

INTERGROUP RELATIONS IN CHIMPANZEES

Michael L. Wilson

The Jane Goodall Institute's Center for Primate Studies, Department of Ecology, Evolution, and Behavior, University of Minnesota, 100 Ecology Building, 1987 Upper Buford Circle, St. Paul, Minnesota 55108; email: wilso198@tc.umn.edu

Richard W. Wrangham

Department of Anthropology, Harvard University, Peabody Museum, 11 Divinity Ave., Cambridge, Massachusetts 02138; email: wrangham@fas.harvard.edu

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■ **Abstract** In the 1970s, researchers provided the first detailed descriptions of intergroup conflict in chimpanzees. These observations stimulated numerous comparisons between chimpanzee violence and human warfare. Such comparisons have attracted three main objections: (a) The data supporting such comparisons are too few, (b) intergroup aggression is the result of artificial feeding by observers, and (c) chimpanzee data are irrelevant to understanding human warfare. Recent studies provide strong evidence against these criticisms. Data from the five long-term sites with neighboring groups show that intergroup aggression is a pervasive feature of chimpanzee societies, including sites where artificial feeding never took place. Recent studies have clarified questions about the functional goals and proximate mechanisms underlying intergroup aggression. Male chimpanzees compete with males in other groups over territory, food, and females, base their decisions to attack strangers on assessments of numerical strength, and strive for dominance over neighboring groups. Human males likewise compete over territory, food, and females and show a preference for low-risk attacks and intergroup dominance. Chimpanzee studies illustrate the promise of the behavioral biology approach for understanding and addressing the roots of violence in our own species.

INTRODUCTION

A widespread assumption in the 1960s and 1970s was that warfare resulted from features unique to the human lineage, such as weapons or the dense populations created by agriculture (e.g., Lorenz 1966, Montagu 1976). The observation of lethal intergroup attacks in wild chimpanzees challenged this view (Goodall et al. 1979). Numerous comparisons between chimpanzee aggression and human warfare followed these first observations (e.g., Trudeau et al. 1981, Goodall 1986, Ghiglieri 1987, Alexander 1989, van Hooff 1990, Hamburg 1991, Manson & Wrangham 1991, Boehm 1992, van der Dennen 1995, Wrangham & Peterson 1996). Shared traits, such as the cooperation of males to defend group resources

and the occurrence of lethal intergroup attacks, suggested that key features of human warfare evolved either in the common ancestor of humans and chimpanzees or independently in the two lineages for similar reasons (Ghiglieri 1989, Manson & Wrangham 1991).

Until recently, however, these comparisons rested on a narrow foundation. Most of the detailed information on intergroup aggression came from two sites in Tanzania, Gombe and Mahale, raising the possibility that patterns of intergroup aggression observed there resulted from some unusual feature of those sites, such as artificial feeding by observers (Power 1991).

In recent years, however, a new generation of studies has advanced our understanding of intergroup relations (reviewed in Wrangham 1999, Boesch & Boesch-Achermann 2000, Mitani et al. 2002). New descriptions of intergroup aggression are emerging from unprovisioned sites, including Taï National Park, Côte d'Ivoire (Boesch & Boesch-Achermann 2000), Kibale National Park, Uganda (Watts & Mitani 2001, Muller 2002), and Budongo Forest Reserve, Uganda (Newton-Fisher 1999). New technologies and methods have enabled researchers to ask new questions and answer previously unanswerable old questions. Entry of data into increasingly powerful computer systems is enabling researchers to examine long-term ranging and grouping data in unprecedented detail (e.g., Williams et al. 2002b). Genetic analysis has enabled researchers to test the proportion of infants born from intergroup mating (Gagneux et al. 1997, Constable et al. 2001, Vigilant et al. 2001). Field experiments have made possible controlled tests of hypotheses that are difficult to test using only observational data (Wilson et al. 2001; I. Herbinger and C. Boesch, submitted manuscript).

In this chapter we review the current information on chimpanzee intergroup relations and discuss how results from recent studies affect prior generalizations. First, we describe the emerging consensus regarding chimpanzee social structure, territory characteristics, and intergroup interactions. Then we examine how recent studies have clarified questions about the functional goals and proximate mechanisms underlying intergroup aggression. Finally, we discuss the relevance of these findings to intergroup aggression in humans.

The comparisons of chimpanzee and human intergroup aggression have attracted three main objections. First, critics claim that the data on intergroup aggression are too few to support claims that chimpanzees are inherently violent (Sussman 1999, Marks 2002). Second, some argue that intergroup aggression results from human influence, especially provisioning chimpanzees with artificial food (Power 1991, Sussman 1999). Third, it has been suggested that chimpanzee violence is irrelevant to understanding human behavior (Sussman 1999, Ferguson 2001, Marks 2002). According to this view, we already know that humans can be violent and that humans can be peaceful as well; what matters for humans are environmental factors such as culture rather than biology.

As we discuss below, recent studies provide strong evidence against these criticisms. First, evidence from classic and more recent studies shows that intergroup aggression, including lethal attacks, is a pervasive feature of chimpanzee societies. Second, the occurrence of intergroup aggression at unprovisioned sites allows us

to reject the hypothesis that intergroup aggression and other patterns of social behavior were the result of provisioning. Instead, chimpanzee intergroup aggression is best explained by principles of behavioral biology that apply to other species such as lions, wolves, and hyenas (e.g., McComb et al. 1994, Mech et al. 1998, Boydston et al. 2001). Third, the argument that, because humans can be both warlike and peaceful, war is not the result of biology or instinct is aimed at an outdated view of biology. Animals, especially large-brained animals such as primates, are no longer viewed as response-stimulus robots but rather as strategic actors who make decisions based on assessments of costs and benefits (Archer 1988, Huntingford & Turner 1987). Recent studies have improved our understanding of the costs and benefits underlying intergroup aggression for chimpanzees. These studies illustrate the promise for obtaining a better understanding of human intergroup aggression using principles generated by behavioral biology.

LONG-TERM STUDY SITES

Chimpanzees have been studied at over forty sites across Africa (Wrangham et al. 1994). Many years are required to fully habituate chimpanzees to the presence of researchers, to learn the identity and group membership of individuals, and to identify patterns of ranging behavior and intergroup interactions. Detailed data on intergroup relations are thus available only from the five long-term study sites with neighboring communities: Gombe, Mahale, Taï, Kibale, and Budongo (Figure 1). [One additional long-term study site, Bossou, Guinea, consists of a single semi-isolated chimpanzee community surrounded by villages (Sugiyama 1989) and therefore is not considered here.] Since 1960, these long-term studies have accumulated over 190 years of demographic and behavioral data from 11 different communities. Researchers at these sites are currently studying nine habituated communities, more than ever before.

In addition to “common” chimpanzees (*Pan troglodytes*), the genus *Pan* includes one other species, bonobos (*Pan paniscus*), which are also (rather misleadingly) called pygmy chimpanzees. Bonobos differ strikingly from chimpanzees in their intergroup relations. Although both species defend group territories (Hohmann et al. 1999, Kano 1992), no indications of attempts to conduct lethal violence have been recorded among bonobos (reviewed in Stanford 1998b, Wrangham 1999). Furthermore, parties from neighboring bonobo communities with friendly relations may intermingle for several hours, during which time members of different communities sometimes groom and copulate without aggression (Idani 1991, White 1996). No comparable peaceful associations have been recorded among chimpanzees. Possible reasons for this difference are discussed elsewhere (Wrangham 1986, Wrangham & Peterson 1996). Because comparisons of human and ape intergroup aggression have focused on chimpanzees, we focus, in this chapter, on the chimpanzee evidence.

Researchers commonly distinguish three chimpanzee subspecies: eastern (*P. troglodytes schweinfurthii*), central (*P. troglodytes troglodytes*), and western (*P.*

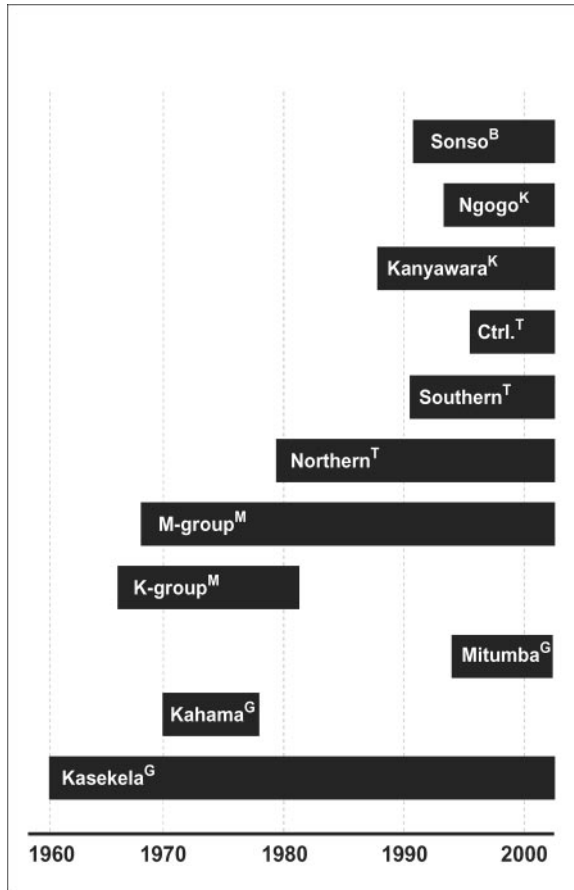


Figure 1 Years of continuous observation for communities at long-term study sites with neighboring communities. Following the community name, a superscript letter indicates whether the community's site is Gombe, Mahale, Taï, Kibale, or Budongo. Start times are approximate and exclude earlier short-term studies; see text for details on duration of habituation and systematic study.

troglodytes verus) (Hill 1969). Apart from Taï chimpanzees, which belong to the western subspecies, the communities with long-term data on intergroup relations are eastern chimpanzees. The subspecies are not very distinct in appearance or behavior (Boesch & Boesch-Achermann 2000, Wrangham 1984). Population differences in behavior appear to depend more on habitat and local traditions than on genetic differences (Boesch & Boesch-Achermann 2000).

The first and longest-running chimpanzee study site is in Gombe National Park, which currently contains three chimpanzee communities: Mitumba, Kasekela, and Kalande. Observers have studied the Kasekela community since 1960 (Goodall

1986). A fourth community (Kahama) separated from Kasekela in the early 1970s and was subsequently exterminated by attacks from Kasekela (Goodall 1986). Efforts to habituate the Mitumba community began in the mid-1980s, with more systematic observations beginning in the mid-1990s [The Jane Goodall Institute's Center for Primate Studies (JGICPS), unpublished data]. Attempts to identify and monitor the Kalande chimpanzees began in 1998 (Greengrass 2000).

A second Tanzanian site, Mahale, has been operating since 1966 (Nishida 1990). Observations initially focused on K-group, which declined in numbers from over 30 individuals in 1974 to effective extinction with the death of the group's last adult male in 1982 (Nishida et al. 1985). Researchers speculated that K-group's decline resulted from attacks by the larger M-group, studied from 1968 to the present (Nishida et al. 1985).

Researchers at both Gombe and Mahale provisioned chimpanzees with cultivated food (mainly bananas and sugarcane) to facilitate habituation and observation. At Gombe, the intensity of provisioning was initially decreased in 1969 (Wrangham 1974) and then halted entirely in 2000 (JGICPS, unpublished data). At Mahale, provisioning was reduced in 1981 and halted in 1987 (Nishida 1990). Due to concerns that provisioning might affect chimpanzee behavior and health, researchers did not provision chimpanzees at sites established in later years (see, for example, Ghiglieri 1984, Boesch & Boesch-Achermann 2000).

Researchers studied chimpanzees without provisioning in Uganda and Côte d'Ivoire. Short-term studies occurred in Uganda as early as 1960. In Budongo, chimpanzees were observed intermittently through the 1960s (Reynolds & Reynolds 1965, Suzuki 1971), with long-term study starting in 1990 (Newton-Fisher 1999). In Kibale, studies have focused on the Ngogo and Kanyawara communities, which are separated from one another by 12 km of forest occupied by unhabituated chimpanzees. Researchers conducted short-term studies at Ngogo from 1976–1978 and in 1981 (Ghiglieri 1984) and at Kanyawara from 1983–1985 (Isabirye-Basuta 1988). Kanyawara has been studied continuously since 1987 (Wrangham et al. 1996). Habituation of Ngogo resumed in 1989, with intensive study continuous since 1995 (Watts & Mitani 2001). The Northern community at Tai has been observed continuously since 1979 (Boesch & Boesch-Achermann 2000). Habituation of Tai's central and southern communities began in 1996 and 1991, respectively (Herbinger et al. 2001; I. Herbinger, personal communication).

SOCIAL ORGANIZATION

Chimpanzees live in groups called communities (van Lawick-Goodall 1968) or unit-groups (Nishida 1968) containing up to at least 150 individuals (Watts et al. 2002). Rather than traveling in a cohesive unit, chimpanzees exhibit fission-fusion grouping patterns. Individuals travel, feed, and sleep in parties containing 1 to 20 or more individuals (Chapman et al. 1994). The entire community rarely or

never comes together. Males tend to be more gregarious than females, especially mothers with infants (e.g., Nishida 1968, Wrangham 2000). Mothers spend much of their time alone with their offspring or in nursery parties with other mothers and young (Wrangham & Smuts 1980, Goodall 1986). During the 10 to 15 days preceding ovulation, female chimpanzees experience a conspicuous swelling of the ano-genital skin and an increase in sexual proceptivity (Graham 1981, Tutin & McGinnis 1981). Mothers are more likely to join mixed-sex parties when they have full sexual swellings (e.g., Matsumoto-Oda 1999; Williams et al. 2002a). Females with offspring typically use an individual home range that is smaller than the total range used and defended by males (Wrangham 1979, Chapman & Wrangham 1993, Wilson 2001, Williams et al. 2002b).

Males and females differ strikingly in their residence and dispersal patterns. Female chimpanzees usually emigrate to another community at adolescence, whereas males remain in their natal group (Pusey 1979). Gombe is unusual among chimpanzee sites in that roughly half of all females remain in their natal community (Pusey et al. 1997).

TERRITORY CHARACTERISTICS

The degree to which chimpanzees occupy and defend distinct territories remained unclear for the first decades of chimpanzee field studies. At least one early report from Gombe described chimpanzees as “strongly territorial,” but this was entirely guesswork (Thomas 1961). Other early observers assumed that chimpanzees did not defend discrete territories (Reynolds 1966, van Lawick-Goodall 1968) and were “free to come and go as they please without restraint by territorial borders” (Power 1991, p. 62).

Various difficulties inherent in studying chimpanzees contributed to the late understanding of territorial behavior. Even in the richest habitats, chimpanzees live at low densities [1–4 per km² (e.g., Table 7.4 in Boesch & Boesch-Achermann 2000, Herbinger et al. 2001)] and occupy large home ranges [of 10–38 km² (Herbinger et al. 2001, Wilson et al. 2001)]. Under such circumstances, it is challenging to simply find and follow any chimpanzees. Moreover, individuals frequently join and leave temporary parties, giving early observers the mistaken impression that friendly relations existed among all chimpanzees in the population. In species that live in stable troops, such as baboons, researchers studying a new troop can see and be seen by all the troop’s members every time they encounter the troop. In such species, habituation and identification of individuals proceed rapidly, taking perhaps a few months. In contrast, in chimpanzees, observers studying an unhabituated chimpanzee community encounter only a few group members at a time. Without provisioning, fully habituating and learning the identity of all community members—necessary steps to learning group and territory boundaries—can take five years or more (Boesch & Boesch-Achermann 2000). An additional obstacle to understanding territorial behavior is that, during the 1960s, observations

at Gombe focused on behavior at the feeding station. Observations of territorial behavior did not occur until researchers began conducting all-day follows of individuals throughout the forest in the 1970s (Goodall 1986).

As habituation improved at Gombe and Mahale, and once researchers began following chimpanzees away from the feeding station at Gombe, researchers found clear evidence for territoriality, including boundary patrolling and hostility to members of neighboring communities (Kawanaka & Nishida 1974, Goodall et al. 1979, Nishida 1979). The striking difference between early and later reports of territorial behavior at Gombe and Mahale suggested to Power (1991) that these reports represented a change in behavior, rather than a changing understanding of existing behavior. Power argued that by provisioning chimpanzees with food, and by limiting access to that food, researchers caused chimpanzee intergroup relations to change from peaceful to hostile. Now that long-term data from several studies of unprovisioned chimpanzees are available, however, it is clear that territorial competition is a pervasive feature of chimpanzee societies, rather than the product of human interference (Wrangham 1999, Boesch & Boesch-Achermann 2000, Watts & Mitani 2001).

Rather than wandering about nomadically, as some early observations suggested, chimpanzees use well-defined home ranges. Barring such disruptions as deforestation or community extinction, a given chimpanzee community can use the same locations for decades. At Gombe, the Kasekela chimpanzees still focus their activities in the valleys they used over 40 years ago, despite variation in the total size of their range (e.g., Williams et al. 2002b).

Recent quantitative analyses of chimpanzee ranging have shown that chimpanzee territories include a heavily used central area surrounded by a less frequently used periphery that may overlap extensively with neighboring territories (Herbinger et al. 2001, Wilson 2001). This pattern of ranging suggests that chimpanzees actively avoid border areas. For example, at Tai, chimpanzees spent 75% of their time in the central 35% of the range (Boesch & Boesch-Achermann 2000, Herbinger et al. 2001). Likewise, at Kanyawara, chimpanzees spent 90% of their time in the central 40% of their total range (Wilson 2001). At Tai, chimpanzees rarely visited border areas even though food was at least as abundant in those regions as in the center of their range (Anderson et al. 2002). Indeed, preliminary evidence suggests that some food items, such as preferred animal prey, may be more abundant in border regions (Stanford 1998a, Wrangham 1999).

Although communities on both sides visit borders infrequently, the risk of encountering neighbors in those regions affects behavior during border visits. Chimpanzees often appear tense or cautious during such visits (Bygott 1979, Boesch & Boesch-Achermann 2000, Watts & Mitani 2001). At Gombe (Bauer 1980) and Kibale (Chapman & Wrangham 1993, Wilson 2001), chimpanzees are more likely to visit borders when in parties with many males. Success during intergroup encounters depends greatly on the number of males on each side (Manson & Wrangham 1991). Chimpanzees thus appear to seek safety in numbers before visiting borders.

INTERGROUP INTERACTIONS

The overall pattern of intergroup interactions is similar across long-term study sites (for detailed accounts, see Boesch & Boesch-Achermann 2000, Chapter 7; Goodall 1986, Chapter 17; Mitani et al. 2002). Hostile intergroup relationships are the norm, in the sense that, in the majority of cases where members of one community detect the presence of neighbors, interactions are immediately aggressive (Boesch & Boesch-Achermann 2000, Wrangham 1999). Within the overall hostile relationship between communities, the nature of a particular interaction depends on the age, sex, and reproductive state of the individuals involved.

Intergroup interactions are most likely to occur during visits to borders. Goodall (1986, p. 489) distinguished two kinds of border visit: patrols and excursions. During patrols, parties consisting mainly of males travel quietly along borders, apparently searching for evidence of neighbors (Bygott 1979, Watts & Mitani 2001). Males on patrol sometimes pause to sniff the ground or listen for distant calls, and they may destroy chimpanzee nests found in border areas (Goodall 1986, p. 490). During excursions, large parties that may include mothers and offspring travel to border areas to feed in particularly rich food patches (Goodall 1986).

Despite the importance of intergroup interactions, both to human observers and to chimpanzees themselves, such interactions occur infrequently. Parties that were followed at least 6 h in a day heard or saw strangers of either sex on 9.5% of follows at Gombe and 11.8% of follows at Tai (Table 7.11 in Boesch & Boesch-Achermann 2000). At Kanyawara, encounters occurred even less frequently [2.8% of days with at least 6 h of observation, January 1998–May 2002 (R.W. Wrangham, unpublished data)]. When chimpanzees do encounter their neighbors, most interactions involve only auditory contact rather than direct visual or physical contact. For example, during a 14-year period at Tai, 70% of intergroup encounters were limited to auditory contact (Table 7.5 in Boesch & Boesch-Achermann 2000).

Auditory encounters typically involve “pant-hoot” calls (Marler 1976), which can be heard for 2 km or more in dense forest (Ghiglieri 1984). Both sexes produce pant-hoots, but males pant-hoot more often than females, with high-ranking males pant-hooting most frequently (Clark 1993, Mitani & Nishida 1993). Most pant-hoots are produced during within-community contexts, such as arrival at fruit trees, during reunions with other community members, and as exchanges between allies that are nearby but out of sight (Mitani & Nishida 1993). The long distance over which pant-hoots are audible enables chimpanzees to advertise their presence and numerical strength to rival communities (Clark 1993, Ghiglieri 1984) and to assess the numerical strength of rivals from a safe distance (Boesch & Boesch-Achermann 2000).

Hearing calls from neighbors usually generates a striking response, including signs of apparent fear and/or excitement, such as open-mouth grinning and bristling of hair, and reassurance gestures, such as embracing and mounting other party members (Goodall et al. 1979, Nishida 1979). They may either listen quietly or respond with a chorus of loud calls. They may retreat, hold their ground, or

approach the calls with varying degrees of apparent caution and excitement. Generally, all members of a party show similar responses, but on occasion differences can occur. Males tend to act more boldly than females, but even among males there can be a mixture of reactions (e.g., Goodall 1986, p. 518).

The circumstances vary under which visual and physical encounters occur. Parties may converge by accident, such as at a shared food resource, in which case approaches to as close as <100 m can occur before the chimpanzees realize each other's presence. Such events are rare, however. More often, encounters appear to be intentional, in which members of one party move rapidly and directly toward pant-hoots or other calls made by neighbors. Such approaches can either be silent, resembling a hunt, or vocal (Boesch & Boesch-Achermann 2000, Watts & Mitani 2001).

Males and females differ in their willingness to approach neighbors. Upon hearing strangers, males often approach them with the apparent intention of attacking, as evidenced by stalking and swift silent movements during their approach, followed by directed aggression after they arrive (Goodall 1986, Boesch & Boesch-Achermann 2000). Females are less likely to join patrols, but they do seek out members of other communities during adolescent dispersal (Pusey 1979). Females usually visit a new community only if they have a full sexual swelling, in which case they are more attractive to resident males. Mothers with infants generally avoid encounters with neighboring communities (Goodall 1986). Mothers rarely transfer unless their current community contains few males (Nishida et al. 1985, Williams et al. 2002b). Females are usually intolerant of stranger females and sometimes attack immigrating females (Pusey 1980, Goodall 1986, Nishida 1989). In contrast to other sites, females at Taï often join males during patrols and intergroup encounters, but they rarely take part in direct physical attacks (Boesch & Boesch-Achermann 2000).

The outcome of direct encounters varies according to each side's party composition. Males are least likely to act aggressively if the stranger is an adolescent female with a sexual swelling. Males may groom and mate with such females, although they may attack if the female attempts to run away (Goodall 1986). Males are sometimes tolerant of stranger mothers, especially when they have a sexual swelling. Remarkably, however, males often attack females, and these attacks can involve considerable brutality, especially if the female has young offspring (Goodall 1986; J. Williams and A.E. Pusey, submitted manuscript). At Gombe, males attacked stranger mothers in 76% of encounters (Goodall 1986). In some cases, males focus their attacks on the female's infant, which they may kill and eat (e.g., Bygott 1972, Watts et al. 2002). At other times, however, males appear focused on attacking the mother rather than the infant [e.g., many cases at Taï (Boesch & Boesch-Achermann 2000)]. Attacks on stranger females can result in severe wounds and, in at least one case, death (Goodall 1986).

Males almost always show fear or hostility to stranger males (Goodall 1986, Boesch & Boesch-Achermann 2000, Watts & Mitani 2001). Males sometimes flee from neighboring parties, particularly if they appear outnumbered (Goodall 1986,

Boesch & Boesch-Achermann 2000, Watts & Mitani 2001). Direct intergroup interactions among males include battles and gang attacks (Manson & Wrangham 1991). In battles, both sides contain many males. Both sides may exchange pant-hoots and other loud calls while displaying at and charging their opponents. The outcome is often indecisive, and severe injuries rarely occur, unless males from one side manage to isolate and surround a rival (Goodall 1986, Boesch & Boesch-Achermann 2000). Gang attacks involve many males attacking a lone individual and are the main source of severe injuries, including fatal ones (Manson & Wrangham 1991).

TERRITORIAL GAINS

Intergroup aggression appears to yield territorial benefits. At Mahale, the larger M-group seasonally invaded the range of the smaller K-group to exploit abundant food resources (Nishida 1979). Following the disappearance of the K-group males, K-group's neighbors (B-group to the north and M-group to the south) expanded their ranges, dividing all of K-group's former range between them (Nishida et al. 1985). Likewise, during the years of the attacks on Kahama chimpanzees, the Kasekela community expanded into Kahama's former range (Goodall 1986). Kasekela's gains proved fleeting, however, when the powerful Kalande community to the south expanded northward (Goodall 1986). Kahama had apparently acted as a buffer state between Kasekela and Kalande (Goodall 1986).

LETHAL ATTACKS: ADULTS

Lethal attacks against both infants and weaned individuals have been observed or inferred at both provisioned and unprovisioned sites. Because theoretical considerations suggest different motivations for killing infants and older individuals (e.g., Arcadi & Wrangham 1999, Wrangham 1999), we discuss the age classes separately, starting with older victims. Table 1 lists all cases with either direct observation of intergroup attacks on adults and adolescents that were known or inferred to result in fatalities or compelling evidence of fatal attacks, such as a freshly killed body with wounds consistent of chimpanzee attack ($N = 14$). Such evidence exists for three sites: Gombe, Mahale, and Kibale. A comparable number of males that disappeared suddenly, without evidence of disease or other factors, are suspected to have died from intergroup aggression. Suspicious disappearances include up to six adult males (and one adolescent) from Mahale (K-group) (Nishida et al. 1985), at least five adult males and four juveniles from Gombe (Kasekela) (Williams et al. 2002b), and five adult males from Kanyawara (R.W. Wrangham, unpublished data).

Until recently, the best-described cases were those that occurred at Gombe in the 1970s. By 1972, the main study community at Gombe had split into two:

TABLE 1 Intercommunity killings of adults and adolescents, 1972–2002

Site	Year	Victim ^a	Aggressors' community	Victim's community	Evidence ^b
Gombe	1972	Unknown	Kahama?	Kalande?	Inf. ¹
Gombe	1974	<i>Godi</i>	Kasekela	Kahama	Obs. ²
Gombe	1974	<i>Dé</i>	Kasekela	Kahama	Obs. ²
Gombe	1975	<i>Goliath</i>	Kasekela	Kahama	Obs. ²
Gombe	1975	Madam Bee	Kasekela	Kahama	Obs. ²
Gombe	1977	<i>Sniff</i>	Kasekela	Kahama	Obs. ²
Gombe	1977	<i>Charlie</i>	Kasekela	Kahama	Inf. ²
Gombe	1998	<i>Unknown</i>	Kasekela	Kalande	Obs. ^{5*}
Gombe	2002	<i>Rusambo</i>	Kasekela	Mitumba	Inf. ⁵
Kibale	1992	<i>Ruwenzori</i>	Rurama	Kanyawara	Inf. ³
Kibale	1998	<i>Unknown</i>	Kanyawara	Sebitole	Inf. ^{3,4}
Kibale	2002	<i>Unknown</i>	Ngogo	Unknown	Obs. ⁶
Kibale	2002	<i>Unknown</i>	Ngogo	Unknown	Obs. ⁶
Kibale	2002	<i>Unknown</i>	Ngogo	Unknown	Obs. ⁶

^aFemales in bold, males in italics.

^bWhether the attack was observed directly (Obs.) or inferred from strong evidence such as finding a body with wounds consistent with chimpanzee attack (Inf.).

References: ¹Wrangham (1975); ²Goodall (1986); ³Wrangham (1999); ⁴Muller (2002); ⁵M.L. Wilson, W. Wallauer, and A.E. Pusey, submitted; ⁶D.P. Watts and J.C. Mitani, personal communication.

*Attack was observed but whether the victim survived is unknown.

Kasekela in the north and Kahama in the south (Bygott 1979). From 1974 to 1977, Kasekela males brutally attacked at least five and probably six or more Kahama chimpanzees. Observers directly witnessed attacks on five individuals (Godi, Dé, Goliath, Madam Bee, and Sniff). The body of a sixth individual, Charlie, was found after fisherman heard sounds of fighting and saw a large group of habituated males, almost certainly from Kasekela (Goodall 1986). With the death of Sniff in 1977, the Kahama community became extinct, and the surviving females joined neighboring communities. One Kasekela male, Faben, disappeared in 1975 and was suspected have been a victim of intergroup aggression (Goodall 1986, p. 64).

Following Kahama's extinction, intergroup relations remained hostile at Gombe. From 1979 to 1990, four juveniles and four adult males disappeared in the absence of injury or illness (Williams et al. 2002b). In recent years, observers have found direct evidence of additional intergroup killing of weaned individuals. In 1998, observers at Gombe witnessed a brutal and possibly fatal attack on a young male from Kalande (M.L. Wilson, W. Wallauer, and A.E. Pusey, submitted manuscript; for video footage from this attack, follow the Supplemental Material link from

the Annual Reviews home page at <http://www.annualreviews.org>). In 2002, the day after an incursion into Mitumba's range by a large party of Kasekela males, observers found the body of an adolescent Mitumba male, Rusambo, whose numerous wounds included severe bites to the throat and elsewhere, bruises, and a torn-off scrotum and penis (M.L. Wilson, W. Wallauer, and A.E. Pusey, submitted manuscript).

At Mahale, K-group (initially about 30 individuals) lost all six of its adult males and one adolescent male from 1970 to 1982 (Nishida et al. 1985). Although K-group was described as "effectively extinct" by 1982 (Nishida et al. 1985), sporadic sightings indicate that a remnant, including a male who was an adolescent in 1982, persisted at least through the 1990s (Nishida et al. 1990, Uehara et al. 1994). Researchers speculated that the K-group males died from attacks by the large M-group (90–100 individuals) (Nishida et al. 1985). In contrast to Gombe, observers at Mahale neither directly observed intergroup killing nor found bodies of victims. Nonetheless, aggressive intergroup encounters did occur during K-group's decline, including the intergroup killing of infants (Nishida et al. 1979). As the number of K-group males declined, M-group expanded its range to include former K-group territory, and most of K-group's females joined M-group.

What caused the disappearance of K-group's males remains unknown. Alternatives to intergroup aggression include disease and predation. In contrast to known disease epidemics (e.g., Nishida et al. 1990), the K-group males were all healthy at the time of their disappearance. Both lions and leopards sometimes prey on chimpanzees and are capable of killing adult males (Boesch 1991, Inagaki & Tsukahara 1993). During the disappearances of the K-group males, however, observers found no evidence of predation—such as wounded survivors of attacks—and/or fresh carcasses with carnivore wounds (cf., Boesch 1991). Circumstantial evidence thus supports intergroup aggression as the cause of at least some of these deaths.

At Kibale, evidence for intergroup killing of adults exists for both the Kanyawara and Ngogo communities. The freshly killed body of a Kanyawara male, Ruwenzori, was found near the site of recent intergroup encounters, huddled face down at the edge of an area trampled by what was apparently the charges and fighting of chimpanzees (Wrangham 1999). In 1998, observers found a large party of Kanyawara males beating on and displaying around the freshly killed body of a male from the Sebitole community (Muller 2002). The victim's body bore numerous wounds consistent with chimpanzee attack, including broken ribs, removal of testes and fingernails, and a ripped-out trachea (Muller 2002). At Ngogo in 2002, observers witnessed lethal intergroup attacks on two adult males and one juvenile male (D.P. Watts and J.C. Mitani, personal communication).

In most cases, the victims did not die immediately after these attacks. Instead, their death was inferred from their subsequent disappearance or the discovery some days later of the victim's body. Nonetheless, observers had the impression that killing was the goal of these attacks (e.g., Goodall 1986). The attacks on Kahama individuals included an intensity of wounding not seen in other contexts,

such as prolonged beating, biting, twisting of limbs, tearing off strips of flesh, and, in one case, drinking blood from the victim's nose (Goodall 1986). Among the more recent attacks, evidence for immediate death of the victim exists in five cases. At Kanyawara, Ruwenzori's body was found on the site of trampled vegetation, indicating he died during or soon after the attack (Wrangham 1999). The Sebitole male inferred to have been killed by Kanyawara males presumably died soon after his trachea was ripped from his throat (Muller 2002). At Gombe, Rusambo had massive damage to the throat and is unlikely to have survived long after receiving those wounds (M.L. Wilson, W. Wallauer, and A.E. Pusey, submitted manuscript). During two of the three fatal intergroup attacks at Ngogo in 2002, the victim died before the attackers left (D.P. Watts and J.C. Mitani, personal communication).

Fatal coalitionary killing attacks are not limited to intergroup contexts (Wrangham 1999). Intragroup killings have occurred at Budongo (Fawcett & Muhumuza 2000), Mahale (Nishida 1996), and Ngogo (D.P. Watts and J.C. Mitani, personal communication). For example, at Budongo, during a time of intense competition for mates, males ganged up on and killed a young male from their own community (Fawcett & Muhumuza 2000). At Mahale, males overthrew and killed Ntologi, who had spent nearly 16 years as alpha male (Kitopeni et al. 1995).

LETHAL ATTACKS: INFANTS

Although discussions of lethal intergroup aggression often focus on conflict between adults (e.g., Gat 1999, Sussman 1999), intergroup attacks have resulted in a comparable number of infant victims. For example, compared to the 14 or more killings of adults (Table 1), 15 infants are known or inferred to be victims of intergroup attack (Table 2). In addition to intergroup infanticide, a similar number of intragroup infanticides have been reported [$N = 12$ in which the mother was known to be a stranger and 3 in which the mother's community was uncertain (Table 6 in Arcadi & Wrangham 1999)].

Intergroup infanticide is more widespread than killing of adults, having been reported for four of the five long-term sites: Budongo, Gombe, Kibale, and Mahale. Six cases of intergroup infanticide occurred at Gombe and Mahale in the 1970s. In three of these cases the attack was observed directly, and in the other cases three males were found eating the infant's freshly killed carcass (reviewed in Arcadi & Wrangham 1999). Recent cases of infanticide include two from Budongo (Newton-Fisher 1999), two from Gombe (M.L. Wilson, W. Wallauer, and A.E. Pusey, submitted manuscript), four from Kibale (Ngogo) (Watts et al. 2002, Watts & Mitani 2000), and one from Mahale (Kutsukake & Matsusaka 2002).

A single ambiguous case of infanticide has been reported for Tai. Observers found females eating an infant, presumably an infanticide victim, near the boundary

TABLE 2 Observed and inferred intercommunity infanticides, 1967–2002

Site	Date	Infant's sex	Aggressors' community	Victim's community	Evidence ^a
Budongo	1995	Unknown	Sonso	N15	Inf. ⁵
Budongo	1995	M	Sonso	N15	Obs. ⁵
Gombe	1971	Unknown	Kasekela	Unknown	Obs. ¹
Gombe	1975	M	Kasekela	Unknown	Inf. ²
Gombe	1975	F	Kasekela	Unknown	Obs. ²
Gombe	1979	Unknown	Kasekela	Unknown	Obs. ⁴
Gombe	1993	F	Kasekela	Mitumba	Obs. ⁹
Gombe	1998	Unknown	Kasekela	Kalande	Obs. ⁹
Kibale	1999	Unknown	Ngogo	Unknown	Obs. ⁶
Kibale	1999	Unknown	Ngogo	Unknown	Obs. ⁶
Kibale	2001	Unknown	Ngogo	Unknown	Obs. ⁷
Kibale	2001	Unknown	Ngogo	Unknown	Inf. ⁷
Mahale	1974	M	K-group	M-group	Inf. ³
Mahale	1976	M	M-group	K-group	Sus. ³
Mahale	2000	M	M-group	Unknown	Inf. ⁸

^aWhether the fatal attack was observed directly (Obs.), inferred from strong evidence such as finding males eating a freshly killed infant (Inf.), or suspected from the sudden disappearance of a healthy individual (Sus.).

References: ¹Bygott (1972); ²Goodall (1977); ³Nishida et al. (1979); ⁴Goodall (1986); ⁵Newton-Fisher (1999); ⁶Watts & Mitani (2000); ⁷Watts & Mitani (2002); ⁸Kutsukake & Matsusaka 2002; ⁹M.L. Wilson, W. Wallauer, and A.E. Pusey, submitted.

of the community's range, but it was not clear whether the infant was from the study community (Boesch & Boesch-Achermann 2000). On a number of occasions, Tāi males captured a female "prisoner" and attacked her with sufficient severity that blood was observed on the female and on the ground following the attack (Boesch & Boesch-Achermann 2000). During such attacks, mothers with infants cowered protectively over their infants, suggesting that Tāi infants do face some risk from male attackers.

Intergroup infanticide typically involves many males attacking a strange mother. Males may beat the mother severely. In contrast to attacks on adults, attacks on infants usually result in the victim's immediate death. In most cases, the attackers killed the infant quickly with a bite to the head or bowels and ate at least part of the carcass (Arcadi & Wrangham 1999). In most cases, the attackers overwhelmingly outnumbered the mother, who was unable to effectively defend herself or her infant. Attackers thus face little risk of injury. In the recent case at Mahale, however, the presumed mother of the infanticide victim attacked and severely injured two human observers, whom she apparently regarded as allies of her attackers (Kutsukake & Matsusaka 2002).

FUNCTIONS OF INTERGROUP AGGRESSION

It is now clear that chimpanzees across Africa defend group territories and respond to members of neighboring groups with aggression, including lethal attacks. Debate continues, however, over the relative importance of different benefits that chimpanzees gain from intergroup aggression. Recent studies have helped clarify long-standing questions about the degree to which males are successful in excluding rival males, the degree to which males can gain females by expanding territory or killing their infants, and the extent to which territorial behavior involves feeding competition.

Excluding Rival Males

For males in many species, females are the limiting resource for reproductive success (Trivers 1972). The primary cause of chimpanzee intergroup aggression is thus widely assumed to be competition for mates: Males cooperate to defend their females from other males (e.g., Ghiglieri 1989, Manson & Wrangham 1991). The routine aggression toward stranger males supports this assumption. Researchers were thus surprised when early genetic paternity tests of Tai chimpanzees indicated that over 50% of infants had fathers from outside the community (Gagneux et al. 1997, 1999). These results suggested that intercommunity mating is widespread and an important feature of chimpanzee social evolution (e.g., Boesch & Boesch-Achermann 2000). Subsequent studies, however, found the earlier reports to be mistaken. Improved lab work and data analysis methods identified within-community fathers for most infants at Tai (Constable et al. 2001, Vigilant et al. 2001). Genetic testing at Gombe found within-community fathers for all infants (Constable et al. 2001). These results indicate that males are largely successful in defending their females from outside males and/or that females choose not to mate with extragroup males.

Gaining Females by Expanding Territory

In addition to defending their females from extragroup males, various authors have proposed that a goal of male intergroup aggression is to obtain females from rival groups (e.g., Boesch & Boesch-Achermann 2000, Ghiglieri 1989, Manson & Wrangham 1991). The degree to which females are obtainable from rivals depends on both the female's age and the extent to which females are loyal to particular communities. Male demonstrations of power during intergroup encounters potentially influence the transfer choices of adolescent females. Direct evidence for factors underlying the decisions of which community females join is limited, however. Females usually have several communities to choose from, with at best one or two of them known to researchers. Nonetheless, some evidence suggests that females choose communities with more males. For example, during K-group's decline, many of K-group's adolescent females transferred to the much larger M-group, and one M-group female that had immigrated to K-group transferred back to M-group (Nishida et al. 1985).

More questionable is the degree to which male intergroup aggression can influence the group membership of adult females with offspring (parous females). Whether male chimpanzees can add parous females to their community by expanding their territory depends on the degree to which females identify with a particular community (Williams et al. 2002b). The degree to which female ranging patterns depended on male territorial boundaries remained unclear for many years. Females spend much of their time alone, and most studies have focused on more conspicuous male behavior such as hunting and fighting.

Wrangham (1979) proposed three alternative models in which female home ranges are either (a) entirely overlapping with male ranges, (b) smaller than male ranges and dispersed within boundaries defended by males, or (c) smaller than male ranges and dispersed independently of boundaries defended by males. The first model can be rejected, with the possible exception of Tai (Boesch & Boesch-Achermann 2000, Wrangham 1979). Distinguishing between the second and third models has proved difficult, but these two models provide contrasting predictions regarding the extent to which males can acquire new females. In the second model, because females identify closely with a single territory defended by males, males cannot directly increase their access to females by expanding territory. Instead, male access to females depends on female immigration patterns. In contrast, in the third model, males can increase their access to females by taking over more land occupied by those females.

Analyzing 18 years of ranging data from Gombe, Williams and colleagues (2002b) found evidence for a variation of Wrangham's second model that might be termed the neighborhood model. Rather than being evenly distributed across the landscape, females settle in different neighborhoods within the male-defended range. Most females live in centrally located neighborhoods, avoid borders, and mate exclusively with males of one community. These females' home ranges expanded when the community's total area grew and contracted when the total area shrank. Some females, however, lived in peripheral neighborhoods and may have maintained friendly relations with more than one community. One possible advantage to having a peripheral home range is that food resources may be more plentiful in the no-man's-land between communities (Boesch & Boesch-Achermann 2000, Wilson 2001). Despite possible access to more abundant food, however, females using the periphery face a higher risk of intergroup aggression and infanticide (Williams et al. 2002b). These observations from Gombe indicate that, over all, males are unlikely to add females to their community simply by expanding their territory. Nonetheless, the diversity of female strategies suggests that, in some cases, peripheral females could change their community loyalties when faced with territorial expansion.

Rival Extermination

The community extinctions reported for Gombe and Mahale suggest that one strategy for males to add females to their community is to kill all the males from a

rival community. The extent to which this strategy occurs is difficult to interpret. Of the two reported community extinctions, Gombe and Mahale, lethal attacks were observed only at Gombe, and extensive female transfers were observed only at Mahale.

At Gombe, Kahama contained at least three adult females and two adolescent females (Goodall 1986). One of these adolescent females, Little Bee, joined Kasekela in the early 1970s, though it is unclear whether Little Bee's immigration was the result of intergroup aggression. The other adolescent, Honey Bee, was briefly seen in Kasekela but then disappeared. Both adolescents were daughters of Madam Bee, who was killed by the Kasekela males through a series of at least five attacks that occurred over the course of a year (Goodall 1986). One additional but uncertain case is that of Joanne, who immigrated to Kasekela in 1978 with her five-year-old son. Based on facial resemblance and the age of her son, researchers suspect that Joanne was the daughter of Wanda, a likely Kahama resident (Williams et al. 2002b). It is thus unclear whether the attacks on Kahama chimpanzees yielded any direct gains in female members for the Kasekela males.

The case for large-scale transfer of females is clear from Mahale. K-group contained a maximum of 6 males and 14 females in the early 1970s. Including females who immigrated and natal females who grew to maturity, a total of 28 females resided in K-group during the group's decline (1970–1983) (Nishida et al. 1985). Seventeen of these females transferred to M-group and five disappeared, presumably transferring to an unhabituated group. Only six females had not emigrated from K-group by 1983; three of these had died. Of the 17 females that transferred to M-group, 5 were K-group natal females that presumably would have left their natal group in any case. (A sixth natal female had returned to K-group to breed, then transferred to M-group after her son was weaned.) The remaining females included females with infants, who usually do not transfer, as well as young females born in M-group who probably would not have returned to their natal group if K-group had survived. In general, K-group females with young infants did not transfer to M-group until their infants were weaned, presumably to minimize infanticide risk (Nishida et al. 1985).

M-group males clearly gained females because of K-group's decline. As discussed above, however, the reasons for K-group's decline remain uncertain. Whether K-group's males were killed mainly by M-group males, as Nishida and colleagues (1985) proposed, or by some other factor, K-group's females showed a strong preference to reside in the group with more males, despite all the potential costs of transferring, such as aggression from the new community's males and females and the risk of infanticidal attacks.

The large-scale transfer of K-group females to M-group suggests that exterminating rival males would be an effective way to gain females. Whether such extermination is the goal of intergroup killing remains unclear. Killing all the males of a rival community takes many years and occurs rarely. Existing evidence suggests that rather than being the goal of intergroup aggression, exterminating all

of a rival group's males is an extreme outcome of a more general strategy: killing individual rivals whenever possible (see below, Imbalances of Power).

Recruiting Females Through Infanticide

In some species, such as gorillas (Watts 1989) and Thomas' langur monkeys (Sterck 1995, Steenbeek 1999), females whose infants were killed by a stranger male during an intergroup encounter have subsequently joined the attacker's group. The logic underlying such transfers is that by killing a female's infant a male demonstrates the inability of a female's current male(s) to protect her and her offspring from such attacks. In chimpanzees, however, there is little or no evidence that females whose infants were killed during intergroup infanticide subsequently joined the attackers' community (reviewed in Arcadi & Wrangham 1999, Watts et al. 2002). Obtaining such evidence is difficult, however, in that the mothers in such cases are usually unhabituated and not individually recognized. Intergroup infanticide seems more likely to result from either attempts to reduce the coalitionary strength of neighboring communities (Nishida & Kawanaka 1985, Takahata 1985) or from a more general strategy of defending feeding territory from all members of rival groups (Pusey 2001; J. Williams and A.E. Pusey, submitted manuscript).

Defending a Feeding Territory

Williams and Pusey (J. Williams and A.E. Pusey, submitted manuscript) argue that males defend a feeding territory for themselves, females, and their offspring. In this view, male territoriality represents parental effort rather than mating effort. Males indirectly gain fitness benefits by providing more territory and thus more food for females and their offspring. In a given habitat, larger territories presumably contain more food such as fruit trees and animal prey. Recent analyses of long-term data at Gombe reveal that females travel in larger parties and have shorter interbirth interval when territory size is larger, both indications of more abundant food (Pusey 2001; J. Williams and A.E. Pusey, submitted manuscript). Additional evidence in support of the view that intergroup aggression involves male parental effort comes from data on participation in border patrols. At Ngogo, males with more mating success, and hence greater probability of having offspring in the community, participated in patrols more often than other males (Watts & Mitani 2001).

The pattern of aggression toward females supports the view that males defend a feeding territory for themselves, their mates, and offspring. If males were attempting to recruit females, they would be expected to affiliate with them rather than attack them. In general, male hostility to a stranger female depends on both the female's cycling status and the presence of offspring. Swollen females without infants receive the least aggression, and nonswollen females with infants receive the most. This pattern of aggression appears based on the female's reproductive value, a measure of a female's expected future reproduction (Wolf & Schulman 1984). Young females without infants are likely to transfer and thus represent possible recruits, whereas older females with infants represent competitors for food and the source of future male rivals.

IMBALANCES OF POWER

Chimpanzees, like many social mammals, compete over territory, food, and females. Why should chimpanzees, but few other mammals, engage in lethal intergroup attacks? The imbalance-of-power hypothesis developed by Wrangham and colleagues (Manson & Wrangham 1991, Wrangham & Peterson 1996) attempts to answer this question by drawing attention to the costs, rather than the benefits, of aggression. A growing number of studies support the view that animals use aggression strategically, when the benefits are likely to outweigh the costs of aggression (Archer 1988, Huntingford & Turner 1987, Wilson 2003). Proximate mechanisms underlying aggression should therefore be sensitive to both costs and benefits. Costs of aggression include the risk of injury and/or death as well as energetic and opportunity costs (time spent fighting could be spent feeding or mating instead). Benefits of aggression include food and females. Decisions about how to interact with neighbors should therefore depend on a variety of factors, including resource distribution and assessing the motivations and capabilities of potential opponents. The imbalance-of-power hypothesis proposes that in chimpanzees fission-fusion social structure, combined with coalitionary bonds among males, creates opportunities for low-cost killing of rivals.

Chimpanzees travel in parties of varying size and composition, which may result in large disparities in party size during intergroup encounters, even among communities that are similar in overall size. In such cases, members of the larger group can kill rivals at very low risk of injury to themselves. During observed lethal intergroup attacks, three or more attackers ganged up on a single victim, who was immobilized by some of the attackers while others beat and bit the victim. Attackers themselves rarely received injuries. The imbalance-of-power hypothesis thus argues that intergroup attacks are lethal not because of unusually high benefits to be obtained from killing, but because the costs of killing are low during gang attacks.

The primary benefit of intergroup killing is thought to be the reduction of the coalitionary strength of rival communities. By reducing the fighting strength of a given community, males increase their chances of success in future battles with that community. More frequent success in battles should result in territory expansion and thus more food for group members, including females and offspring.

Both observational and experimental evidence support the prediction that chimpanzees modify their response to intergroup threat based on the relative number of opponents. At both Ngogo and Taï, parties containing many males were more likely to approach intruders (Boesch & Boesch-Achermann 2000, Watts & Mitani 2001). The actual number of intruders was unknown in these cases. To obtain a more controlled test, Wilson and colleagues (2001) used playback experiments to simulate intergroup encounters. These experiments involved playing a single pant-hoot from a stranger male to parties of varying size and composition. Parties with only females remained silent, and in some cases females dropped down from the trees and moved away from the speaker. Parties with one or two males also

remained silent, but in about half the cases the males moved slowly and cautiously toward the speaker. Parties with three or more males usually responded with loud calls immediately after the playback and quickly approached the speaker. These results indicate that chimpanzees are able to assess the numerical strength of their own side compared to the opposition and are more likely to respond aggressively when the odds are in their favor. More recent experiments conducted at Tai will refine our understanding of how numerical assessment interacts with other factors, such as familiarity with the opponent(s) (I. Herbinger and C. Boesch, submitted manuscript).

Additional observational evidence supports the view that the number of males in a community is crucial to the community's success in intergroup encounters. At Tai, the Northern group's territory was larger when it contained more males (Lehmann & Boesch 2003). At Gombe, territory size did not depend on the number of adult males alone but did depend on the number of adult males divided by an index of intergroup threat (J. Williams and A.E. Pusey, submitted manuscript). The exceptionally large Ngogo community in Kibale has over 150 members, including 23 adult males (Watts et al. 2002). The large number of males at Ngogo enables that community to engage in high rates of cooperative aggression, both within and between species. In a single year, 2002, Ngogo males killed two adults and a juvenile male from neighboring communities and also killed an adult male in their own community (D.P. Watts and J.C. Mitani, personal communication). In addition to killing adults, Ngogo males have killed four infants from neighboring communities in the past four years (Watts et al. 2002). The large number of males at Ngogo also leads to extraordinary success in coalitionary killing of their preferred prey, red colobus monkeys (Mitani & Watts 1999).

Killing Future Rivals

The imbalance-of-power hypothesis predicts that a primary benefit of intergroup infanticide is to reduce the future coalitionary strength of rival communities. To ensure the killing of future rivals rather than potential future mates, attackers should kill male rather than female infants. Observers were able to determine the sex of the victim in 7 of 14 infanticide cases (Table 2). Two victims were female and five were male. The occurrence of female victims suggests either that intergroup infanticide serves some function besides reducing the number of future male rivals or that attackers do not face a high cost from making mistakes in identifying the victim's sex.

RELEVANCE TO HUMANS

The first four decades of research on wild chimpanzees have produced evidence of important similarities between aspects of chimpanzee and human intergroup aggression. Comparisons between the two species are made difficult, admittedly,

by many factors. In chimpanzees, the description of intergroup aggression is still in an early phase. In humans, quantitative data from the most relevant groups (hunter gatherers) are so rare that different authors reach widely differing conclusions about the frequency of aggression (e.g., Ferguson 2000, Gat 2000a).

Yet despite these problems, it is clear that intergroup aggression has occurred among many, possibly all, hunter-gatherer populations and follows a rather uniform pattern (Gat 1999). From the most northern to the most southern latitudes, the most common pattern of intergroup aggression was for a party of men from one group to launch a surprise attack in circumstances in which the attackers were unlikely to be harmed. Attacks were sometimes unsuccessful but were, at other times, responsible for the deaths of one or many victims. Women and girls were sometimes captured (Gat 1999).

One factor that complicates efforts to compare patterns of intergroup aggression in humans and chimpanzees is that in chimpanzees the only large social group is the community, whereas no precise equivalent of the chimpanzee community exists for humans. Instead, human group membership always exists on several levels: residential group, clan, tribe, nation, and so on (Boehm 1992, Durkheim 1933). The existence of these multiple types of group complicates the comparison of aggressive patterns between chimpanzees and humans because it means that aggression between groups can occur at many more levels among humans than among chimpanzees. At one extreme, aggression can be found between residential groups that both belong to the same linguistic, cultural, and tribal unit, within which individuals can move and intermarry [internal warfare (Otterbein 1997)]. At the other extreme, it can occur between culturally distinct groups having different languages (or dialects) and little or no tendency for intermarriage or friendly contact (external warfare).

Despite this variation, a useful comparison can be made between chimpanzees and humans by identifying the level at which relations are essentially anarchic, i.e., characterized by the lack of any central or cultural authority. Human societies normally feature such a level (Rodseth & Wrangham 2003). The Ache, for example, lived in bands of 10 to 70 individuals who, in turn, formed groups of up to 550 (Hill & Hurtado 1996). Within these regional groups, the only form of culturally sanctioned violence among men was the club fight. By contrast, "anyone not in the group, including other Ache, could be shot on sight" (Hill & Hurtado 1996, p. 70).

Among foraging societies, such regional groups frequently included around 500 individuals (e.g., Birdsell 1968, Tindale 1974). Both the size and internal structure of such groups varied extensively, however, in relation to ecological and cultural factors, as indicated by the wide variety of terms used to describe them (e.g., dialect group, maximum band, tribe).

Whatever the name used, this level of grouping suggests a similarity to the chimpanzee community because aggressive interactions at this level are not regulated by the predictable intervention of allies (Rodseth & Wrangham 2003). This essential similarity suggests that shared principles may help explain the occasionally

intense escalation of interactions between such groups. But of course the similarity gives way to major differences in scale and organization, given that humans can expand their regional groupings all the way to nation-states containing hundreds of millions of individuals living in complex networks.

Chimpanzees and hunter gatherers, we conclude, share a tendency to respond aggressively in encounters with members of other social groups; to avoid intensely aggressive confrontations in battle line (typically, by retreating); and to seek, or take advantage of, opportunities to use imbalances of power for males to kill members of neighboring groups.

These similarities have been explained in parallel ways in the two species, using concepts from evolutionary ecology (Gat 2000b,c; Wrangham 1999). The essential notion is that natural selection has favored specific types of motivational systems (Gat 2000b). In particular, motivations have been favored that have tended, over evolutionary time, to give individuals access to the resources needed for reproduction.

The motivations that drive intergroup killing among chimpanzees and humans, by this logic, were selected in the context of territorial competition because reproduction is limited by resources, and resources are limited by territory size. Therefore, it pays for groups to achieve dominance over neighboring groups so that they can enlarge their territories. To achieve dominance, it is necessary to have greater fighting power than the neighbors. This means that whenever the costs are sufficiently low it pays to kill or damage individuals from neighboring groups. Thus, intergroup killing is viewed as derived from a tendency to strive for status (Gat 2000c, Wrangham 1999). According to this view, these several aspects of human intergroup aggression do not appear exceptional compared to other animals (Gat 2000a).

Many other aspects of human intergroup aggression, however, differ extensively from chimpanzees, such as the ability of residential groups to form alliances, the possibilities for expressing formal peace relations, the capacity for symbolic domination [through cannibalism, for example (Gat 2000c)], the ability to kill large numbers at a time, and the integration of intergroup relations with ideology. Such differences suggest to some critics that human warfare cannot usefully be compared to chimpanzee aggression (Lewontin 1999, Marks 1999, Sussman 1999). No ultimate explanation has yet been offered, however, as an alternative to the hypothesis that territorial competition for resources for reproduction favors a drive for intergroup dominance (cf., Gat 2000a).

Finally, it is important not to confuse levels of explanation. The comparison of chimpanzees and humans is useful in suggesting common principles generating evolved psychological tendencies. But it is not useful in directly accounting for intraspecific variation, which is the central concern of the anthropology of war (e.g., Otterbein 2000). As with chimpanzees and other species, however, models based on evolutionary principles (such as behavioral ecology) provide powerful tools for understanding intraspecific variation (e.g., Daly & Wilson 1988, Mesquida & Wiener 1996).

LETHAL RAIDING IN *PAN* AND *HOMO*: HOMOLOGY OR HOMOPLASY?

It is currently unclear whether the patterns of intergroup aggression seen in humans and chimpanzees result from homology (shared evolutionary history) or homoplasy (convergent evolution). Various lines of evidence suggest that our common ancestor with chimpanzees was very much like a chimpanzee (Wrangham & Pilbeam 2001). In the five to seven million years that followed the divergence of the lines leading to *Pan* and *Homo*, however, the human lineage developed into a bushy tree (Wood & Collard 1999). A variety of woodland apes (Wrangham & Peterson 1996) evolved, including *Ardipithecus*, *Australopithecus*, and *Paranthropus*. These creatures do not closely resemble any living species, and we can make only educated guesses about their feeding ecology and social structure. Considerable behavioral diversity exists among extant apes; woodland apes probably varied as well, with societies that evolved to meet different ecological challenges. We know that social behavior can change quickly over evolutionary time. The two extant species of *Pan*, chimpanzees and bonobos, differ considerably in their intergroup relations despite generally similar feeding ecology, morphology, and recent date of divergence. Fossils can provide only a limited amount of information about social behavior. For example, lions and tigers differ strikingly in their social behavior, despite being closely related enough to interbreed. If we had only fossils of lions and tigers, it is hard to imagine that we would be able to infer cooperative territory defense for the one and solitary seclusion for the other.

The relevance of chimpanzee violence to the evolution of human warfare does not depend on the possibility that both species inherited this trait from a common ancestor. Instead, chimpanzees provide a valuable referential model. Before observers reported accounts of chimpanzee intergroup aggression, anthropologists assumed that human warfare resulted from some factor unique to the human lineage, such as social stratification, horticulture, high population density, or the use of tools as weapons. The observation of warlike behavior in chimpanzees demonstrated that none of these factors was required. A similar lesson could be drawn from the warlike behavior of social carnivores, such as lions, wolves, and spotted hyenas (Wrangham 1999). The relevance of carnivore behavior to human evolution might be discounted, however, given that carnivores possess many specialized traits; intergroup killing in carnivores could be a byproduct of morphological and behavioral evolution for cooperative hunting. The benefit of using chimpanzees as a referential model is that, as our evolutionary cousins, they give us a more realistic picture of traits our ancestors may have possessed.

The benefits and limitations of using chimpanzee data to understand the evolution of human warfare are similar to those presented by data on another trait shared by chimpanzees and humans: hunting. In both species, hunting is conducted mainly by males, who often hunt in groups. As Mitani & Watts point out (2003), chimpanzee hunting differs in various ways from human hunting. For example, chimpanzees pursue prey through the trees and kill with their hands and

teeth, whereas humans pursue prey on the ground and kill with weapons. Chimpanzees hunt opportunistically, and the degree of cooperation involved remains the subject of debate, whereas human hunting clearly involves planning and cooperation. We don't know if "*Pan prior*" (Wrangham 2001) hunted, and the extent to which the various early woodland apes hunted or scavenged continues to be debated. Nevertheless, much like the case with intergroup aggression, data from chimpanzees (and other primates, such as baboons) challenged previous views that humans were the only hunting primate, and ongoing studies continue to provide valuable insight for guiding our thinking about human evolution.

CONCLUSION

Recent studies have shown that the patterns of intergroup aggression reported from Gombe and Mahale in the 1970s are, in many ways, typical of chimpanzees. Chimpanzees at all long-term study sites defend group territories, and chimpanzees at four out of five sites have conducted lethal attacks on members of neighboring groups. Studies of unprovisioned communities demonstrate that these patterns of intergroup aggression are not the result of provisioning. Indeed, the Ngogo community, which Power (1991) considered a prime example of peaceful intergroup relations, turns out to have an exceptionally high rate of intergroup violence.

Instead of being a maladaptive aberration, chimpanzee intergroup aggression appears to be typical of aggression in other wild animals in that it tends to provide fitness benefits for the aggressors. Two sets of genetic paternity tests demonstrate that males successfully kept outside males from mating with females in their community, a result supported by consistent behavioral observations. Females reproduced more quickly when territories were larger, indicating that both females and males benefit from defense and acquisition of feeding territory.

The chimpanzee studies suggest that our understanding of human intergroup aggression, particularly small-scale non-state violence, would benefit from more extensive testing of hypotheses generated by behavioral biology. The few studies that have focused on testing evolutionary principles (e.g., Chagnon 1988, 1992) have provoked hostile critiques (e.g., Ferguson 2001, Tierney 2000). The hostility apparent in such critiques reflects a widespread concern that "biological" is equivalent to "fixed" or "unchangeable." Contemporary behavioral biology, however, views primate aggression as a strategic response to appropriate environmental conditions. Rather than viewing human aggression as inevitable, an approach rooted in behavioral biology would provide more focused predictions for when aggression is likely to occur and how aggression can be reduced.

Even among chimpanzees, rates of intergroup aggression vary considerably among sites and over time within sites. Understanding the factors responsible for that variation constitutes the next frontier in studies of chimpanzee intergroup relations. The range of variation may well prove greater than so far observed. For example, under appropriate conditions, captive chimpanzees can be induced to

accept new adult males into their group, something not yet observed in the wild (Seres et al. 2001). Newly introduced males are predictably aggressive to one another, but appropriate management can lead to eventual acceptance.

Such observations indicate both that biology provides chimpanzees with clear dispositions (e.g., hostility toward stranger males) but also that even chimpanzees, under the right conditions, can learn to overcome such hostility. A fully developed behavioral biology of human intergroup aggression offers similar hope for understanding—and addressing—the roots of violence in our own species.

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LITERATURE CITED

- Alexander RD. 1989. Evolution of the human psyche. In *The Human Revolution*, ed. P Mellars, C Stringer, pp. 455–513. Edinburgh: Edinburgh Univ. Press
- Anderson DP, Nordheim EV, Boesch C, Moermond TC. 2002. Factors influencing fission-fusion grouping in chimpanzees in the Tai National Park, Côte d'Ivoire. In *Behavioral Diversity in Chimpanzees and Bonobos*, ed. C Boesch, G Hohmann, LF Marchant, pp. 90–101. Cambridge, UK: Cambridge Univ. Press
- Arcadi AC, Wrangham RW. 1999. Infanticide in chimpanzees: review of cases and a new within-group observation from the Kanyawara study group in Kibale National Park. *Primates* 40:337–51
- Archer J. 1988. *The Behavioural Biology of Aggression*. Cambridge, UK, New York: Cambridge Univ. Press
- Bauer HR. 1980. Chimpanzee society and social dominance in evolutionary perspective. In *Dominance Relations: Ethological Perspectives of Human Conflict*, ed. DR Omark, FF Strayer, D Freedman, pp. 97–119. New York: Garland
- Birdsell J. 1968. Some predictions for the Pleistocene based on equilibrium systems among recent hunter-gatherers. In *Man the Hunter*, ed. DR Lee, I DeVore, pp. 229–40. Chicago: Aldine
- Boehm C. 1992. Segmentary 'warfare' and the management of conflict: comparison of East African chimpanzees and patrilineal-patrilocal humans. In *Coalitions and Alliances in Humans and Other Animals*, ed. AH Harcourt, FMB de Waal, pp. 137–73. Oxford, UK: Oxford Univ. Press
- Boesch C. 1991. The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour* 117:220–42
- Boesch C, Boesch-Achermann H. 2000. *The Chimpanzees of the Tai Forest: Behavioral Ecology and Evolution*. Oxford, UK: Oxford Univ. Press
- Boydston EE, Morelli TL, Holekamp KE. 2001. Sex differences in territorial behavior exhibited by the spotted hyena (*Hyaenidae, Crocuta crocuta*). *Ethology* 107:369–85
- Bygott JD. 1972. Cannibalism among wild chimpanzees. *Nature* 238:410–11
- Bygott JD. 1979. Agonistic behaviour and dominance among wild chimpanzees. See Hamburg & McCown 1979, pp. 405–27

- Chagnon NA. 1988. Life histories, blood revenge, and warfare in a tribal population. *Science* 239:985–92
- Chagnon NA. 1992. *Yanomamo*. Fort Worth, TX: Harcourt Brace
- Chapman CA, White FJ, Wrangham RW. 1994. Party size in chimpanzees and bonobos: a reevaluation of theory based on two similarly forested sites. In *Chimpanzee Cultures*, ed. RW Wrangham, WC McGrew, FBM de Waal, PG Heltne, pp. 41–58. Cambridge, MA: Harvard Univ. Press
- Chapman CA, Wrangham RW. 1993. Range use of the forest chimpanzees of Kibale: implications for the understanding of chimpanzee social organization. *Am. J. Primatol.* 31:263–73
- Clark AP. 1993. Rank differences in the production of vocalizations by wild chimpanzees as a function of social context. *Am. J. Primatol.* 31:159–79
- Constable JL, Ashley MV, Goodall J. 2001. Noninvasive paternity assignment in Gombe chimpanzees. *Mol. Ecol.* 10:1279–1300
- Daly M, Wilson M. 1988. *Homicide*. Hawthorne and New York: Aldine de Gruyter
- de Waal FBM, ed. 2001. *Tree of Origin*. Cambridge, MA: Harvard Univ. Press
- Durkheim E. 1933. *The Division of Labor in Society*. New York: Free Press
- Fawcett K, Muhumuza G. 2000. Death of a wild chimpanzee community member: possible outcome of intense sexual competition. *Am. J. Primatol.* 51:243–47
- Ferguson RB. 2000. The causes and origins of “primitive warfare”: on evolved motivations for war. *Anthropol. Q.* 73:59–65
- Ferguson RB. 2001. Materialist, cultural and biological theories on why Yanomami make war. *Anthropol. Theory* 1:99–116
- Gagneux P, Boesch C, Woodruff D. 1999. Female reproductive strategies, paternity and community structure in wild West African chimpanzees. *Animal Behav.* 57:19–32
- Gagneux P, Woodruff DS, Boesch C. 1997. Furtive mating in female chimpanzees. *Nature* 387:358–59
- Gat A. 1999. The pattern of fighting in simple, small-scale, prestate societies. *J. Anthropol. Res.* 55:563–83
- Gat A. 2000a. The causes and origins or “primitive warfare”: reply to Ferguson. *Anthropol. Q.* 73:165–68
- Gat A. 2000b. The human motivational complex: evolutionary theory and the causes of hunter-gatherer fighting. Part I. Primary somatic and reproductive causes. *Anthropol. Q.* 73:20–34
- Gat A. 2000c. The human motivational complex: evolutionary theory and the causes of hunter-gatherer fighting. Part II. Proximate, subordinate, and derivative causes. *Anthropol. Q.* 73:74–89
- Ghiglieri M. 1984. *The Chimpanzees of Kibale Forest: a Field Study of Ecology and Social Structure*. New York: Columbia Univ. Press
- Ghiglieri MP. 1987. Sociobiology of the great apes and the hominid ancestor. *J. Hum. Evol.* 16:319–58
- Ghiglieri MP. 1989. Hominid sociobiology and hominid social evolution. See Heltne & Marquardt 1989, pp. 370–79
- Goodall J. 1977. Infant killing and cannibalism in free-living chimpanzees. *Folia Primatol.* 22:259–82
- Goodall J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, MA: Belknap Press
- Goodall J, Bandora A, Bergman E, Busse C, Matama H, et al. 1979. Intercommunity interactions in the chimpanzee population of the Gombe National Park. See Hamburg & McCown 1979, pp. 13–53
- Graham CE. 1981. Menstrual cycle physiology of the great apes. In *Reproductive Biology of the Great Apes*, ed. CE Graham, pp. 286–303. New York: Academic Press
- Greengrass E. 2000. The sudden decline of a community of chimpanzees at Gombe National Park. *Pan Africa News* 7:[http://jinrui.zool.kyoto-u.ac.jp/PAN/7\(1\)/7\(1\)-05.html](http://jinrui.zool.kyoto-u.ac.jp/PAN/7(1)/7(1)-05.html)
- Hamburg DA. 1991. An evolutionary perspective on human aggression. In *The Development and Integration of Behavior: Essays in Honor of Robert Hinde*, ed. P Bateson, pp.

- 419–58. Cambridge, UK: Cambridge Univ. Press
- Hamburg DA, McCown ER. 1979. *The Great Apes*. Menlo Park, CA: Benjamin/Cummings
- Heltne PG, Marquardt LA. 1989. *Understanding Chimpanzees*. Cambridge, MA: Harvard Univ. Press
- Herbinger I, Boesch C, Rothe H. 2001. Territory characteristics among three neighboring chimpanzee communities in the Tai National Park, Ivory Coast. *Int. J. Primatol.* 22:143–67
- Hill K, Hurtado MA. 1996. *Ache Life History: the Ecology and Demography of a Foraging People*. New York: Aldine de Gruyter
- Hill WCO. 1969. The nomenclature, taxonomy, and distribution of chimpanzees. In *The Chimpanzee*, ed. GH Bourne, pp. 22–49. Basel, Switz.: Karger
- Hohmann G, Gerloff U, Tautz D, Fruth B. 1999. Social bonds and genetic ties: kinship association and affiliation in a community of bonobos (*Pan paniscus*). *Behaviour* 1999:1219–35
- Huntingford F, Turner A. 1987. *Animal Conflict*. New York: Chapman and Hall
- Idani G. 1991. Cases of inter-unit group encounters in pygmy chimpanzees at Wamba, Zaire. In *Primate Today: Proceedings of the XIIIth Congress of the International Primatological Society*, ed. A Ehara, pp. 235–38. Amsterdam: Elsevier
- Inagaki H, Tsukahara T. 1993. A method for identifying chimpanzee hairs in lion feces. *Primates* 34:109–12
- Isabirye-Basuta G. 1988. Food competition among individuals in a free-ranging chimpanzee community in Kibale Forest, Uganda. *Behaviour* 105:135–47
- Kano T. 1992. *The Last Ape: Pygmy Chimpanzee Behavior and Ecology*. Stanford, CA: Stanford Univ. Press
- Kawanaka K, Nishida T. 1974. Recent advances in the study of inter-unit-group relationships and social structure of wild chimpanzees of the Mahale Mountains. In *Proceedings of the 5th Congress of the International Primatological Society*, ed. S Kondo, M Kawai, A Ehara, S Kawamura, pp. 173–85. Tokyo: Jpn. Sci. Press
- Kitopeni R, Kasagula M, Turner L. 1995. Ntologi falls?! *Pan Africa News* 2:9–11
- Kutsukake N, Matsusaka T. 2002. Incident of intense aggression by chimpanzees against an infant from another group in Mahale Mountains National Park, Tanzania. *Am. J. Primatol.* 58:175–80
- Lehmann J, Boesch C. 2003. Social influences on ranging patterns among chimpanzees (*Pan troglodytes verus*) in the Tai National Park, Côte d'Ivoire. *Beh. Ecol.* In press
- Lewontin RC. 1999. The problem with an evolutionary answer. *Nature* 400:728–29
- Lorenz K. 1966. *On Aggression*. New York: Harcourt Brace
- Manson JH, Wrangham RW. 1991. Intergroup aggression in chimpanzees and humans. *Curr. Anthropol.* 32:369–90
- Marks J. 1999. Demonic males: apes and the origins of human violence (review). *Hum. Biol.* 71:143–46
- Marks J. 2002. *What It Means to Be 98 Percent Chimpanzee: Apes, People, and Their Genes*. Berkeley: Univ. Calif. Press
- Marler P. 1976. Social organization, communication and graded signals: the chimpanzee and gorilla. In *Growing Points in Ethology*, ed. PPG Bateson, RA Hinde, pp. 239–77. Cambridge, UK: Cambridge Univ. Press
- Matsumoto-Oda A. 1999. Mahale chimpanzees: grouping patterns and cycling females. *Am. J. Primatol.* 47:197–207
- McComb K, Packer C, Pusey A. 1994. Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Animal Behav.* 47:379–87
- Mech LD, Adams LG, Meier TJ, Burch JW, Dale BW. 1998. *The Wolves of Denali*. Minneapolis: Univ. Minn. Press
- Mesquida CG, Wiener NI. 1996. Human collective aggression: a behavioral ecology perspective. *Ethol. Sociobiol.* 17:247–62
- Mitani JC, Nishida T. 1993. Contexts and social correlates of long-distance calling by male chimpanzees. *Animal Behav.* 45:735–46
- Mitani JC, Watts DP. 1999. Demographic

- influences on the hunting behavior of chimpanzees. *Am. J. Phys. Anthropol.* 109:439–54
- Mitani JC, Watts DP. 2003. Seasonality in hunting by nonhuman primates. In *Primate Seasonality: Implications for Human Evolution*, ed. DK Brockman, CP van Schaik. Cambridge, UK: Cambridge Univ. Press. In press
- Mitani JC, Watts DP, Muller MN. 2002. Recent developments in the study of wild chimpanzee behavior. *Evol. Anthropol.* 11:9–25
- Montagu A. 1976. *The Nature of Human Aggression*. New York: Oxford Univ. Press
- Muller MN. 2002. Agonistic relations among Kanyawara chimpanzees. In *Behavioural Diversity in Chimpanzees and Bonobos*, ed. C Boesch, G Hohmann, LF Marchant, pp. 112–23. Cambridge, UK: Cambridge Univ. Press
- Newton-Fisher NE. 1999. Infant killers of Budongo. *Folia Primatol.* 70:167–69
- Nishida T. 1968. The social group of wild chimpanzees in the Mahale Mountains. *Primates* 9:167–224
- Nishida T. 1979. The social structure of chimpanzees of the Mahale Mountains. See Hamburg & McCown 1979, pp. 73–121
- Nishida T. 1989. Social interactions between resident and immigrant female chimpanzees. See Heltné & Marquardt 1989, pp. 68–89
- Nishida T. 1990. A quarter century of research in the Mahale Mountains: an overview. In *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies*, ed. T Nishida, pp. 3–35. Tokyo: Univ. Tokyo Press
- Nishida T. 1996. The death of Ntologi, the unparalleled leader of M Group. *Pan Africa News* 3:[http://jinrui.zool.kyoto-u.ac.jp/PAN/3\(1\)/nt.death.html](http://jinrui.zool.kyoto-u.ac.jp/PAN/3(1)/nt.death.html)
- Nishida T, Hiraiwa-Hasegawa M, Hasegawa T, Takahata Y. 1985. Group extinction and female transfer in wild chimpanzees in the Mahale National Park, Tanzania. *Z. Tierpsychol.* 67:284–301
- Nishida T, Kawanaka K. 1985. Within-group cannibalism by adult male chimpanzees. *Primates* 26:274–85
- Nishida T, Takasaki H, Takahata Y. 1990. Demography and reproductive profiles. In *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies*, ed. T Nishida, pp. 63–97. Tokyo: Univ. Tokyo Press
- Nishida T, Uehara S, Nyundo R. 1979. Predatory behavior among wild chimpanzees of the Mahale Mountains. *Primates* 20:1–20
- Otterbein KF. 1997. The origins of war. *Crit. Rev.* 11:251–77
- Otterbein KF. 2000. A history of research on warfare in anthropology. *Am. Anthropol.* 101:794–805
- Power M. 1991. *The Egalitarians—Human and Chimpanzee: an Anthropological View of Social Organization*. Cambridge, UK: Cambridge Univ. Press
- Pusey A, Williams JM, Goodall J. 1997. The influence of dominance rank on the reproductive success of female chimpanzees. *Science* 277:828–31
- Pusey AE. 1979. Intercommunity transfer of chimpanzees in Gombe National Park. See Hamburg & McCown 1979, pp. 464–79
- Pusey AE. 1980. Inbreeding avoidance in chimpanzees. *Animal Behav.* 28:543–82
- Pusey AE. 2001. Of genes and apes: chimpanzee social organization and reproduction. See de Waal 2001, pp. 9–38
- Reynolds V. 1966. Open groups in hominid evolution. *Man* 1:441–52
- Reynolds V, Reynolds F. 1965. Chimpanzees of the Budongo forest. In *Primate Behavior: Field Studies of Monkeys and Apes*, ed. I DeVore, pp. 368–424. New York: Holt, Rinehart & Winston
- Rodseth L, Wrangham RW. 2003. Human kinship: a continuation of politics by other means? In *Kinship and Behavior in Primates*, ed. B Chapais, CM Berman. New York: Oxford Univ. Press. In press
- Seres M, Aureli F, de Waal FBM. 2001. Successful formation of a large chimpanzee group out of two preexisting subgroups. *Zoo Biol.* 20:501–15
- Stanford CB. 1998a. *Chimpanzee and Red Colobus: the Ecology of Predator and Prey*. Cambridge, MA: Harvard Univ. Press
- Stanford CB. 1998b. The social behavior of chimpanzees and bonobos: empirical

- evidence and shifting assumptions. *Curr. Anthropol.* 39:399–420
- Steenbeek R. 1999. Tenure related changes in wild Thomas's langurs. I. Between-group interactions. *Behaviour* 136:595–625
- Sterck EHM. 1995. *Females, foods and fights: a socioecological comparison of the sympatric Thomas langur and long-tailed macaques*. Unpubl. PhD thesis, Univ. Utrecht, Utrecht
- Sugiyama Y. 1989. Population dynamics of chimpanzees at Bossou, Guinea. See Heltne & Marquardt 1989, pp. 134–45
- Sussman RW. 1999. The myth of man the hunter, man the killer and the evolution of human morality (evolutionary and religious perspectives on morality). *Zygon* 34:453–72
- Suzuki A. 1971. Carnivory and cannibalism observed in forest-living chimpanzees. *J. Anthropol. Soc. Nippon* 74:30–48
- Takahata Y. 1985. Adult male chimpanzees kill and eat a newborn infant: newly observed intragroup infanticide and cannibalism in Mahale National Park, Tanzania. *Folia Primatol.* 44:161–70
- Thomas DK. 1961. The Gombe Stream Game Reserve. *Tanganyika Notes Rec.* 56:34–39
- Tierney P. 2000. *Darkness in El Dorado: How Scientists and Journalists Devastated the Amazon*. New York: Norton
- Tindale NB. 1974. *Aboriginal Tribes of Australia*. Los Angeles: Univ. Calif. Press
- Trivers RL. 1972. Parental investment and sexual selection. In *Sexual Selection and the Descent of Man 1871–1971*, ed. B Campbell, pp. 136–79. London: Heinemann
- Trudeau MB, Bergmann-Riss E, Hamburg DA. 1981. Towards an evolutionary perspective on aggressive behavior: the chimpanzee evidence. In *Biobehavioral Aspects of Aggression*, ed. DA Hamburg, MB Trudeau, pp. 27–40. New York: Alan Liss
- Tutin CEG, McGinnis PR. 1981. Chimpanzee reproduction in the wild. In *Reproductive Biology of the Great Apes*, ed. CE Graham, pp. 239–64. New York: Academic Press
- Uehara S, Nishida T, Takasaki H, Kitopeni R, Kasagula MB, et al. 1994. A lone male chimpanzee in the wild: the survivor of a disintegrated unit-group. *Primates* 35:275–81
- van der Dennen JMG. 1995. *The Origin of War: the Evolution of a Male-Coalitional Reproductive Strategy*. Groningen, The Neth.: Origin Press
- van Hooft JARAM. 1990. Intergroup competition and conflict in animals and man. In *Sociobiology and Conflict: Evolutionary Perspectives on Competition, Cooperation, Violence and Warfare*, ed. JMG van der Dennen, VSE Falger, pp. 23–54. London: Chapman and Hall
- van Lawick-Goodall J. 1968. Behaviour of free-living chimpanzees of the Gombe Stream area. *Animal Behav. Monogr.* 1:163–311
- Vigilant L, Hofreiter M, Siedel H, Boesch C. 2001. Paternity and relatedness in wild chimpanzee communities. *Proc. Natl. Acad. Sci. USA* 98:12,890–95
- Watts DP. 1989. Infanticide in mountain gorillas: new cases and a reconsideration of the evidence. *Ethology* 81:1–18
- Watts DP, Mitani JC. 2000. Infanticide and cannibalism by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Primates* 41:357–65
- Watts DP, Mitani JC. 2001. Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour* 138:299–327
- Watts DP, Mitani JC, Sherrow HM. 2002. New cases of inter-community infanticide by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Primates* 43:263–70
- White FJ. 1996. Comparative socio-ecology of *Pan paniscus*. In *Great Ape Societies*, ed. WC McGrew, LF Marchant, T Nishida, pp. 29–41. Cambridge, MA: Cambridge Univ. Press
- Williams JM, Liu H, Pusey AE. 2002a. Costs and benefits of grouping in female chimpanzees at Gombe. In *Behavioral Diversity in Pan*, ed. C Boesch, G Hohmann, L Marchant, pp. 192–203. Cambridge, UK: Cambridge Univ. Press
- Williams JM, Pusey AE, Carlis JV, Farm BP, Goodall J. 2002b. Female competition and male territorial behavior influence female

- chimpanzees' ranging patterns. *Animal Behav.* 63:347–60
- Wilson ML. 2001. *Imbalances of power: how chimpanzees respond to the threat of intergroup aggression*. Unpubl. PhD thesis, Harvard Univ., Cambridge, MA
- Wilson ML. 2003. Environmental factors and aggression in non-human primates. In *Neurobiology of Aggression: Understanding and Preventing Violence*, ed. M Mattson. Totowa, NJ: Humana Press. In press
- Wilson ML, Hauser MD, Wrangham RW. 2001. Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Animal Behav.* 61:1203–16
- Wolf K, Schulman SR. 1984. Male response to "stranger" females as a function of female reproductive value among chimpanzees. *Am. Nat.* 123:163–74
- Wood B, Collard M. 1999. The human genus. *Science* 284:65–71
- Wrangham R. 1974. Artificial feeding of chimpanzees and baboons in their natural habitat. *Animal Behav.* 22:83–93
- Wrangham RW. 1975. *The behavioural ecology of chimpanzees in Gombe National Park, Tanzania*. Unpubl. PhD Thesis, Cambridge Univ., Cambridge, UK
- Wrangham RW. 1979. Sex differences in chimpanzee dispersion. See Hamburg & McCown 1979, pp. 481–89
- Wrangham RW. 1984. Chimpanzees. In *The Encyclopedia of Mammals*, ed. DW MacDonald, pp. 422–42. New York: Andromeda Oxford Ltd.
- Wrangham RW. 1986. Ecology and social relationships in two species of chimpanzee. In *Ecological Aspects of Social Evolution: Birds and Mammals*, ed. DI Rubenstein, RW Wrangham, pp. 352–79. Princeton, NJ: Princeton Univ. Press
- Wrangham RW. 1999. The evolution of coalitional killing. *Yearb. Phys. Anthropol.* 42:1–30
- Wrangham RW. 2000. Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In *Primate Males: Causes and Consequences of Variation in Group Composition*, ed. PM Kappeler, pp. 248–58. Cambridge, UK: Cambridge Univ. Press
- Wrangham RW. 2001. Out of the *Pan*, into the fire: from ape to human. See de Waal 2001, pp. 119–43
- Wrangham RW, Chapman CA, Clark-Arcadi AP, Isabirye-Basuta G. 1996. Socio-ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In *Great Ape Societies*, ed. WC McGrew, LF Marchant, T Nishida, pp. 45–57. Cambridge, UK: Cambridge Univ. Press
- Wrangham RW, McGrew WC, de Waal FBM, Heltne PG. 1994. *Chimpanzee Cultures*. Cambridge, MA: Harvard Univ. Press
- Wrangham RW, Peterson D. 1996. *Demonic Males: Apes and the Origins of Human Violence*. Boston: Houghton Mifflin
- Wrangham RW, Pilbeam D. 2001. African apes as time machines. In *All Apes Great and Small. Volume 1: Chimpanzees, Bonobos, and Gorillas*, ed. BMF Galdikas, N Briggs, LK Sheeran, GL Shapiro, J Goodall, pp. 5–18. New York: Plenum/Kluwer
- Wrangham RW, Smuts BB. 1980. Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. *J. Reprod. Fertil., Suppl.*, 28:13–31