979; de Waal, 1982; Goodall, 1986; Nishida, 1994). Selection is expected to favor the effort to rise in dominance because dominant individuals (or groups) tend to have high fitness, and accordingly, individuals opportunistically take advantage of any perception of changes in power asymmetry (Chapais, 1995).

Sometimes, admittedly, the expectation that higher dominance leads to higher fitness is not met. Thus, in around half of the studies between dominance and reproductive success within primate groups, there was no relationship. However, in the other half, dominants had higher fitness than subordinates (Harcourt, 1987; de Ruiter and van Hooff, 1993; Ellis, 1995). This means that even though increased dominance does not always lead to higher fitness, it pays on average.

Therefore, according to the dominance-drive hypothesis, a necessary and sufficient condition for intercommunity aggression is a perception that an opponent is sufficiently vulnerable to warrant the aggressor(s) attacking at low risk to themselves.

The dominance drive hypothesis appears useful for explaining why carnivores share lethal coalitionary violence with chimpanzees. As expected by both the proximate competition and dominance drive hypotheses, fission-fusion grouping and intergroup hostility occur in these species (Table 6). The proximate competition hypothesis also predicts, however, that the type of food supplies, mating system and/or coalitionary bond should be similar in allowing benefits to be gained from raiding or killing neighbors. However, the four species of carnivores in which lethal coalitionary violence has been recorded show various combinations of mating systems and coalitionary bonds, all different from those found in chimpanzees (Table 6). For example, intergroup transfer is in some species primarily by males, in others primarily by females. Therefore, lethal violence cannot be uniformly explained as resulting from competition over females. Because the carnivore species in Table 6 vary in the type of benefits to be gained by

TABLE 6. *Intergroup aggression in fission-fusion species with group territoriality*[1]

	Chimpanzee	Human	Wolf	Lion	Spotted hyena	Cheetah
Battles	Y	Y	Y	Y	Y	?
Kill adults	Y	Y	Y	Y	Y	Y
Lethal raid	Y	Y	Y	Y?	Y?	?
Food supplies	Dispersed	Variable	Clumped	Clumped	Clumped	Dispersed/ clumped
Coalitionary bonds among	Males	Males	Pair + Helpers	Females; Males	Females	Males

[1] "Kill adults" is shown separately from "Lethal raid" because, in hyenas and lions, it is not clear if killing of neighbors occurs with lethal raids, or merely when invaders are discovered and killed by residents. "Dispersed" food supplies imply that individual food-patches are not defensible, whereas "clumped" foods can be individually defended (e.g., carcasses). Coalitionary bonds are bonds in which adults support each other in aggression against others. Sources for mating system and coalitionary bonds are Kruuk (1972) (spotted hyenas), Grinnell et al. (1995), and McComb et al. (1994) for lions, and Mech et al. (1998) for wolves. For other sources, see text.

intergroup dominance, the dominance drive hypothesis explains similarities in their tendency to use lethal violence more easily than the proximate competition hypothesis.

The proximate competition and dominance drive hypotheses are closely related, because in both cases, the ultimate benefits of dominance are increased success in resource competition. The proximate competition hypothesis is favored if raiding is elicited by the presence of stealable resources, or if benefits accrue immediately after a raid. On the other hand, unprovoked deep incursions and attacks on males without any obvious reward are better explained by the dominance drive hypothesis. To differentiate these hypotheses more clearly, data are needed on the proximate stimuli that elicit aggression. Since current information suggests that chimpanzee raids are often initiated without the raiders perceiving mates or food sources, the dominance drive hypothesis appears relevant to explaining the timing and direction of lethal raiding.

Sex differences in territoriality and aggressiveness

Among chimpanzees, males have to date been the only observed killers and aggressors in intergroup interactions, and males are also more likely than females to be victims (Table 4). Among humans, warriors are also overwhelming male (Adams, 1983). This contrasts with spotted hyenas, where females are more aggressive than males (Kruuk, 1972; Frank, 1986; East and Hofer, 1991; Henschel and Skinner, 1991); and with wolves, where both sexes are killed at high rates, and there is no evidence of a sex difference in aggressiveness (Mech et al., 1998). Why, therefore, are males the principal perpetrators of aggression in chimpanzees and humans?

Traditional explanations are that males are more expendable, or that males have more to gain simply because they have higher variance in fitness than females do (reviewed by van der Dennen, 1995). However, such general explanations do not account for species variation in the intensity of female participation. Nor does the degree of sexual dimorphism in body size, because among nonhuman primates, sexual dimorphism in body size is not correlated with female involvement in intergroup aggression (Manson and Wrangham, 1991).

Male bonding, which is especially pronounced among chimpanzees and humans, has often been proposed to be an important influence (reviewed by van der Dennen, 1995). This idea is supported by the fact that both in humans and nonhuman primates, populations with more patrilocal residence (or male philopatry) have relatively greater tendency for aggressors to be male (Adams, 1983; Manson and Wrangham, 1991).

The ultimate origins of male bonding are still debated. In chimpanzees, males are more gregarious than mothers, possibly because, as a result of carrying and waiting for infants, mothers travel slowly (Wrangham, 1999a). The relative mobility and gregariousness of males means that they can use allies to dominate access to their home ranges, excluding other males and thereby forcing male philopatry. As a result, a system evolves in which it pays to eradicate males from neighboring communities (Wrangham, 1999a,b).

According to this logic, therefore, male bonding has two effects. First, it contributes to the development of male philopatry and the benefits of excluding nongroup males, thereby raising the stakes in territorial encounters. Second, it makes available allies that enable a larger party to dominate a smaller party.

None of this means, however, that male participation is a necessary condition for the evolution of lethal violence in territorial interactions. As wolves, spotted hyenas and ants show, coalitionary territoriality can be carried out by both sexes, or even primarily by females. The comparative evidence, therefore, suggests that lethal raiding in chimpanzees and humans cannot be attributed to the fact that bonds among adults are primarily among males.

Bonobos: exceptions that support the rule?

Intercommunity relations among bonobos sometimes involve fights between large parties, but as a species they appear to be substantially less hostile to each other than are chimpanzees (reviewed by Wrangham and Peterson, 1996; Stanford, 1998a). First, bonobos have never been seen to engage in lethal raiding, nor indeed in any components of such behavior (Table 2). Second, they can include markedly peaceful interactions, in which individuals from neighboring communities rest, travel, copulate, play, and groom together (Idani, 1991; White, 1996). In contrast, peaceful interactions involving males of neighboring communities have not been seen among chimpanzees.

In view of the anatomical and phylogenetic similarities between chimpanzees and bonobos these differences are remarkable. Three kinds of explanation suggest themselves.

First, the facts may be misleading; more prolonged observation may reveal lethal raiding in bonobos (Stanford, 1998a). However, this eventuality appears unlikely because at Gombe, Mahale, Taï, and Kibale components of lethal raiding were seen shortly after individuals were observed near the community range borders. Among bonobos, by contrast, interactions are seen at range borders without the components of lethal raiding.

Second, relatively peaceful intercommunity relationships in bonobos may be an incidental result of a reduction in the level of within-community violence compared to chimpanzees. For example, fewer violent behavioral interactions of all kinds occur among bonobos: no sexual coercion, no infanticide, no brutal fights among males or females competing for dominance, no male beatings of females (Wrangham and Peterson, 1996; Furuichi et al., 1998). The same is true in captivity (de Waal and Lanting, 1997; Stanford, 1998a). Collateral evidence comes from a survey of cranial and postcranial skeletal trauma that concluded that in chimpanzees (and gorillas), but not in bonobos, there was evidence of serious risk from interindividual aggression (Jurmain, 1997) and from the generally less robust and less sexually dimorphic morphology of bonobos than chimpanzees (Zihlman and Cramer, 1978; Shea, 1984). Pending further data, bonobo males consistently appear to be less violent than chimpanzees.

Accordingly, a possible hypothesis is that selection may have favored a generally less aggressive male temperament in bonobos, as opposed to a loss of motivation specifically for lethal raiding. The reasons why male bonobos are generally less aggressive than male chimpanzees could derive from the dominance of males by powerful female–female coalitions, or the greater importance of mothers than other males as allies for individual males, or other social dynamics occurring within communities (Kano, 1992; Parish, 1996; Wrangham and Peterson, 1996; de Waal and Lanting, 1997). The important point is that the reduced tendency for lethal raiding would be viewed as an incidental consequence of a more general reduction in male aggression. This hypothesis is challenged, however, by species that have aggressive intergroup interactions despite having peaceful relationships within groups (e.g., female lions). Furthermore, the tendency to engage in lethal raiding seems unlikely to be selectively neutral, considering its potentially large effects on dominance relationships between groups and the time and effort spent on raids. I therefore conclude that the low tendency for lethal raiding in bonobos is not merely an incidental consequence of the benefits of within-community peacefulness.

The third kind of explanation is that among bonobos, important components of lethal raiding has been specifically selected against. Under what circumstances could this occur? According to the imbalance-of-power hypothesis, lethal raiding is favored by a combination of coalitionary territoriality and imbalances of power sufficient to allow one party to kill victims of the rival community with impunity. Since lethal raiding is absent even though coalitionary territoriality occurs among bonobos, the imbalance-of-power hypothesis predicts that compared to chimpanzees, bonobos must experience greatly reduced power imbalances between rival parties.

In general, variance in bonobo party size is less than among chimpanzees, even when average party size is similar (Chapman et al., 1994). This is as expected from the imbalance-of-power hypothesis. However, the more critical question is how often bonobos are forced to travel alone, because individuals can be killed (at minimal cost to the aggressors) only when they are found alone by a rival party. The two principal bonobo study sites both indicate that lone travel is rarely forced by ecological pressures. In Wamba, bonobos usually range as one or two large mixed parties averaging more than ten individuals (Hashimoto et al., 1998). In Lomako, where feeding competition appears more intense than in Wamba, females remain in multi-female parties even during the seasons when fruit is least available (White, 1998). Such observations suggest that compared to chimpanzees, the intensity of feeding competition is substantially reduced among bonobos (Chapman et al., 1994; Wrangham et al., 1996; White, 1998). As a result, extreme imbalances of power appear unlikely to occur between parties meeting from neighboring communities.

Whether the apparent difference in the intensity of feeding competition between chimpanzees and bonobos is sufficient to satisfy the imbalance-of-power hypothesis, however, remains to be proven. In Lomako, male bonobos spend increased time alone during periods of fruit scarcity (White, 1998). White (1998) suggests that these males choose to travel alone in order to track the increasingly dispersed female parties, but according to the imbalance-of-power hypothesis, it should be dangerous for them to do so. However, if solitary travel is a social option rather than a strategy dictated by ecological pressures, it may be possible for bonobos to restrict their solitary periods to times and locations when they can assess that they are safe. More quantitative data will be needed to test such ideas.

One of the only other species of primate in which lethal raiding might be expected from the imbalance-of-power hypothesis are spider monkeys *Ateles* spp., because spider monkeys have a fission-fusion grouping system like chimpanzees: individuals sometimes travel alone and sometimes in larger parties. Furthermore, males are more gregarious than mothers, and they form coalitionary bonds with each other against neighboring groups (Chapman et al., 1995). On the other hand, spider monkeys are wholly arboreal, which may reduce their ability to use coalitionary aggression. Among baboons *Papio anubis,* for example, coalitions of low-ranking males are effective in defeating a single higher-ranking male on the ground, but not in trees (Smuts, 1986). Further data on the effect of arboreality on power asymmetries between coalitions and solitaries is therefore desirable.

The imbalance-of-power hypothesis and the evolution of human warfare

Peace is the normal human condition, in the sense that most human groups, for most of the time, are not at war (Ferguson, 1989; Sponsel, 1996). Nevertheless, ethnographic and historical records clearly show that warfare is a frequent practice (Keeley, 1996; Manson and Wrangham, 1991; van der Dennen, 1995). Increasingly, archaeological data suggest that violence has often been a statistically important source of death, and it is sometimes possible to infer that the violence was coalitionary (Keeley, 1996; Larsen, 1997). In small-scale societies, the commonest form of war interaction is a raid (e.g., Turney-High, 1949; Keeley, 1996; Maschner and Reedy-Maschner, 1998). Even if humans are routinely peaceful, therefore, war needs to be explained. Because warfare includes a variety of types of interaction (such as raids and battles), it will require multiple explanations.

The myriad hypotheses proposed to explain why humans practice raids and other forms of warfare fall into three general classes. Maladaptive hypotheses suggest that warfare results from an originally adaptive aggressive tendency that, as a result of subsequent developments such as the invention of weapons, became disadvantageous even to the winners (e.g., Lorenz, 1966). They suffer from the theoretical problem that if warring tendency is indeed disadvantageous, it has such large effects that it should be selected against rapidly. However, it seems unlikely that winners fare badly.

Neutral hypotheses are currently more popular, though they also suffer from the selective-disadvantage problem. They suggest that warfare should be regarded as deriving merely from a capacity, or potential, resulting from our cognitive creativity. Neutral hypotheses consider warfare to be elicited by environmental and social stimuli that have no evolutionary significance (e.g., Bock, 1980; Keeley, 1996; Gould, 1996). They are often based on the (erroneous) premise that behaviors that vary among populations cannot be explained in terms of natural selection without assuming genetic differences between populations (see Discussion).

The imbalance-of-power hypothesis exemplifies a third kind of hypothesis that views warfare as adaptive and rooted in genetic predispositions. It suggests that raiding derives from the advantages of gaining intergroup dominance and an ability to assess power imbalances in an environment of intergroup hostility and power imbalances between parties from neighboring communities. As in chimpanzees, it raises the question of why territories are defended by males rather than females. By analogy with the argument for chimpanzees, male rather than female territoriality derives from the high cost of travel experienced by mothers (Wrangham, 1999a). This cost reduces mothers' ability both to defend a range and to form alliances.

Both intergroup hostility and a fission-fusion grouping system are universal in contemporary human populations, whether tribal or nation-state (Rodseth et al., 1991). Whether these features were characteristic of humans in prehistory is unknown. However, with the exception of brain size, human morphology has changed relatively little during the last 1.9 million years (Wolpoff, 1998), suggesting that the essential ecology of human prehistory may been rather stable prior to agriculture. The essence of theories about fission-fusion grouping in chimpanzees is that fission is a response to high costs of scramble competition (Chapman et al., 1995); scramble competition is expected to be more intense in species that depend on rare, high-quality foods (Janson and Goldsmith, 1995), and humans appear adapted to high-quality foods (Milton, 1987; Leonard and Robertson, 1997). Following this line of argument, fission-fusion grouping is expected to have been characteristic of human evolutionary history.

Based on the ubiquity of xenophobia and ingroup-outgroup bias in contemporary populations, intergroup hostility is normally assumed to have been routine in human prehistory. The likelihood of intergroup hostility in prehistory is supported also by its prevalence among nonhuman primates (Cheney, 1986). The form of hostility can be inferred as being territorial, because among primates, territories tend to be found in species with long day ranges in relation to home ranges, and are predicted to occur more easily where groups are split into multiple parties (Mitani and Rodman, 1979; Lowen and Dunbar, 1994). The long day ranges of contemporary forager men [e.g., 9 km (Bailey, 1991)] and the probability of fission-fusion foraging suggest that territoriality would have been possible where home ranges were not immense.

The imbalance-of-power hypothesis is thus compatible with conventional views of human prehistory. It can in theory be challenged by evidence that recent prehistoric ancestors foraged in stable parties, or had ways of reducing power imbalances between rival parties, or had little intergroup hostility, though such evidence would in practice be difficult to obtain.

On cladistic grounds, various authors have hypothesized that lethal raiding in humans and chimpanzees shared a common origin around 5–6 mya, and has been present continuously in the subsequent evolution of each species (Wrangham, 1987; Ghiglieri, 1988; Wrangham and Peterson, 1996; Otterbein, 1997). This hypothesis is currently untestable. A key issue for human ancestry is whether australopithecine ancestors of humans foraged in temporary parties (i.e., with fission-fusion) or in stable groups. Answers to such questions are needed before we can be confident whether lethal raiding in chimpanzees and humans represents a synapomorphy or a homoplasy.

CHALLENGES TO THE IMBALANCE-OF-POWER HYPOTHESIS

Uncertainty in the chimpanzee data

The evidence of lethal raiding in chimpanzees comes from few cases and a small number of populations, some of which have experienced significant anthropogenic influences. This has led to doubts about the importance of lethal raiding as a species trait among chimpanzees (Power, 1991; Sussman, 1997).

For example, Power (1991) accepts that the descriptions of chimpanzees in Gombe, Mahale, and Kibale as violent and status-striving are accurate, but regards the behaviors as nonadaptive consequences of excessive ecological stress. A central concern for Power (1991) is why there was a shift in the perception of chimpanzee society from peaceful to violent, beginning in the 1970s based on observations after the first 5 years of Goodall's study (1960–1965). She argues that the 1960s view of chimpanzees living in a peaceful society was the "correct" one, and that subsequent observations of violence reflect a social environment stressed by various kinds of human-induced disturbance. In support, she cites the fact that intense aggression was seen rarely in early chimpanzee studies, especially at Gombe, Budongo, and Kibale (Ngogo community). She notes that in studies where violence has been reported, either humans have provided food for the chimpanzees (Gombe, Mahale), or the forest has been disturbed by encroachment or logging (Kibale, Ngogo, and Kanyawara).

However, the relative lack of observations of violence in the early years of chimpanzee studies cited by Power (1991) is easily understood without reference to the effects of disturbance. Where there was no provisioning, early observations were relatively few compared to later years, and they were mostly of poorly habituated individuals, more concerned about humans than each other [e.g., contrast early observations by Ghiglieri (1984), Kibale, Ngogo community, Isabirye-Basuta (1989), Kibale, Kanyawara community, Reynolds and Reynolds (1965), Budongo, and Sugiyama (1973), Budongo] with those based on well-habituated individuals by Watts (1999) (Kibale, Ngogo community), Wrangham et al. (1992) (Kibale, Kanyawara community), and Newton-Fisher (1997) (Budongo). With increased observation of habituated individuals, studies of the Kanyawara, Ngogo, and Budongo communities conform to the essential Gombe-Mahale model of dominance-motivated and strategically violent males. Power (1991) appears not to have appreciated the difficulty of observing dominance behavior and violence among poorly habituated and little known individuals.

Provisioning complicates the issue because it confounds increased observability with a concentrated food resource that is liable to promote aggression. In the case of Gombe, Goodall's introduction of banana feeding in 1962 led to the chimpanzees becoming habituated quickly, so individuals were watched at close quarters during the first decade. Once the chimpanzees were habituated, they were observed almost entirely in the banana-feeding area (ca. 50 × 50 m, approximately 1/5,000th of their territory of 12 sq km or more), and not followed toward territorial boundaries. Much aggression during intense banana-feeding years of 1965–1969 was clearly directed toward obtaining bananas (Wrangham, 1974). During 1969, banana feeding was reduced, and fewer aggressive incidents occurred in the banana-feeding area (Wrangham, 1974).

Power (1991) argued that a particularly important feature of the banana-feeding system was that, after 1965, chimpanzees were frustrated by their lack of control. She characterized the observation period 1960–1965 as "naturalistic" (implying undisturbed by humans) because the bananas were given freely, i.e., they were never withheld. From 1965 onward, in attempts to reduce the banana-induced aggression of the 1962–1965 era, bananas were made available in metal boxes equipped with doors that were controlled in various ways by observers. It was this system that Power argued caused chimpanzees to express their potential for aggression, because it frustrated them.

In the absence of controlled experiments, no hypothesis can be rejected. Two points relevant to the imbalance-of-power hypothesis can be made, however. First, even if the frustration-aggression hypothesis is correct in explaining why the Kasekela community attacked the Kahama community, it does not explain why coalitional lethal aggression was elicited relatively easily in these chimpanzees, or why it occurs in males, whereas it has not been seen in any other species faced with similarly frustrating contexts. [For example, baboons obtained bananas regularly at the banana-feeding-area, though observers tried to prevent them (Wrangham, 1974). There has been no hint of any behavior resembling lethal raiding in these baboons, despite intense study in subsequent years]. Thus, as Power (1991) herself says, whether or not feeding frustration contributed to the social tensions at Gombe, there remains a problem to be explained. Why are male chimpanzees easily prompted to adopt intense coalitionary violence as a solution to social problems?

Second, the frustration-aggression hypothesis has much against it. The idea is that "frustration causes a distinct behavioral change in the condition of an organism" (Power, 1991, p 3). This implies that under natural conditions, chimpanzees are not naturally frustrated, which is clearly not true. For example, intense aggressive competition occurs regularly in all study sites over prized foods, such as meat (Goodall, 1986; Boesch and Boesch, 1989). On the other hand, whatever behavioral change occurred among the post-1965 Kasekela chimpanzees (compared to chimpanzees at other sites) is not easily viewed as "distinct." The series of attacks that began in January 1974 occurred almost a decade after the start of the problematic banana-feeding-system, and took place several kilometers from the feeding station. Power (1991) implies that this long delay can be accommodated by the hypothesis of a permanent behavioral/psychological reorganization, but clearly the behavior must also be viewed in the context of ongoing social tensions (see Goodall, 1986 for an account of the relationships between the alpha-males of the Kasekela and Kahama communities that may have helped precipitate the aggression).

The incidence of aggression in the banana-feeding-area was closely related to the number of bananas that chimpanzees obtained. Party size increased in the feeding area compared to the natural habitat, but within minutes of the chimpanzees leaving the feeding area the expected party size was restored (Wrangham, 1994). These and similar results show that there were indeed short-term influences related to the availability of bananas, but no long-term influences have been detected (Wrangham, 1974; Goodall, 1986). The accumulation of data from other, nonprovisioned sites continues to challenge the view that chimpanzees are naturally averse to violence.

The claim that biology is irrelevant for human warfare

Some critics reject evolutionary explanations of warfare out of hand, based on the misconception that the only behavioral patterns explicable by biology are "instincts," i.e., behaviors that are obligatory and/or invariable. According to this logic, since warfare is not "instinctual," biological adaptations cannot explain the propensity for war (Keeley, 1996; Sussman, 1997; Regal, 1998). This error seems remarkable, because behavioral ecologists have long stressed that psychological adaptations are expected to respond in a contingent way to appropriate contexts (e.g., Hrdy, 1990; Barkow et al., 1995; Krebs and Davies, 1997). In the words of Otterbein (1997, p 272), "Man is neither, by nature, peaceful nor warlike. Some conditions lead to war, others do not."

The imbalance-of-power hypothesis is entirely compatible with the observations that many people live wholly peaceful lives, that some cultures have periods of peace lasting for several generations, and that some chimpanzee populations have no lethal raiding for long periods. Indeed, such variation is to be expected. The imbalance-of-power hypothesis conforms well to some theories of peace, such as the idea that nonviolence is an adaptive response by societies to violence by stronger neighbors (Dentan, 1992). Admittedly, males are expected by this hypothesis to take advantage of power over neighbors, especially when unfettered by social or cultural constraints. They are also expected to probe for weaknesses in perceived opponents, and to be willing to fight in a wide variety of circumstances where elevated status is predictable or perceived opponents will be wounded or destroyed at low cost. But the essence of the imbalance-of-power hypothesis, like other behavioral hypotheses for large-brained mammals, is that expression of the behavior depends on context. Whether or not an individual employs violence is expected to depend on the proximate stimuli, about which we still know little. What leads individuals to classify others as "opponents"? How do social and ideological pressures affect the ease with which men, or women, respond to incitements to violence? How is "dominance" perceived? How are risks perceived, for instance, when Ego is embedded within a hierarchy of alliances? How do institutional war relationships influence individual neuroendocrinology, and vice versa? Such questions are critical for understanding who becomes violent, and when.

In the current context, the imbalance-of-power hypothesis suggests that selection has favored certain emotional predispositions in males that cause aggressive behavior to be elicited relatively easily under certain circumstances. The challenge of defining the eliciting circumstances is the province of disciplines that probe local variations, including not only biological anthropology, but also social psychology, behavioral ecology, social anthropology, cultural ecology, or social ecology. Those disciplines, together with biological anthropology, are the places to seek answers about population variations.

The assumption that evolutionary analysis implies genetic determinism seems oddly old-fashioned in an era when we are beginning to understand the nuances of psychoneuroendocrinological adaptations of different species and sexes. To Keegan (1993, p 3), war reaches into "the most secret places of the human heart, places where self dissolves rational purpose, where pride reigns, where emotion is paramount, where instinct is king." If psychology can describe those secret places, it is the task of evolutionary anthropology to explain how they arose.

IMPLICATIONS OF THE IMBALANCE-OF-POWER HYPOTHESIS

Chimpanzee and human psychology

Different versions of the CVH pay varied attention to such factors as cognitive ability, weapons, brain size, male-bonding, territoriality, sexual dimorphism, and imbalances of power (van der Dennen, 1995). They are united, however, in providing adaptive rationales for chimpanzee and human violence, and therefore in proposing that lethal raiding has a substantial evolutionary history, possibly since our split from a common ancestor with chimpanzees.

The implication is that there has been selection for a male psyche that, in certain circumstances, seeks opportunities to carry out low-cost attacks on unsuspecting neighbors. The psychological mechanisms that would make such a complex function possible have not been studied, but a partial list might include: the experience of a victory thrill, an enjoyment of the chase, a tendency for easy dehumanization [or "dechimpization," (Goodall, 1986), i.e., treating nongroup members as equivalent to prey], and deindividuation (subordination of own goals to the group), ready coalition formation, and sophisticated assessment of power differentials. Sex differences can be expected in at least some of these traits, unless developmental constraints interfere. Some features of a lethal-raiding psychology are not easily predicted, such as the mechanisms by which expected costs and benefits are assessed.

A sharp alternative to the CVH is the standard social science model (SSSM), that human males have no inherent propensity to take advantage of power differentials. Instead, according to the SSSM, humans merely have a capacity for violence, and since "the range of possible cultural results is not explicable by natural selection" (Bock, 1980; p. 76; cf. Gould, 1996), evolutionary history is claimed to be irrelevant. This line of thinking has several problems. It does not account for the species distribution of coalitional aggression. It treats biology and cultures as alternatives, rather than as mutually interacting influences. It does not account for the predictability of human aggressive patterns, and it is easily subsumed under adaptive theories of violence, which can account both for the fact that individuals choose to manipulate others (whether through ideology or other ways) and for the fact that they are so easily manipulated.

The complexity of war

Even in the complex human world, some of the processes that regulate aggression among large groups are analogous to those that occur at the individual or face-to-face level (Hinde, 1993). Both at the large group and the individual level, for example, personal relations between leaders of opposing groups can play an important role, with a threat to the interests or values of the actor being capable of instigating aggression. Placatory signals or actions (e.g., donations) are used to deter aggression. Aggressiveness can be augmented by a greater asymmetry of power, or reduced by a probability of punishment. Hinde (1993) found more than 20 such analogies, of varying significance and distinctness, linking the behavioral interactions among individuals and large groups. This suggests that, in some ways, the logic of aggressive interaction among individuals can be applied to large groups.

Nevertheless, so many cultural and linguistic novelties complicate warfare that the connection to biology can appear tenuous at best. Among factors such as the number of military and strategic options available, the ability to discuss options and manipulate others, the adoption of cultural goals, and the unpredictable potential for shifting alliances, a particularly important trait distinguishing humans from chimpanzees is that human groups incorporate more levels of social dynamics (Hinde, 1993). At each such level, "level-specific properties" influence and are influenced by adjacent levels. For example, group processes and institutional influences modify the motivational ideals of individuals. In modern nation-states, the military-industrial-scientific complex tends to precipitate and maintain war, e.g., by producing increasingly sophisticated weaponry. War as an institution can in theory be maintained by the inertia of subinstitutions, such as the belief that capitalism needs militarism for its continued growth (Hinde, 1993). Dynamics like these mean that a propensity for lethal raiding cannot be translated directly into an explanation of the complexities of human warfare.

Is a propensity for lethal raiding of the chimpanzee type at all relevant to human warfare? Among people living in small politically independent groups, lethal raiding appears strikingly similar to the patterns among chimpanzees. In both cases, small parties of males aim to make undetected incursions into the ranges of neighbors, attack unsuspecting victims, and retreat without being drawn into a battle (Turney-High, 1949; Chagnon, 1992; Keeley, 1996). Although the psychological processes remain undescribed, the imbalance-of-power hypothesis might suggest that selection has favored various complex traits, such as a tendency to classify others as in-group or out-group, to regard members of out-groups as potential prey, to be alert to (or search for) power asymmetries between in-group and out-group parties, and to be ruthless in attacking out-group parties when the perceived power asymmetry is sufficiently great. A list of traits such as these can in theory describe an evolutionarily selected "propensity for lethal raiding."

Such traits appear obviously relevant to some aspects of intergroup relations (e.g., the planning and execution of military engagements). Among humans, the complexity of society means that individual propensities sometimes have less direct impact on social outcomes than among chimpanzees. Nevertheless, the imbalance-of-power hypothesis may explain why culturally derived information is used in certain ways. For example, as a result of cultural beliefs or social pressure, individuals can either broaden or contract their concept of where an in-group/out-group boundary falls, or of how important it is. Idealogues can persuade their followers that sufficient power asymmetry exists to make attacks on an outgroup worthwhile. Culture can thus manipulate the information an individual uses to assess whether an attack is desirable.

The imbalance-of-power hypothesis can be reconciled with the power of culture; therefore, if human males have a tendency to search for, and take advantage of, power asymmetries sufficient to enable them to safely kill rivals, while social pressures modify the concept of "rival," "ally," and "sufficient power asymmetry." It accordingly suggests an explanation for why human males become dangerous when they obtain, or believe they have, large power advantages over others. (Whether, in novel circumstances, they use such power adaptively is an open question.) It also suggests the importance of systems that reduce power asymmetry, such as intergroup alliances through trade, marriage or treaty.

When large power asymmetries do not occur, relationships between groups are often peaceful, as expected from the imbalance-of-power hypothesis (Knauft, 1991; Bueno de Mesquita and Lalman, 1992; van der Dennen, 1995). Even when there is a balance of power, however, lethal battles and wars can occur among humans, in contrast to the pattern among chimpanzees (Singer, 1989, Boehm, 1992). Coalitionary aggression occurring between opponents with balanced power requires other kinds of explanation than the imbalance-of-power hypothesis, such as the cultural exaggeration of motivating forces or the development of self-deceptive assessment strategies (Boehm, 1992; van der Dennen, 1995; Wrangham, 1999b).

The relation between lethal raiding and hunting

Both lethal raiding and hunting are carried out primarily by adult males acting in coordinated groups: both involve otherwise unusual actions such as searching for large prey, stalking, chasing, seizing, wounding, and killing; both are more elaborated in humans and chimpanzees than in other primates. Furthermore, the behaviors shown by chimpanzees toward mammalian prey are partly similar to those they show toward conspecific victims, including quiet stalking during a hunt, intense arousal during the attack phase (pilo-erection, intimidation displays), and ambivalence toward the victim. In contrast, the behaviors shown by specialized carnivores toward their prey are not like those directed toward conspecifics. For example, social carnivores do not show signs of excitement when killing prey, and tend to use a killing bite (van der Dennen, 1995).

Such observations suggested to Eibl-Eibesfeldt (1975) and Goodall et al. (1979) that among chimpanzees similar motivational factors may be involved in intraspecific killing and hunting. Eibl-Eibesfeldt (1975) specifically proposed that, "Motivationally, hunting behavior in chimpanzees has probably been derived from intraspecific aggression" (translated and quoted by van der Dennen, 1995, p 192). The essential logic is that if hunting had arisen independently, it should be expected to show more similarities to the patterns displayed by social carnivores. Van Hooff (1990) agreed, suggesting that if selection favored the ability to hunt and kill conspecifics, the psychological mechanisms that evolved would be easily co-opted toward obtaining meat.

Note that these ideas are opposite to the killer ape hypothesis. The killer ape hypothesis suggested that intraspecific violence evolved from hunting, whereas Eibl-Eibesfeldt (1975), Goodall (1986), and van Hooff (1990) proposed that hunting evolved from intraspecific violence. As van der Dennen (1995) notes, the relationship between intraspecific killing and hunting probably now involves multiple directions. For example, in some human populations hunting may provide practice for warfare (Otterbein, 1997). Disentangling these relationships will therefore not be easy.

Nevertheless the idea that violence begat hunting is useful because it suggests a new way to solve a puzzle about bonobos, namely, that bonobos show no evidence of monkey hunting. Thus, no monkey hunting or monkey eating has been recorded at the long-term bonobo sites (Wamba and Lomako), or in the shorter-term studies of Yalosidi, Lake Tumba, or Lilungu, even though these studies have provided sufficient data to record, for example, termite-eating in four of the sites (Thompson, 1997). Bonobos do eat meat occasionally, however, which they obtain individually by seizing young antelope. The lack of monkey hunting by bonobos is striking given that they not only prey on terrestrial mammals, but also complete with each other to eat meat, and sometimes interact socially with monkeys, in grooming and play. On three occasions, they have even kidnapped young monkeys during play, but not eaten them (reviewed by Wrangham and Peterson, 1996).

Stanford (1998b) suggested that the reason why male bonobos hunt rarely is that hunting has a low pay-off, because they tend to lose meat to females. Against this, low-ranking male chimpanzees often lose meat to high-ranking males, but still hunt frequently (Goodall, 1986). Furthermore it is monkey hunting, rather than meat eating, that appears to be lacking in bonobos, not only among males but also among females. Stanford's proposal is therefore not supported.

Another possible explanation for the lack of observations of monkey hunting by bonobos is stochastic. Hunting traditions might vary among bonobo populations. If so, monkey hunting may be observed in the future, in populations that have not yet been studied. However, there is no evidence that any chimpanzee population fails to hunt monkeys, provided monkeys are present. Chimpanzees prey on monkeys in at least 12 sites, including all the long-term sites [Gombe, Mahale, Taï, Kibale, and Budongo (Goodall, 1986)] as well as seven lesser-known populations [Chambura, (B. Fahey, personal communication; Kahuzi-Biega, DRC (Basasose and Yamagiwa, 1997), Lopé, Gabon (Tutin and Fernandez, 1993), Mt. Assirik, Senegal (McGrew et al., 1979), Outamba-Kilimi, Sierra Leone (Alp, 1993), Sapo, Liberia (Anderson et al., 1983), Tongo, DRC (A. Lanjouw, personal communication). There is, therefore, a strong contrast between the widespread occurrence of monkey hunting in chimpanzees and its absence in bonobos. Contrary to the stochastic hypothesis, this suggests that compared to chimpanzees, bonobos have a weaker motivation to hunt monkeys.

As a third possibility, therefore, Wrangham and Peterson (1996) noted that the lack of monkey hunting among bonobos might be explained as a consequence of their low interest in intraspecific killing. For example, if bonobos evolved from a chimpanzee-like ancestor, they began with a tendency for lethal raiding which was lost or inhibited when they acquired relatively stable parties. Accordingly, the evolution of inhibitions against lethal raiding may have inadvertently caused monkey hunting to be inhibited also, if the two patterns are indeed motivationally related (Eibl-Eibesfeldt, 1975; van Hooff, 1990). This proposal implies that monkey hunting is motivationally more similar to lethal raiding, and relatively distinct from the killing of terrestrial ungulates. Important similarities between monkey hunting and lethal raiding could include the necessity for coordination and planning and the ability to assess an adequate power imbalance between predators and prey.

In summary, it is admittedly speculative to propose that monkey hunting has been lost in bonobos as a result of selection against propensities relevant to lethal raiding. However, this idea appears to explain the facts better than alternative hypotheses. It suggests a correlation between group hunting and lethal raiding in humans, chimpanzees and bonobos that challenges traditional thinking, and draws attention to the need for further data.

Morality

This paper suggests that violent propensities of a particular kind have been positively selected among male chimpanzees and humans. Biologically, this is unsurprising. Likewise, propensities for particular types of altruistic and cooperative behavior have probably also evolved through selection, and are neither more nor less important biologically than violence.

But anthropologists' views on violence tend to be interpreted politically. For example Otterbein (1997) labeled anthropologists as "Hawks" or "Doves" according to whether they consider evolutionary biology relevant or irrelevant to warfare (Otterbein, 1997). Although Doves (e.g., Power, 1991; Sussman, 1997) suggest that Hawks (e.g., Ghiglieri, 1984; Goodall, 1986; Wrangham and Peterson, 1996) are culturally biassed in thinking that male chimpanzees strive aggressively for status and use violence adaptively in intergroup interactions, there is no evidence for a positive correlation between anthropological Hawkishness (in the Otterbein sense) and political beliefs. Indeed, some notable "anthropological Hawks" have been prominent in the search for peace. For example, Hamburg (1991) argued for the importance of biological similarities in chimpanzee and human violence, and in the same spirit co-chaired a multi-year effort to reduce the frequency and intensity of international violence (Carnegie Commission, 1997). There is no moral high ground to be held by virtue of being an anthropological Dove.

Admittedly, any theory of violence has moral implications, because biological analyses can be misused. But no theory, however benign or malevolent or whether based on biology, psychology, or culture, is immune to co-option by ideologues and propagandists. While German military philosophy was backed by Darwinism in the First World War, French military philosophy was backed by Bergson's theory of creative evolution (Tuchman, 1962). On either side, opposing theories of evolution were used to bolster the waging of war. Military organizations can be expected to deceive themselves and their followers using any available materials (Wrangham, 1999b).

I see no better course than to follow Darwin (1871, p 405): ". . .we are not here concerned with hopes or fears, only with the truth as far as our reason permits us to discover it." Lethal violence appears strikingly frequent among chimpanzees and humans, and appears explicable by relatively simple adaptive rules. Current evidence suggests it has been a major selective pressure for significant periods of chimpanzee and human evolution. Until lethal violence is shown to be a strange new phenomenon, we should consider it sufficiently ancient to have influenced the temperaments of both species, particularly of males, in ways that should be taken seriously. The more we understand about the evolutionary origins and persistence of intergroup violence, the better we can predict and avert it.

CONCLUSION

Despite some important unsolved problems, chimpanzee lethal raiding appears generally well explained by the imbalance-of-power hypothesis, which states that successful attacks on rivals are favored because they increase the dominance status of the aggressors. A combination of three points likewise suggests that selection has favored unprovoked intergroup violence in human males: the prevalence of human war raiding, the similarities of chimpanzee and human lethal raiding, and the ability of the imbalance-of-power hypothesis to explain the mammalian distribution of lethal violence. Until an alternative model exists, chimpanzees and humans are, therefore, best regarded as species in which a dominance drive by male groups has been positively selected.

If this conclusion has merit, anthropology has given inadequate consideration to coalitionary violence as a force in human evolution. As anthropologists, we have a duty to acknowledge the horrors of our evolutionary past, partly for the sake of truth, and partly to consider how such behavior can be avoided in the future. By combining primatological, paleontological and behavioral-ecological evidence, anthropologists can provide especially rich tests of evolutionary hypotheses. These will offer a solid base from which evolutionary anthropology can work with other disciplines to understand cultural variation and the proximate stimuli that elicit violence.

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