

RESEARCH ARTICLE

Intergroup Conflicts Among Chimpanzees in Tai National Park: Lethal Violence and the Female Perspective

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Intercommunity aggression in chimpanzees and primitive warfare in humans possess striking similarities, such as the common occurrence of large male coalitions, systematic control of territory boundaries, and lethal attacks on isolated individuals from neighboring groups. However, an important apparent contrast is the absence of recurrent peaceful interactions between neighboring groups of chimpanzees. We observed a remarkable range of behavior in intergroup encounters among three habituated communities of chimpanzees in Tai National Park, Côte d'Ivoire. Lethal attacks are documented in these study groups for the first time, as well as year-long exchanges of parous adult females and peaceful intergroup visits of mothers with infants. Demographic factors, including group size and number of adult males, are shown to affect the nature of intergroup interactions in ways not considered previously. A reconsideration of the difference in intergroup interactions between eastern and western chimpanzees is proposed including a more important consideration of the female's perspective. The inclusion of the new complexities in intergroup interactions in chimpanzees allows new parallels to be drawn with the evolution of primitive warfare in humans. *Am. J. Primatol.* 70:519–532, 2008. © 2008 Wiley-Liss, Inc.

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INTRODUCTION

Animals should enter intergroup contests when the benefit appears to outweigh the costs. This is especially true if fitness is closely correlated with access to food resources and territorial enlargement increases access to resources. Direct aggression between groups has been observed in many social animal species, whereby group members physically confront members of neighboring groups or total strangers with levels of aggression at least similar to, if not exceeding, those observed within groups [lions; Grinnell et al., 1995; Packer et al., 1988; African wild dogs; Creel & Creel, 2002; wolves; Mech & Boitani, 2003; white faced capuchins; Gros-Louis et al., 2003; red colobus monkey; Starin, 1994; black and white colobus; Harris, 2006; spider monkey; Aureli et al., 2006; chimpanzees; Boesch & Boesch-Achermann, 2000; Goodall et al., 1979; Watts et al., 2006; Wilson & Wrangham, 2003].

Chimpanzees live in social groups or “communities” occupying specific territories and containing multiple adult males and females and their offspring [Boesch & Boesch-Achermann, 2000; Goodall, 1986; Nishida, 1968]. Chimpanzee males spend their entire lives in their natal groups, and display remarkable levels of cooperation with other group males, including joint participation in intergroup encounters

[Boesch & Boesch-Achermann, 2000; Goodall, 1986; Mitani et al., 2002]. Large coalitions of males have regularly been observed to patrol the boundaries of their territory, sometimes violently fighting intrusions by neighboring chimpanzees and making deep incursions into neighboring territories [Boesch & Boesch-Achermann, 2000; Goodall, 1986; Goodall et al., 1979; Kawanaka & Nishida, 1974; Mitani & Watts, 2005; Nishida et al., 1985; Watts & Mitani, 2000; Watts et al., 2006; Wilson et al., 2004]. Transfer between groups is mostly limited to young nulliparous estrous females, who are readily accepted by the resident males and can be rapidly integrated into new groups [Boesch & Boesch-Achermann, 2000; Goodall, 1986; Nishida, 1989]. Though, under some specific circumstances, parous females have been seen to be incorporated in new communities with their

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offspring [Emery Thompson et al., 2006; Nishida et al., 1985]. In contrast, adult males and sometimes mothers with infants have been subject to extreme violence leading in some cases to the death of the attacked individuals [Goodall et al., 1979; Nishida & Kawanaka, 1985; Watts et al., 2006; Wilson et al., 2004]. The killing of adult males from neighboring groups can be particularly violent with prolonged and vicious gang attacks leading to numerous injuries including emasculation by amputation of testes and penis followed sometimes by very rapid killing [Goodall et al., 1979; Watts et al., 2006]. In cases of stranger parous females with dependant infants, many instances of infanticide, often followed by cannibalism, have been documented [Goodall et al., 1979; Suzuki, 1971; Wilson et al., 2004]. In one instance, intergroup violence has been observed to lead to the complete dissolution of whole social groups with the deaths of all the males in Gombe National Park, Tanzania [Goodall, 1986], and it was suspected but not observed in another case in Mahale Mountains National Park, Tanzania [Nishida et al., 1985].

Lethal intergroup aggression in chimpanzees has been proposed to present similarities with primitive warfare in human populations, based mainly on observations that both species regularly use large male coalitions, systematic patrolling of territory boundaries, and violent killing of adults from neighboring groups that can lead to the annihilation of a whole group [Beltzig, 1988; Boehm, 1992; Boesch & Boesch-Achermann, 2000; van der Dennen, 1995; Gat, 1999, 2000; Goodall, 1986; Manson & Wrangham, 1991; Wrangham & Peterson, 1996]. This view has been critically received by others who highlight dissimilarities between the two species, mainly that sexual, marital, and social friendly contacts persist over extended periods of time between opponent groups in humans [Alexander, 1989; Foley, 1995; Kelly, 2005; Knauff, 1991; Otterbein, 2004].

However, the sometimes dramatic nature of intergroup aggression in chimpanzees has led to underappreciation of the fact that such lethal violence represents only the minority of the encounters between communities in wild chimpanzees [Goodall, 1986; Kawanaka & Nishida, 1974; Watts et al., 2006]. Most notably, after more than 18 years of observation of the chimpanzees of the Taï National Park, Côte d'Ivoire, initially of one community and then of three neighboring ones, no lethal violence was observed despite regular aggressive interactions between communities and the systematic employment of macro-coalitions by the males [Boesch & Boesch-Achermann, 2000; Herbinger et al., 2001]. Especially striking is the fact that observers had not seen infants of stranger mothers to be killed nor to be subject to intense aggressions by the attacking males and the injuries suffered by the females were minor compared to the reports

provided from other chimpanzee populations [Boesch & Boesch-Achermann, 2000]. Therefore, a key to understand the evolution of intergroup violence is to ask why we observe such differences between chimpanzee populations in the level of intergroup aggression.

Two different perspectives concerning chimpanzee lethal violence in intercommunity interactions have appeared. First, some have suggested that high levels of violence are abnormalities resulting from increased level of stress owing to either artificial food provisioning, as was provided to the Gombe and Mahale chimpanzees, or resulting from increased human encroachment on their ranges including the presence of human observers [Clark, 2002; Hart & Sussman, 2005; Power, 1991]. Power [1991] proposed that reports of possible peaceful encounters between groups from early studies on chimpanzees were more representative of the species, such as those of the Budongo forest [Reynolds, 1965] and the observations from Taï chimpanzees. However, evidence contradicting such an explanation includes new lethal incidents in additional non-provisioned populations like the chimpanzees of the Kibale National Park [Watts et al., 2006; Wilson & Wrangham, 2003], and an apparent intergroup killing in a non-habituated chimpanzee population in Loango National Park, Gabon [Boesch et al., 2007].

A second, more widely held perspective considers intergroup violence to be a typical aspect of chimpanzee sociality. However, no consensus has emerged about the evolutionary basis of such intergroup violence in wild chimpanzees. The killings of infants of stranger females suggest that males may use such violence to gain access to more females, as in infanticide by males in species such as lions, gorillas, and langurs [Hrdy, 1977; Packer et al., 1988, 1991; Robbins, 1995; Watts, 1996]. In chimpanzees, however, there is as yet no convincing evidence that females are more likely to immigrate into the group of the infanticidal males. On the other hand, it has been proposed that the main function of such violence is to physically eliminate male competitors [van der Dennen, 1995; Knauff, 1991; Manson & Wrangham, 1991; Wrangham, 1999]. If this would seem to explain the dramatic cases of adult males killed by coalitions of neighboring attackers that have been observed first in Gombe chimpanzees and then in other East African populations, we still need to explain what males would gain from this. A complementary explanation posits that, as fitness would increase with territory size, different level of violence might be expected depending on feeding competition, as land gain results in access to more resources [Williams et al., 2004].

Until now, intergroup violence in chimpanzees has been largely considered from the perspective of the gains or losses to the males [but see Williams

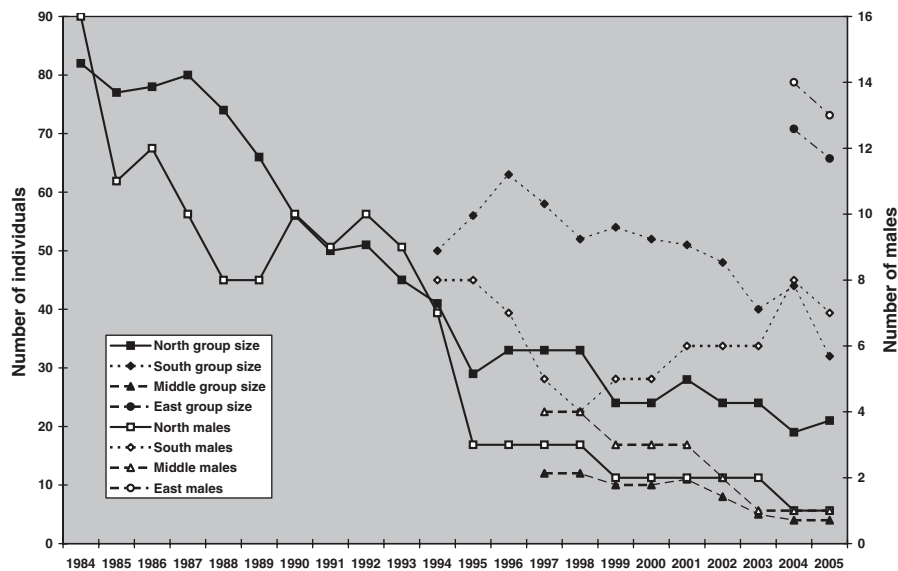


Fig. 1. Community size and number of adult and adolescent males in four chimpanzee communities of the Tai forest between 1984 to 2005.

et al., 2004, for considering more the female perspective]. Females in chimpanzees have been shown under some demographic conditions to implement much of their preference when it comes to sexual partners [Stumpf & Boesch, 2005, 2006]. This may go as far as females producing infants with males who are not members of their own group; ~10% of the offspring in Tai result from extra-group paternities [Boesch et al., 2006; Vigilant et al., 2001], and a similar proportion of extra-group paternity was inferred from Gombe and Bossou [Constable et al., 2001; Sugiyama et al., 1993]. Also, most females transfer between communities before maturity and seem to select communities with large numbers of adult males [Boesch & Boesch-Achermann, 2000; Nishida et al., 1985]. Therefore, females may have more reasons to interact with neighboring community than has hitherto been realized.

Here, we describe 485 intergroup encounters involving four communities of chimpanzees of known composition from 1982 to 2005 in the Tai National Park, Côte d'Ivoire. We present new evidence of lethal violence in this population, but confirm that fatal violence is less common than documented for other chimpanzee populations. We discuss these findings in relation to the importance of mating strategies in intergroup relationships and stress the importance of considering female strategies for a complete perspective on intergroup conflicts.

METHODS

We observed four neighboring chimpanzee communities in the Tai National Park, Côte d'Ivoire [for more details, see Boesch & Boesch-Achermann, 2000]. Observations started with the North Group

in 1979, with habituation to human observers achieved by 1982, and constant observation since involving daily all-day follows (see Fig. 1 for the demography data of the four communities). During the first 6 months of 2003, civil unrest interrupted research. The North Group's territory is about 6 km from the western park boundaries and is surrounded by chimpanzee groups on all sides. The Middle Group was fully habituated in 1995 and was under daily observation until summer 2004, when its size had decreased to five individuals, and we switched to demographic monitoring for 1 week every 3 months. The Middle Group shares a territory limit in the north with the North Group and in the south with the South Group [see map in Herbing et al., 2001]. This South Group was fully habituated in 1993 and has since been under constant observation by field assistants and students (see Fig. 1). Habituation of the East Group started in 2000, and by February 2005, 11 adult males had been identified and at least two more males were suspected to be present. Twelve females have been identified but the total number of females is still unknown (see Fig. 1, numbers for the East Group are provisional, because community size was estimated by assuming that the age structure and sex ratio were the same as in the other three communities). The intergroup interactions reported here come from 25, 12, and 9 years of observations on the North, South, and Middle Groups, respectively.

Individual targets were selected every morning and followed as long as possible [average follow time: 9.7 hr; Lehmann & Boesch, 2004]. Detailed data collection was done on standardized check sheets by well-trained field assistants and students. Basic data collection included systematic recording of party composition, party size, presence of estrous females,

and all signs of neighboring communities. Daily protocols were interrupted when the presence of neighbors was confirmed so that the interactions between the two communities could be recorded in detail.

Intercommunity encounters take many forms: target individuals can discover neighbors by surprise, be surprised by them, or be involved in intentional searches for them during patrols of territory boundaries. We considered only situations in which neighboring chimpanzees were seen or heard as intercommunity encounters. Chimpanzees may sometimes behave as if they have noticed neighboring chimpanzees by suddenly becoming excited and reassuring one another, then silently moving off as if to surprise some chimpanzees. However, they often direct such a behavior to members of their own communities. Because visibility is low at Tai, patrolling rarely results in visual encounters with neighbor chimpanzees, and auditory detection is the principle means of detecting neighbors. Daily follows involved only a minority of the community members and therefore we missed some intercommunity encounters. If non-target individuals encountered neighboring group members, we might become aware of the encounter only after initial contact and thus have missed part of the interaction. Since smaller communities tend to be more cohesive [Boesch & Boesch-Achermann, 2000], this bias is more important for larger communities. However, as auditory detection is the most common way of spotting neighbors and auditory contact between individuals includes most group members [Boesch, 1991], we suspected that we were aware of most of them. We did not include transfers of adolescent females as intergroup encounter.

Human presence influences interactions with non-habituated chimpanzees. Typically, naive chimpanzees immediately run away when seeing humans independently of the intensity of the intergroup conflict, although human presence only marginally affects the frequency of encounters.

The identity of the community encountered by the habituated communities was relatively easy to confirm as their position in the forest was precisely known. For non-habituated neighboring communities, we assumed that each chimpanzee community had only four neighboring communities based on what we saw from the South and Middle groups that had clearly only one neighbor in the north, south, or east.

Because not all community members can be observed at all times, ascertaining why apparently healthy individuals sometimes disappear is a challenge, and some authors have suggested that intergroup violence is the most likely explanation for the sudden disappearance of healthy full-grown adult individuals [Nishida et al., 1985; Wrangham & Peterson, 1996]. For example, the disappearance of

seven males of K Group in the Mahale chimpanzees during an 8-year period without any direct observation or corpse remains found was suggested to be owing to intergroup violence [Nishida et al., 1985]. However, sudden disappearances of healthy individuals could have many causes besides chimpanzee violence, such as predation by lions or leopards [Boesch, 1991; Tsukahara, 1993], human poaching [Boesch, personal observation; Reynolds, 2005], and disease [Boesch & Boesch-Achermann, 2000; Leendertz et al., 2004, 2006]. Although predation by big cats can sometimes be excluded owing to their rarity or known absence, such as in Gombe and Kibale National Parks, and poaching by humans can sometimes be excluded, such as possibly in Mahale and Gombe National Parks, disease affects all chimpanzee populations [Boesch & Boesch-Achermann, 2000; Goodall, 1986; Nishida et al., 1985]. Chimpanzees rarely show disease symptoms before disappearing [Boesch & Boesch-Achermann, 2000; Leendertz et al., 2006], and some diseases, such as anthrax or Ebola, can lead to startlingly rapid deaths of adult chimpanzees [Boesch & Boesch-Achermann, 2000; Formenty et al., 1999; Leendertz et al., 2004]. For example, the alpha male of the Middle Group died from anthrax within 3 hr after showing the first symptoms of weakness [Leendertz et al., 2004]. Therefore, the assumption that disappearance of a healthy adult individual is a sign of violent death through intergroup hostility is tenuous and will lead to an over-estimation of the frequency of intergroup killings. However, contrary to Hart and Sussman [2005], we think that the fieldworkers' judgments about the causes of death should be trusted when they find fresh chimpanzee corpses.

Mortality in Tai chimpanzees has been high in recent years, but we have been able to infer the causes of most deaths. During the last 15 years, 66 individuals disappeared or died from the North Group, of which 16, including eight adults, disappeared for unknown reason. Thirty probably died from disease, 11 infants died of starvation after their mothers died, five died owing to predation by leopards, one died in a tree fall, one died from poaching, one died by infanticide, and one died of old age. In the last 7 years in the South Group, 43 individuals died. Eleven individuals, including three adults disappeared for unknown reasons. Five were killed by leopards and eight by poachers, whereas 13 from disease, five starved after the deaths of their mothers, and one died from injuries.

RESULTS

Table I summarizes all 485 intergroup encounters recorded from 1982 to 2005. After the habituation of both the South and Middle groups, we could collect data on encounters between neighboring groups of known demographic compositions. Of all

TABLE I. All Auditory and Visual Intergroup Encounters Observed Within Three Chimpanzee Communities in the Tai Forest (N = 485)

Year	North Group		Middle Group			South Group		
	Total	MG only	Total	NG only	SG only	Total	MG only	EG only
1982–1996	137							
1997–2005	157	36	86	21	16	105	29	44

When encounters involved two habituated groups we present the data for known neighbors. As different observers were following different groups at different times, the numbers of observed encounters do not correspond between the different groups. MG, Middle group; NG, North Group; SG, South Group; EG, East Group.

TABLE II. Summary of Intergroup Encounters Observed in Three Chimpanzee Communities in the Tai Forest

Community	Observation time	Contact		Prisoner	Kill	Support	Sexual interaction (♀ visit)
		Auditory	Visual				
North Group	12-1982 to 4-2005	224	70	9	0	20	13 (1)
Middle Group	9-1999 to 2-2004	64	22	5	0	2	14 (9)
South Group	11-1996 to 12-2005	64	41	4	2	11	18 (16)

encounters, 42% (146 out of 348) occurred between two of the study groups. Human presence did not affect these encounters, so detailed observation was possible. Three main types of encounters were observed. The most frequent type was encounters that were auditory only; the second type was aggressive encounters and the third was affiliative encounters that involved parous adult females.

Table II presents observations of visual encounters classified according to whether they were mainly violent, resulted in death, or included sexual interactions. In what follows, we present an example for each type of encounter.

Lethal Violence Between Communities

For the first 23 years of the Tai chimpanzee project, no lethal attacks were witnessed. However, in the past 3 years, two cases of fatal intercommunity attacks have been observed, both perpetrated by South Group males.

Case 1: 8th September 2002: Infanticide (observers: Nicaise Oulai and Camille Bolé). A large party that included five adult males and nine adult females of the South Group was moving north into the western part of the territory of the Middle Group, when they heard neighbors from the west drum (16:06). They advanced silently, listening carefully, and looking in all directions. After 6 min, two south males drummed and pant hooted, and the neighbors answered as the South Group continued to advance, drumming two more times. At 16:27, they surprised a party of the neighbors in a fruiting tree. The neighbors ran west, pursued by some of the South Group males. A young adult male, Sagu,

realized that an infant male has been left in the tree and is whimpering. He climbed the tree, seized the infant, and descended, then hit the infant against the ground. Responding to the screams of the infant, the neighbors made loud calls, but only one adult female, who was immediately chased away by some South Group chimpanzees, came into view. Sagu climbed the tree with the infant and hit it against the branches, while some South Group members looked on. At 16:39, Sagu started to bite the infant and the sound of breaking bones could be heard, then he twisted one foot of the infant, who screamed loudly. In response, the two groups exchanged calls. At 16:50, Sagu let the infant fall to the ground and seven adults of the South Group looked carefully at him for 12 min. At 17:12, Gogol bit the infant in the throat, probably killing him, then broke the infant’s fingers, feet, and some articulations and extracted some foot bones without eating anything. After 11 min, Gogol left the corpse on the ground with others, but Duna came back 2 min later and dragged the infant on the ground to a *Sacoglottis* tree where others were eating fruits. The neighbors called again in the west. At 17:33, the last chimpanzees of the South Group moved toward the south and returned to their territory with some drumming, leaving the dead infant on the ground.

This attack took place in an area where the Middle Group and the West Group overlap, and since no Middle Group infants disappeared at that time, we assume that the killed infant belonged to a female of an unhabituated group in the west. The killers showed no interest in cannibalizing their victim.

Case 2: 1st March 2005: Adult male killed (observer: Emmanuelle Normand). A party of the

South Group, including the four adult males of the community, two adolescent males, and four adult females, heard the east neighbors and all ran silently toward them. When the observer caught up with them, all the South Group individuals, including three females, Sumatra, Zora, and Wapi, had gathered around a young adult male chimpanzee of the East Group. The observer could see the victim clearly in the mass of the aggressors, and saw that all, except Taboo, bit and hit him violently. At one point, Sumatra is ejected from the group, and hit by Kaos who jumped on her back. After this, they both rejoined the attacker mass. All individuals present were very excited and screamed. Twenty-two minutes after the beginning of the attack, East Group chimpanzees farther eastward were heard to drum. All the South Group members rushed to attack them, leaving the victim alone but he had by now much difficulty to move and just succeeded to sit. Two minutes later, Zora came back to sit near the stranger. He had a lot of fresh cuts around the mouth and ears but his throat was still intact. Five minutes later, three of the four adult males from the South Group, including Sagu and Gogol, came back to the stranger and attacked him viciously for 1 min. The observer had the impression that this was the moment when the victim was badly injured at the throat. The victim is now unable to move. The south party started to move away, but twice Gogol came back and bit his arm and the noise of the breaking bones could be heard. Each time Sumatra followed him to chase him off the victim. After 39 min, the victim seemed dead. They left the inanimate body 46 min after the beginning of the attack.

The victim was dead, probably owing to a wide 10 cm gash in his throat and upper chest. The testis and penis had been removed. It was impossible to say when the emasculation happened. Later that day, observers saw that Sagu had three fresh cuts on his head, neck, and one foot, and that Sumatra and Zora each had one fresh cut as well. The attack took place in the overlapping zone between the South and East Groups. The victim could have been a young adult male of the East Group called Néron who sometimes foraged on his own in the periphery of the east territory and who disappeared exactly at that time. Owing to his numerous facial injuries and the rapid post-mortem changes, we could not confirm his identity.

Aggressive Non-Lethal Encounters Between Groups

Although the majority of encounters between groups involved only auditory contact, we followed 118 visual encounters (25% of all encounters) of which 47 included physical contacts (10% of all encounters). Here, we describe two of them that occurred between habituated groups to illustrate some specific aspects of violent encounters.

Case 3: Multiple encounters between Middle Group and North Group (observers: Catherine Crockford for the Middle Group and Honora Kapazhi for the North Group). On 2nd May 2000, the day after the Middle Group males took Goma, a female from the North Group, prisoner (see below), the entire Middle Group of three adult males and three adult females slowly and silently returned to the same area where they surprised Goma. As they came close they heard drumming in the north possibly from one of the two remaining males of the North Group. The Middle Group listened silently, continued to advance for 8 min to stop, and listened for 10 min. Remaining silent they headed south toward the Middle Group territory.

Three days later, on 5th May 2000, all three Middle Group males began a patrol of the North Group territory, starting at the same *Treculia* tree where they found Goma. They patrolled deep into the North Group territory, right into their core area, drumming once. They remained in the core area for 2 hr, listening continuously and intently. They drummed once again as they left the core area. No reaction was discernable from the North Group at any time. Six hours after starting the patrol, they returned to the border area of the two territories, to the same *Treculia* tree as in the morning.

On the 7th of May, Urs and Bob from the Middle Group returned to the same *Treculia* tree where they captured Goma. They approached the tree slowly and silently, and stopped to sniff some leaves. Both appeared unaware that Marius and Nino, the two adult males of the North Group, were silently sitting some 25 m north watching them intently. After 2 min, Urs after looking around made an initial movement to retreat, at which immediately Marius and Nino charged at them. Urs and Bob fled southward back into their territory. Marius and Nino chased the two males while giving loud barks for about 2 min. A minute after losing the Middle Group, Marius drummed. Five minutes later, Urs and Bob drummed after retreating several hundred meters to the south. Both groups of males continued drumming for some time. Next, Marius and Nino came back to the same area and rested.

Two hours and 50 min later, Léo, the alpha male of the Middle Group, moved alone northward, whimpering and pant hooting, seemingly looking for Urs and Bob. He arrived in the same area as the morning encounter and ate two *Sacoglottis* fruits. Suddenly he stood bipedally with piloerection, while looking around intently. After 2 min, the two males of the North Group, Marius and Nino, appeared from the undergrowth in a full charge toward Léo. Léo screamed loudly and fled south back into his territory. Marius and Nino chased him for 40 ms then stopped to bark and drum. Léo continued to flee southward, screaming continuously for 4 min, and Marius and Nino continued drumming for 1 hr.

The behavior of the male, Léo, demonstrates how risky foraging in the forest can be for a lone individual, particularly when moving toward the periphery of the community, and this illustrates how the male in case 2 could get caught in such an unequal and deadly situation.

Female Prisoners Taken by Neighboring Males

In Tai chimpanzees, the search for appropriate mating partners seems to play a key role in intergroup contacts. As mentioned in Boesch and Boesch-Achermann [2000], females can be made prisoners by males of a neighboring group, kept temporarily and unwillingly separated, and actively prevented from moving away. Here, we describe such a situation with minimal human influence as it happened between the North and Middle Groups.

Case 4: 30th April 2000: North Group female taken prisoner for 22 hr by Middle Group males (observer: Catherine Crockford). At 16:21, the three adult males of the Middle Group, Urs, Bob, and Léo, moved north into the North Group range and suddenly rushed forward and surprised two adult females of the North Group, Goma and Fossey, with their two infants and two juveniles. Goma, whose running abilities have been impaired for months by a handicap in both hips, bent over to cover her 4-year old daughter, Gisèle, whereas the males displayed around her, hitting and jumping on her for 1 min. Fossey and one juvenile disappeared immediately, whereas Fossey's 6-year old daughter remained sitting and observing from a branch in a tree. The aggressive actions of the males toward Goma stopped rapidly. Then, Urs made his first friendly contact to Goma with an open-mouth kiss, followed by Bob 2 min later. All three males performed genital inspection on Goma who had no sexual swelling and was lactating. Four minutes after the initial encounter, Gisèle left her mother to greet Léo, the alpha male of the Middle Group. Gisèle tried repeatedly to greet the males, but Goma whimpering tried to have her come back to her. Urs tried without success to mate with Goma. After 15 min, Fossey's daughter disappeared as well, leaving Goma and Gisèle alone with the males. When Goma tried to climb a tree, Urs hit her many times but then open-mouth kissed her and groomed her. Léo successfully mated with her after 45 min. The males fed a little bit on *Treculia* fruits, but Goma just looked at them. At 19:30, they all made their nests in nearby trees, the males making their nest near the one of Goma.

The next morning, the males tried to lead Goma south into their territory but it took Goma 2 hr to leave her nest and come to the ground. Urs displayed twice at her, and for the very first time Léo hit Gisèle. Afterward many reassurances between Goma and Léo were observed, as males tried to lead Goma east into their territory. Léo mated twice with Goma,

whereas Urs tried two more times without success. Three hours after leaving the nest, Goma tried to move back westward, in the direction of the North Group territory. Léo mated with her. Urs and Léo groomed Goma. Gisèle and Goma received some fruit remains from Bob and Léo and ate for the first time since their capture. At 12:22, for the first time a drumming from the North Group was heard far in the west. The males tried to lead Goma to the east, whereas Goma tried to head in the direction of the drumming. As a result, little progress was made in any direction. Around 14:30, Goma started to move west for short distances, but the males came back to her twice. The third time, at 14:45, the males reacted too slowly and Goma escaped toward the west and hid in a dense tree fall, the males not trying hard to find her. Eighteen minutes later, Marius, the alpha male of the North Group, drummed close to the Middle Group males. The three Middle Group males retreated to the south, back in their territory, eventually drumming and pant hooting (see case 3 for the subsequent interactions).

As shown in Table II, such kidnapping of females has been seen regularly (North Group: $N = 9$, Middle Group: $N = 5$, South Group: $N = 4$) and the duration they are kept prisoners is a direct function of the rapidity of the support provided by their group males. In 11 of these 13 cases, sexual activities were observed between the female and her male aggressors. In the majority of the cases, noisy support from the victim group came within minutes, and kidnapers always first faced them, thus granting victims the time to escape. As observed previously [Boesch & Boesch-Achermann, 2000], in no, but one, instances were the infants of these females directly hurt by the members of the other community.

Females' Active Involvement in Aggressive Intergroup Interactions

Tai females have been recorded as being active participants of some of the intergroup encounters led by males [Boesch & Boesch-Achermann, 2000]. Our new observations confirm this; see cases 1, 2, and 4 above. In addition, we have seen that females on their own could be quite aggressive toward strangers (case 5) and might take risks in doing so (cases 6 and 7).

Case 5: 3rd August 2005: Females of South Group take a female prisoner from West Group (observer: Nicaise Oulai). At 8:56, a large party of 14 adults of the South Group heard drumming in the west; they screamed, and then moved silently in that direction. At 9:00, whereas the adult males of the group were ahead, chasing the West Group, five adult females of the South Group surprised a young West Group female in a tree. Some females immediately climbed the tree and pulled her to the ground, where all females present attacked her and Sumatra

blocked her. Young adolescent males Woodstock, Utan, and Taboo tried to protect her, but the adult females continued the attack. After 2 min, Woodstock hit Sumatra who released the stranger to respond to this attack. The stranger then ran. South Group females pursued her, but she escaped.

In another instance, seven resident females of the South Group were aggressive against a female infant pair while three males of the South Group tried to stop them from attacking her. Whereas the stranger female was injured and bleeding from cuts on the face and body, some females of the South Group were injured by South Group males during this confrontation. The support from some males of stranger female community interrupted this attack after 8 min.

Case 6: 17th August 2002: A female of Middle Group chasing females from the West Group (observer: Louis-Bernard Bally). At 9:21, Jessica, alone, with her two offspring was eating some fruits in a tree of *Scotellia coriacea*, when she heard whimpers from a baby chimpanzee coming from the west. Jessica made a silent open grin face, took her 9-month old daughter on her back and climbed down followed by her 4-year old juvenile daughter. Her baby moved to Jessica's belly and the juvenile daughter climbed on her mother's back. After listening for 6 min, Jessica started to move very carefully toward the west. At 9:37, she arrived under a *Sacoglottis gabonensis* tree where chimpanzees had been eating very recently. She smelled the fresh food-wedges that were on the ground and after 4 min she started to eat. At 9:53, she climbed with her daughters a tree, faced west, and stayed apparently listening for 2 hr and 13 min. She then moved slowly and very silently toward the west. At 13:18, she heard a little noise of a chimpanzee close by and both her daughters climbed onto her, the baby on the belly and the juvenile on her back. She moved very slowly toward the sound and at 13:24 standing she looked up in a *Upaca* tree where two stranger females were eating some fruits, one with a little baby and the other with a juvenile female. At 13:25, Jessica barked loudly and displayed toward the tree. The stranger females in the tree immediately screamed and rushed down disappearing toward the west. Jessica barked and screamed for 2 min while drumming once. The stranger females remained silent. Jessica continued to bark five times during the following 20 min and advanced for 60 m. At 13:53, Jessica retreated.

Jessica's behavior was remarkable for two reasons. First, she is part of the Middle Group that was already very small (one adult male and two adult females) and she could therefore not receive much support from her group. Second, being alone, it seems as if she was counting on the surprise effect of her appearance in such a low-visibility environment.

Case 7: 24th January 1991: Goma, an adult female of the North Group, rescuing an adult male

from a West Group's gang attack (observer: Christophe Boesch). After arriving in the southernmost ridge region of their territory, the chimpanzees of the North Group spread out to feed on *Landolphia* fruits. Macho and Goma were together. She climbed a tree with her 5-year old daughter to eat some fruits, whereas Macho continued south to climb another tree to feed. At 12:50 loud calls came suddenly from where Macho was eating. Without hesitation, Goma with her daughter on her belly rushed down and ran toward the screams with aggressive barks. The attackers took some time to check who was attacking them and Macho used that moment to immediately escape and ran to Goma and both individuals fled toward the observer. Two of the attackers followed them but ran away after seeing the observer. At 12:52, three adult males arrived silently in support of Macho, and with him they immediately chased the neighbors away over a distance of 300 m. During this short attack, Macho received 18 cuts over all his body, including one that missed his right eye by 1 cm. The quick reaction of Goma apparently prevented him from receiving more serious injuries.

Voluntary Visits of Parous Females to Neighboring Groups

Although voluntary visits by young nulliparous females before transfer into new groups have been reported in all study chimpanzee populations, voluntary visits to neighboring males by multiparous adult females with or without infants have been rarely documented. The one exception was the secondary transfers of mothers after the dramatic decrease in the number of males within K Group in Mahale Mountains, Tanzania [Nishida et al., 1985, but see Emery Thompson et al., 2006, for other potential cases in Budongo chimpanzees]. Voluntary visits by multiparous females to neighboring groups were observed several times in our three study groups. We detail one situation that involved only individuals from habituated groups.

Case 8: 6th June 2002: Nadesh, a Middle Group multiparous female makes a repeated visit to the South Group (observers: Nicaise Oulai and Camille Bolé). By June 2002, the Middle Group had lost two adult males, leaving only one adult male and no adolescent males in the group. Nadesh, an adult female estimated to be 40 years old, just lost her second known infant to anthrax 4 months earlier. At 17:19 Nadesh, with a maximally swollen sexual swelling, joined a party of the South Group including four adult males and five adult females in a fig tree. At her arrival, she was greeted by some calls. A south female, Olivia, tried to attack her, but she was immediately chased away by Sagu, the alpha male of the South Group. Three adult males, including Sagu, and one adolescent male were observed to mate with

Nadesh. Olivia attacked Nadesh once more, but Sagu and another male, Zyon, chased Olivia and another female away. Later, two males and two females groomed Nadesh. Nadesh spent the night with the South Group, making her nest in the same tree as some males.

The next day, Nadesh remained with the South Group males and was seen to interact quite freely with them. She copulated four times and was seen to be groomed by three adult males and three adult females. She had to sustain six attacks by three females but was each time vigorously protected by the males. She made her nest in the same tree as some of the males. The 8th of June started as the day before, she copulated twice with young males and was protected by the males in the three attacks by females. She left the group silently at 14:26 and entered her Middle Group range the same day. Eight days later, on the 16th of June, she appeared again in the South Group and mated four times with the males but left early the next morning.

She returned in September 2002 to stay 44 hr with the South Group males and mated with two of them. Nadesh gave birth to a new baby in July 2003, but unfortunately the baby died in December 2004 before samples for determining its paternity could be collected.

Thereafter, Nadesh reappeared for the first time in the South Group on 2nd May 2005. She was observed for hours every day in the South Group until the 10th of July. During these 9 days, she was seen to copulate 15 times with South Group males. However, the aggression of the resident females against her remained persistent, whereas the support of the south males was less systematic than before, so that she had to escape from the females repeatedly during this time. She came back for a 1-day visit on the 9th of September 2005 where she was seen to mate three times with adult males. In October 2005, Nadesh was not seen in the Middle Group and she might have been visiting another group. However, she remained a member of the Middle Group, which had now decreased to include only one adult male, Bob, and another adult female, Jessica. In October 2006, Nadesh was seen with a new baby that was born sometime in January 2006. If we count an 8-month pregnancy period, she would have conceived in May 2005, which coincides with her visit to the South Group.

Similar voluntary visits have also been observed with non-habituated multiparous females with infants visiting members of each of the study groups (North: $N = 1$, Middle: $N = 2$, South: $N = 1$), but owing to the presence of the human observers they were much shorter and observations were far less detailed. Intriguingly, in three of those instances the females with infants were anestrus, suggesting that they might have visited previously. When a female with an infant visited the study groups, no threats or

violence from resident group members were directed at the infants and the infants even sought direct contact with adult members of the new group (see also case 4).

Inter-Population Comparison of Intergroup Conflicts

Population differences in the occurrence of lethal violence in intergroup interactions in chimpanzees are revealed by a comparison of data on intergroup encounter and death rates for nine chimpanzee communities in five populations (Table III). On average, for Tai, Mahale, and Ngogo chimpanzees, encounters with neighboring groups take place between 1 and 1.5 times per month and visual contact occurs in one out of three to four contacts. Encounter rates are similar for Tai and Ngogo, despite different patrolling rates [Ngogo: 95 in 48 months; Watts et al., 2006; Tai: 38 in 45 months].

Most striking is the variation in the rate of intergroup killings (Table III), with Ngogo chimpanzees having the highest rate at two deaths per year of observation, whereas at Tai none have been observed in two of the three groups despite decades of observations. This difference cannot be attributed to study duration, since some groups with shorter observation times have high death rates. Nor could it be attributed to the number of neighboring groups: if the low death rate at Bossou could be explained by the absence of neighboring groups, and the intermediate intergroup death rates observed in Gombe and Mahale communities may be due to them bordering the Tanganyika Lakes and having few neighbors, the lowest and highest rates are found in the three study communities at Tai and at Ngogo with neighbors in all directions. Finally, the number of males in the community does not seem to explain the differences in intergroup death rates (all populations: $r_s = 0.496$, $N = 9$, $P = 0.176$).

The intergroup death rate will likely be influenced by the number of individuals present during encounters. This includes support by other group members once encounters have started [Boesch & Boesch-Achermann, 2000]. Support can change the balance of power between opponents and influence encounter outcomes. Chimpanzee communities seem to vary in the extent to which supporting individuals join intergroup encounters (Table IV). Supports by additional community members at the scene after an individual has directly encountered neighbors has been observed in 28% of all visual contacts in Tai chimpanzees and is almost systematic in cases where one or two females were made prisoners (83%, $N = 15$ of the 18 cases). In 13 cases, support arrived before an individual had been isolated by the attackers and thereby probably prevented the attackers from concentrating on one individual and inflicting severe injuries.

TABLE III. Comparisons of Intergroup Encounter Rates and Intergroup Death Rates in Different Chimpanzee Populations

Populations	Number of contacts		Observation duration, month (year)	Encounter rate, auditory (visual)	Number of deaths (Ad+Inf)	Intergroup death rate	Number of adult males
	Auditory	Visual					
Tai NG	288	66	221 (22)	1.30 (0.30)	0+0	0.00	6.6
Tai MG	85	18	54 (6)	1.57 (0.33)	0+0	0.00	2.55
Tai SG	95	34	87 (9)	0.96 (0.39)	1+1	0.27	6.25
Budongo ^a			(10)		0+6 ^b	0.60	16.0
Mahale M ^c	37	8	12 ^d (20)	3.08 (0.66)	1+2	0.15	16.1
Mahale K			(17)		(7) ^e +1	0.06 (0.47)	4.6
Gombe, Kasakela ^{f,g}			144 (12)		6+4	0.83	10.5
Kanyawara ^h			(14)		3+0	0.21	12.7
Ngogo ⁱ	68	20	48 (7)	1.41 (0.42)	4+7	1.83	24.0
Loango			20		1+1	1.20	

Encounter rate = #contact/# month of observation; Intergroup death rate = (# death/(# month of observations/12)). NG, North Group; MG, Middle Group; SG, South Group.

^aReynolds [2005].

^bIn Budongo chimpanzees, seven bodies of unknown infants suspected to be killed as a result of intergroup encounters have been seen by observers; however, one was suggested to belong to one female of the study community [Reynolds, 2005].

^cNishida et al. [1985] and Nishida and Hiraiwa-Hasegawa 1985 for the period 1965 to 1983 and Kutsukake and Matsusaka 2002 for the period 2000.

^dEncounter rate were provided only for the year 1974, thus the observation time for them is 12 months [Nishida, 1979].

^eIn Mahale chimpanzees, the disappearance of seven males of the K Group was described in detail and attributed to violent interactions with the larger M Group [Nishida et al., 1985]. However, none of those interactions were witnessed nor were any of the bodies found. Keeping in line with our criteria, they would not qualify as intergroup violence victims and we consider them as such only in brackets. On another occasion, one female from the K Group was seen to be attacked badly twice by the M Group and her life spared twice thanks to the direct intervention of the researchers [Nishida and Hiraiwa-Hasegawa, 1985].

^fGoodall [1986] (observational period: 1971–1982).

^gWilson et al. [2004] (observational period: 1993–2002).

^hWrangham et al. [2006].

ⁱWatts et al. [2004, 2006, personal communication] and Sylvia Amsler [personal communication] shared the observation of four intergroup encounters that occurred during 2005 and 2006. Death rate accordingly includes 2 more years of observations.

This seems to be in dramatic contrast to what has been reported from other chimpanzee populations (see Table IV) where no support has been described in Gombe in the 25 cases where individuals were trapped by neighboring attackers [Goodall, 1986; Wilson et al., 2004]. In the 24 cases of physical intergroup contacts reported in Ngogo chimpanzees, there were only three instances where supporting chimpanzees were noted to approach the site of the attacks. Although the supporters did not come into view and join those engaged in the physical contact with neighbors, observers had the impression that the attackers were nonetheless influenced by their approach [Amsler, personal communication; Watts et al., 2002; Watts et al., 2006]. No mention of support could be found in the reports about Mahale encounters [Nishida et al., 1985]. It remains difficult to interpret these data as support may have gone unreported in some instances. In addition, it is known that Tai chimpanzees are more gregarious than other chimpanzee populations, and it might be that support is not always available when needed in other populations. On the other side, if support, like in Tai, would have directly influenced the outcome of the interactions, we would expect them to be reported.

Two additional striking differences emerge from the comparative data collated in Table IV, and these involve the treatment of adult females during intergroup contact. In Tai, 17 females have been isolated from members of their own communities by males from neighboring communities, but not subjected to severe or life-threatening aggression. Aggression was mostly limited to slapping and biting of sexual swellings and its intensity was similar to that observed during within-community aggression. Infants, when present, were not subject to violence. In comparison, Gombe females were subject to severe aggression in 75% of encounters, and such violence was suspected to lead to several deaths [Goodall, 1986]. A review of the data including more recent observations suggested that aggression against stranger females occurred in 45% of encounters at Gombe and was most frequently directed at non-swollen females [Williams et al., 2004]. This implies that 55% of encounters with stranger females were peaceful, but because [in contrast to Goodall, 1986] this study included observations of young nulliparous females in the process of transfer, this difference might reflect the fact that generally transferring females are accepted by males, so we have not included them in Table IV. In Mahale, violent

TABLE IV. Comparison of Intergroup Behavior in Different Chimpanzee Populations (Same References as for Table III)

Chimpanzee population	Number of visual contacts	Prisoner						
		Sex	With severe attack	Attack against infant	Sexual interactions	Support	Female visit	
Tai NG	66	♀	7 (2) ^a	0	0	13	19	1
		♂	1	0	–	1		
Tai MG	18	♀	4	0	0	14	2	9
Tai SG	34	♀	4	0	0	18	10	16
		Inf	1 ^b	1	–	–	1	
Tai (all)	118	♂	1 ^b	1	–	–	0	
			18	2	0	45	33	26
Gombe ^c	97	♀	19	16	3	3	0	0
		♂	6 ^b	6	–	–	0	
Gombe (Wilson)		♀	2	2	3	0	0	0
		♂	2 ^b	–	–	–	–	
Mahale ^d		♀	5 (1)	5	3	6		6
Ngogo ^e	24	♀	10 (6 ^f)	5	10	0	3	0
		♂	11 ^{b+1}	11	–	–	0	
Kanyawara		♀	1	–	–	–	1	0
		♂	3 ^b	3	–	–	–	

Under female visit, we include only cases where adult parous female voluntarily visited neighboring group members. NG, North Group; MG, Middle Group; SG, South Group.

^aIn two occasions, two females were made prisoners at the same time.

^bIndividuals were killed during the encounters.

^cGombe: Data included visual contact number for the period 1975–1992 [Williams et al., 2004] but detailed data on interactions from Goodall [1986]. In 74 of the 97 encounters involving females, 41 of them were peaceful. Seventeen of those peaceful encounters included parous females with at least one infant, and in three instances mating with a swollen female was seen [Pusey, personal communication]. The remaining 33 encounters with females were classified as aggressive of which 16 were described to be severe [Williams et al., 2004].

^dMahale: Nishida et al. [1985] provide only data on the number of identified females of K Group that visited M Group and not information about the number of visits as we presented for Tai.

^eNgogo: Unpublished data to complement the published material on Ngogo chimpanzees were kindly provided by David Watts and Sylvia Amsler [personal communication]. The descriptions of support so far are limited to hearing calls of neighboring group members.

^fLow visibility or late arrival at the site prevented observer from seeing the beginning of the attacks. The resulting infanticide was assumed to result from females being seized by attackers before their infant was snatched away from them.

attacks against parous females were also reported (Table IV), and that despite the fact that under some specific demographic conditions peaceful transfers between communities of parous females have been observed [Nishida et al., 1985]. Similarly, at Ngogo, adult females suffered severe attacks in at least five cases, and possibly more [Watts et al., 2002, 2006].

Finally, in Tai sexual interactions between members of different communities have been observed in 39% of the intergroup encounters with 30% of the later instances resulting from voluntary visits of parous females (Table IV). As seen in case 3, the males' interest in sexual interactions was observed with anestrus mothers as well as with estrous females. If sexual interactions with parous females have been observed in Gombe chimpanzees [Goodall, 1986; Williams et al., 2004], observers in Ngogo have not seen males mate with parous females from neighboring communities [Watts, personal communication]. In addition, voluntary visits by adult parous females have not been reported in Gombe or at Ngogo (Table IV). In Mahale, voluntary transfer of parous females was described following the strong decline in the number of males in the K

Group, when mothers started to pay visit to the neighboring groups, including M Group, before definitive transfer [Nishida et al., 1985; Table IV]. A similar process of permanent transfer of parous females has been suggested recently in relation to a possible increase in female number among Budongo chimpanzees [Emery Thompson et al., 2006].

DISCUSSION

These new observations on intergroup encounters in Tai chimpanzees confirm earlier suggestions that, in all known chimpanzee populations with enough observations, intergroup encounters are mostly aggressive and occur regularly throughout the period of study [Boesch & Boesch-Achermann, 2000]. Our initial observations made with the North Group have been confirmed with two additional communities in Tai forest. These data as well as recent data coming from chimpanzees in other populations [Ngogo; Watts et al., 2002, 2006; Budongo; Newton-Fisher, 1999; Reynolds, 2005; Gombe; Wilson et al., 2004; Loango; Boesch et al., 2007] confirm the general occurrence of intergroup

competition in chimpanzees. In addition, using data from three Tai chimpanzee groups, we have highlighted some aspects of intergroup conflicts that seem more specific to the Tai chimpanzees than to other populations, such as the high level of participation of females in intergroup encounters whether violent or friendly, the reduced level of violence displayed toward stranger infants by attacking males, and the possible more frequent occurrence of support to attacked individuals.

Direct observations of lethal aggression during intergroup conflicts in Tai chimpanzees show that this extreme behavior is general and not only restricted to East African chimpanzees [Wrangham, 1999; Wrangham et al., 2006]. Similar intergroup attacks by coalitions of many males who inflict numerous injuries on their victims, sometimes including removal of testes and penis, have been observed throughout the range of the chimpanzees in Africa. This strengthens the claim that this behavior is natural in chimpanzees, contrary to claims that humans induce it [Hart & Sussman, 2005; Power, 1991].

The frequency of lethal violence varies dramatically between chimpanzees. The Tai groups have undergone striking changes in size, particularly in the number of adult males. Demographic data reveal that only in the South Group was the general decline in community size associated with an increase in the number of adult males (Fig. 1). Given that females preferably transfer into communities with more than six adult males [Boesch & Boesch-Achermann, 2000], recently observed lethal attacks in Tai could represent male efforts to signal their strength and to attract female immigrants. Gogol and Sagu, two young but high-ranking males of the South Group, were very active in both lethal attacks and probably inflicted deadly injuries, which seems to illustrate this proposition. Variations in intergroup death rate between populations have been reported previously and seem not to be easily explained by the number of neighbors or the number of males in the community.

Tai communities are also notable because females are more gregarious that is typical for eastern chimpanzees, and they are "bisexually bonded" [Boesch & Boesch-Achermann, 2000; Lehmann & Boesch, 2004, 2005]. Tai females take part in many of the intergroup encounters and initiate some of them. Visits and subsequent transfer of females from communities with decreasing number of males were nicely illustrated by the visits of Nadesh from the Middle Group to the larger South Group. Similar observations have been made with some females of the decreasing Kalande community in Gombe [Pusey et al., 2007], from the decreasing K Group in Mahale [Nishida et al., 1985], and were inferred from Budongo recently [Emery Thompson et al., 2006]. However, we suggest female visits to neighboring groups to happen recurrently, as well

illustrate in the two cases of extra-group paternity in the South Group at a time when seven adult and adolescent males were still present [Boesch et al., 2006]. In addition, data in Table IV suggest that females in Tai chimpanzees participate in intergroup interactions more than reported in other populations and stress the possibility that sex might play a more important role in influencing intergroup interactions.

The difference observed in the frequency of support is intriguing, because support can strongly modify the costs of intergroup encounters. Support in Tai chimpanzees has allowed many individuals to be rescued before they were injured, at little cost to supporters. We suggested previously that the low visibility within Tai forest favors such interventions compared to higher visibility environment like in Gombe [Boesch & Boesch-Achermann, 2000]. However, the mainly forested nature of the environment at Ngogo and Kanyawara would be equally favorable to support and its rare occurrence requires an explanation. In Ngogo, observers describe three instances in which the presence of supporters made attackers wary and retreat more rapidly [Amsler, personal communication; Watts et al., 2002]. Because detailed descriptions of many of those encounters are missing, support might be underreported. However, a combination of higher gregariousness, owing to predation pressure in Tai, and lower visibility, reducing the accuracy of numerical assessment, could make support more frequent and more efficient in Tai chimpanzees compared to other populations. Support in intergroup conflicts makes imbalance of power between opponents uncertain. Therefore, support functions in a similar way as weaponry in humans by making imbalances of power less predictable and thereby altering the possible costs of intergroup conflicts [Kelly, 2005; Knauft, 1991]. This also illustrates the importance of cooperation in chimpanzees, even in situations that are extremely risky and where the costs to supporters could be very high.

When should chimpanzees initiate an intergroup contact? Different options have been proposed, one suggesting that a drive to violence in males combined with imbalance of power would explain some of the intergroup interactions [Wrangham, 1999; Wrangham & Peterson, 1996], whereas another expected more variability depending upon the demographic and ecological conditions of the communities under study [Boesch & Boesch-Achermann, 2000; Mitani et al., 2002; Williams et al., 2004]. The observation presented here shows that supports regularly change the balance of power and thus create unpredictability. Second, small communities do not refrain from attacking larger communities (for example, when the Middle Group members attacked the much larger South Group or when the South Group members attacked the larger East Group), even

when in very small parties. Our general impression is that chimpanzees can take large risks when potential benefits are large or when failure to do so could inflict larger costs [see Grinnell et al., 1995, for examples in male lions]. Males in communities with a relatively small number of sexually active females might take more risks to attack groups with more females to try and improve their reproductive success, even if those groups have many more males.

In conclusion, intergroup conflicts regularly occur at Tai. They take many forms, involve participation by both sexes, often include sexual interactions or support to targets of attacks, and rarely involve infanticide. Nevertheless, fatal violence has now been observed, but at considerably lower rates than found in other chimpanzee populations. Intergroup violence is general in chimpanzees, but aggression intensity and the role of females vary considerably among populations. Thus, multiple factors may account for the evolution of intergroup violence in this species, and we need more demographic data on neighboring communities if we want to understand intergroup conflict dynamics.

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