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RESEARCH ARTICLE

Lethal Intergroup Aggression by Chimpanzees in Kibale National Park, Uganda

DAVID P. WATTS[1*], MARTIN MULLER[2], SYLVIA J. AMSLER[3], GODFREY MBABAZI[4], AND JOHN C. MITANI[3]
[1]*Department of Anthropology, Yale University, New Haven, Connecticut*
[2]*Department of Anthropology, Boston University, Boston, Massachusetts*
[3]*Department of Anthropology, University of Michigan, Ann Arbor, Michigan*
[4]*Ngogo Chimpanzee Project, Fort Portal, Uganda*

Chimpanzees (*Pan troglodytes*) have hostile intergroup relations throughout most or all of their geographic range. Hostilities include aggressive encounters between members of neighboring communities during foraging and during patrols in which members of one community search for neighbors near territory boundaries. Attacks on neighbors involve coalitions of adult males, and are sometimes fatal. Targets include members of all age/sex classes, but the risk of lethal intergroup coalitionary aggression is highest for adult males and infants, and lowest for sexually swollen females. The best-supported adaptive explanation for such behavior is that fission-fusion sociality allows opportunities for low-cost attacks that, when successful, enhance the food supply for members of the attackers' community, improve survivorship, and increase female fertility. We add to the database on intergroup coalitionary aggression in chimpanzees by describing three fatal attacks on adult males, plus a fourth attack on an adult male and an attack on a juvenile that were almost certainly fatal. Observers saw four of these attacks and inferred the fifth from forensic and behavioral evidence. The attackers were males in two habituated, unprovisioned communities (Ngogo and Kanyawara) in Kibale National Park, Uganda. We also summarize data on other intercommunity attacks at Ngogo. Our observations are consistent with the ''imbalance of power'' hypothesis [Manson & Wrangham, Current Anthropology 32:369–390, 1991] and support the argument that lethal coalitionary intergroup aggression by male chimpanzees is part of an evolved behavioral strategy. Am. J. Primatol. 68:161–180, 2006.

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*Correspondence to: David P. Watts, Dept. of Anthropology, Yale University, P.O. Box 8277, New Haven, CT 06520-8277. E-mail: david.watts@yale.edu

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INTRODUCTION

In several mammalian species, dyadic contests between adults can lead to fatal injuries (e.g., red deer (*Cervus elaphus*) [Clutton-Brock et al., 1982], pronghorn (*Antilocapra americana*) [Byers, 1997], wedge-capped capuchins (*Cebus olivaceous*) [Miller, 1998], white-faced capuchins (*Cebus capucinus*) [Gros-Louis et al., 2003], and mountain gorillas (*Gorilla gorilla beringei*) [Watts, 1988]. Additionally, infanticide, mostly by adult males, occurs in many primate taxa (reviewed in van Schaik [2000]). In contrast, the killing of conspecifics other than infants by coalitions of multiple individuals is known only in a few social carnivores (e.g., lions (*Panthera leo*) [Grinnell et al., 1995], African wild dogs (*Lycaon pictus*) [Creel & Creel, 2002], and wolves [Mech & Boitani, 2003], and a few primate species (e.g., western red colobus (*Procolobus badius temmincki*) [Starin, 1994], diana monkeys (*Cercopithecus diana*) [McGraw et al., 2002], white-faced capuchins [Gros-Louis et al., 2003], and chimpanzees (*Pan troglodytes*) [Wilson & Wrangham, 2003]).

Chimpanzees stand out quantitatively and qualitatively among the nonhuman primate species in which lethal coalitionary aggression is known. Researchers have documented such behavior in four wild populations (Budongo [Fawcett & Muhumuza, 2000; Newton-Fisher, 1999], Gombe [Goodall, 1986; Goodall et al., 1979; Wilson et al., 2004], Kibale [Muller, 2002; Watts, 2004; Wrangham & Peterson, 1996], and Mahale [Nishida, 1996], and at the Arnhem Zoo [de Waal, 1986] (also see reviews by Wrangham [1999] and Wilson and Wrangham [2003]). Fatal attacks have been made almost exclusively by adult and adolescent males, whereas female involvement may be relatively more common in other species. Gros-Louis et al. [2003] described a fatal attack by a male coalition of white-faced capuchins at Lomas Barbudal; however, females participated in other lethal attacks in this population. Female coalitions have fatally attacked adult males in western red colobus monkeys [Starin, 1994], and McGraw et al. [2002] described a lethal attack on an adult female by a coalition of female diana monkeys. Some fatal attacks involving chimpanzees have occurred within communities [Fawcett & Muhumuza, 2000; Nishida, 1996; Watts, 2004] or during encounters between foraging parties from different communities (below), but many have happened during patrols by groups of males along the borders of their territories or in the territories of neighboring communities [Wilson & Wrangham, 2003; Wrangham, 1999]. Male spider monkeys (*Ateles* spp.) also patrol territory boundaries and make incursions into neighboring territories (F. Auerli, N. Gibson, personal communication). Fatal attacks have not been seen in this taxon, and such behavior is otherwise unknown in nonhuman primates. Adult or adolescent males have been the targets in most between-group attacks in chimpanzees (excluding infanticides), but members of all age/sex classes, except females with sexual swellings, risk potentially lethal aggression from males outside their groups, and this aggression is not associated with immigration attempts [Goodall, 1986; Wilson & Wrangham, 2003; Wrangham, 1999]. In other nonhuman primates, dyadic and polyadic aggression that leads to potentially fatal wounds is restricted more to same-sex competitors or to potentially threatening immigrants (e.g., barbary macaques [Kuester & Paul, 1992], eastern red colobus (*Procolobus badius tephrosceles*) [Struhsaker, 2000], western red

colobus [Starin, 1994], and Peruvian squirrel monkeys (*Saimiri boliviensis*) [Mitchell, 1994]).

Fission-fusion sociality makes it possible for a large male party from one chimpanzee community to surprise a small party or a lone individual from a neighboring community and attack with little risk (the ''imbalance of power'' hypothesis [Manson & Wrangham, 1991; Wrangham, 1999]). Boundary patrols can create opportunities for low-risk attacks, but similar power imbalances can also occur during encounters between foraging parties from neighboring communities. Several functional explanations for such attacks have been proposed [Manson & Wrangham, 1991; Pusey, 2001; Williams et al., 2004; Wilson & Wrangham, 2003; Wrangham, 1999]. Support is strongest for the argument that dominance over neighboring communities provides indirect reproductive payoffs to males because it increases the availability of food resources for their mates and offspring. Notably, long-term Gombe data show a positive relationship between territory size and female reproductive success [Pusey, 2001; Williams et al., 2004]. Similar logic may apply to between-community infanticide in chimpanzees [Pusey, 2001; Watts et al., 2002; Wilson et al., 2004]. Also, territory expansion and elimination of neighboring males can directly increase male mating opportunities by incorporating more females into a community, as happened at Gombe [Goodall, 1986] and perhaps Mahale [Nishida et al., 1985], although females may alter their movement patterns rather than associate with neighboring males (Gombe [Pusey, 2001; Williams et al., 2002]). Finally, given the existence of potentially lethal aggression, killing dangerous neighboring males can improve survivorship for all community members [Wrangham, 1999].

Here we describe two lethal coalitionary intergroup attacks on adult males at the Ngogo research site in Kibale, as well as severe attacks on an adult male and a juvenile male that were almost certainly fatal. The attacks occurred while field work was being conducted in 2002 and 2004. We also provide comparative data regarding a fatal attack on an adult male at Kanyawara, in the same habitat [Muller, 2002], and summarize observations of other attacks on individuals older than infants during other intergroup encounters at Ngogo. We do not have enough life history data to test hypotheses about the function of intergroup aggression, but the Kibale evidence supports the argument that lethal coalitionary aggression between groups is part of the natural behavioral repertoire of chimpanzees and is consistent with the ''food defense'' hypothesis.

MATERIALS AND METHODS

Study Site and Subjects

Kibale National Park is located in western Uganda between 0° 13′ and 0° 41′ N and 30° 19′ and 30° 32′ E. The Makerere University Biological Field Station maintains two main research sites in Kibale: Kanyawara in the northwest, and Ngogo in the center. Butynski [1990], Chapman and Chapman [1999], Lwanga et al. [2000], and Struhsaker [1997] have provided detailed descriptions of the study areas, which comprise a mixture of mid-altitude mature forest, forest at various stages of regeneration from past human disturbance, *Pennisetum purpureum* grassland, and other, less extensive vegetation types (e.g., swamp forest dominated by the palm *Phoenix reclinatum*). Ngogo is about 120 m lower than Kanyawara, and receives slightly less rainfall [Struhsaker, 1997]. Vegetation composition and floristics differ slightly between the sites, partly because of different disturbance histories [Chapman & Lambert, 2000; Lwanga et al., 2000; Struhsaker, 1997]. For example, commercial logging occurred at various

intensities in parts of the Kanyawara study area in the 1960s and 1070s, whereas Ngogo was not commercially logged, and mature forest covers more of the Ngogo study area [Struhsaker, 1997]. Some tree species that are important chimpanzee food sources at one site are rare or absent at the other (e.g., *Pterygota mildbraedii* and *Ficus mucuso* are common at Ngogo but rare at Kanyawara). Nevertheless, the diets of the chimpanzees at at these two sites are broadly similar [Wrangham et al., 1991]. Chimpanzees were first studied at Kanyawara in the mid-1980s [Isibirye-Basuta, 1989] and have been observed continuously since 1988. Ghiglieri [1984] studied chimpanzees at Ngogo in the late 1970s and early 1980s. After a hiatus, research resumed there in 1991, and the community there has been habituated and under continuous observation since 1995. Kibale now enjoys strictly protected status and neither study area has experienced any encroachment by humans during the history of these research projects.

At the time the observations reported here were made, the Kanyawara community had 50 members, including 11 adult males and one adolescent male. The Ngogo community is the largest known in the wild [Mitani & Amsler, 2003; Watts, 1998; Watts & Mitani, 2001]. When the first attacks on an adult male (case 1 below; June 2002) and a juvenile male (case 5 below; August 2002) occurred, the community had about 145 members, including 24 fully adult males, 16 adolescent males (several of which outranked the lowest-ranking adult males), and at least 45 adult females. Two adult males had died by the date of the second attack on an adult male (case 2 below; November 2002). Ngogo had 24 adult males, 15 adolescent males, and about 145 members at the time of the third attack on an adult male (case 3 below; August 2004).

Observation Methods

Chimpanzees have been habituated without provisioning at both Kanyawara and Ngogo. Researchers and field assistants at both sites use several methods to locate chimpanzees (e.g., listening for vocalizations and checking trees with currently attractive fruit crops) and can usually follow even small parties easily, especially if the parties contain several males. Observers document the location, context, and sequence of events for all known encounters between communities. Many of these encounters occur when chimpanzees foraging in single or mixed sex parties hear neighbors. Such auditory contact can lead to several responses, sometimes including silent approach. Other encounters occur during boundary patrols, which are performed mostly by males. Patrolling males stay close to each other and travel in file formations. They are extremely vigilant and sometimes stop to listen for neighbors, and are uncharacteristically silent [Goodall, 1986; Mitani & Watts, 2005; Watts & Mitani, 2001; Wrangham, 1999]. Chimpanzees at Ngogo also go on hunting patrols [Mitani & Watts, 1999; Watts & Mitani, 2002]. These sometimes take chimpanzees into boundary areas, but differ from boundary patrols in several respects, including the common presence of females and dependent young on hunting patrols; vigilant scanning of the canopy during hunting, but not boundary, patrols; stops to sit and listen during boundary, but not hunting, patrols; and bypassing large groups of red colobus monkeys in vulnerable situations (e.g., young forest on the edge of grasslands) during boundary patrols. In both contexts, males tolerate humans following them at short distances, and observers have routinely accompanied patrolling males at Kanyawara since 1993 and at Ngogo since 1997. The observations reported here were made ad libitum during intercommunity encounters, and case 3 was partly reconstructed from trail signs and forensic evidence (below). Also, D. Watts

videotaped parts of three of the attacks. The video record for case 2 was almost complete, and analyzing it provided many more details on the attack. The record for case 3 was less complete because thick vegetation obscured some of the action, but it still added details to those gained by direct observation. Video of a short segment of case 4 was not useful as a documentary record because the thickness of the vegetation and swiftness of the action made it impossible to identify individual males.

The Ngogo data discussed here involve only 41 months in 1997–2003 when either D. Watts or J. Mitani, or both were present at the site. We documented 95 boundary patrols and 68 intercommunity encounters in other contexts during that time. This cannot be a complete sample, even though observers find and follow the chimpanzees almost every day, because they do not find all community members. We also note that boundary patrols and intercommunity encounters are nonrandomly distributed in time, and are relatively common during periods when males routinely form large parties, often in response to the availability of large fruit crops, such as when the attacks described below occurred [Mitani & Watts, 2005] (Mitani and Watts, unpublished data).

RESULTS

Case 1: Attack by Ngogo Males on an Adult Male From the Eastern Community, 3 June 2002

On 1 June 2002, J. Mitani, S. Amsler, and field assistant Godfrey Mbabazi followed 10 adult, two adolescent, and two juvenile males (Table I) on a boundary patrol along the eastern edge of the Ngogo chimpanzees' territory. The males

TABLE I. Participants in Inter-community Attacks and Associated Boundary Patrols Described in the Text

Case	Site	Date	Adult Males	Adolescent males	Others
1[a]	Ngogo	6/1/02	BF, BRU, BT, DO,EL, HA HO, LO, MG, MO	COR, DX, GTZ	2 juvenile ♂♂ (PP, ?)
1	Ngogo	6/3/02	BF, BRU, EL, GA, GRA, HA, HO, LO, MG, MO, OR, ST	COR, DX, TA	
2	Ngogo	11/23/02	BE, BF, BRU, BS, BT, DO, EL, GA, HA, MG, MI, MO, MW, OR, PA PI, ST	BRA, COR, DX, MOR[b], RAH[b], RI, ROL[b], TA, WAL	
3	Ngogo	8/1/04	BE, BS, BT, HA, HO, MO, MOR, OR, PA	TA, WB	Ad♀MA
4		Kanyawara	10/25/98	BB, MS, AJ, LB, LK, SL, SY, ST, TU, YB	COR, DX, GTZ, MOR, RI
5	Ngogo	8/9/02	AA, BE, BS, BT, DO, EL, HA, HO, MG, MI, MO, PA		

[a]Boundary patrol two days prior to the interground killing.
[b]MOR, RAH, and ROL participated in attack; other adolescent males present at encounter, but apparently did not join in arrack.

made a deep incursion into the territory of their neighbors, but did not contact any chimpanzees. They eventually returned to the edge of their own territory and dispersed. Early the next morning, Mitani and Amsler located adult males BT (the alpha male), LO, and MO, which had patrolled the previous day, displaying under a *Pseudospondias microcarpa* tree near the boundary of their territory. All three returned to the center of the Ngogo territory, where they split up. Observers followed BT to a large party containing an estrous female and 12 males, none of which had patrolled the day before.

Around 0800 hr on the morning of 3 June 2003, G. Mbabazi found 12 adult and three adolescent males, 10 of which had participated in the boundary patrol 2 days before (Table I) in the eastern part of the Ngogo chimpanzees' territory. They started another boundary patrol by quickly and quietly moving south and then east. At 0830 hr, they moved east through a field of elephant grass (*Pennisetum purpureum*), then reentered the forest and went toward the spot where BT, LO, and MO had been displaying 1 day before and the area where Ngogo males had patrolled the day before that. As they reentered the forest, the Ngogo chimpanzees met chimpanzees from another community. The neighboring chimpanzees were feeding quietly on *Pseudospondias microcarpa* fruit in the same tree under which BT, LO, and MO had displayed. G. Mbabazi could not ascertain the precise number of chimpanzees from the neighboring group, but he saw least two females with infants, one juvenile, and one adult male that immediately fled northeast with the Ngogo chimpanzees in pursuit. The Ngogo chimpanzees caught up to the strange adult male after chasing him for about 100 m and surrounded him. Adult Ngogo male EL began to pummel the intruder, and adults BF, BRU, LO, and MO quickly joined him. The strange male tried to escape down a small hill but could not elude these five Ngogo males and others that joined them. The Ngogo males, led by EL, continued to beat, bite, and kick him for 20 min, and dragged him farther down this hill into a small stream valley about 50 m away from the spot of his initial capture, where he died during or shortly after the attack. All of the Ngogo males remained in the area after the stranger was killed. Several circled his body and some sniffed it, while others sat nearby. After about 30 min, all of the Ngogo chimpanzees moved southwest, angling toward the center of their range. Members of the patrol hunted red colobus (*Procolobus badius tephrosceles*) monkeys later that day and made five kills.

G. Mbabazi, J. Mitani, and S. Amsler returned to the scene the next day to conduct a postmortem examination. Careful inspection showed that the victim suffered wounds across his entire body (Table II), including a deep gash to the bone on the left humerus and a deep puncture on the left side of the thorax near the heart. The only missing body part was the victim's testes, which were recovered 50 m away, near where he was initially captured. None of the bite wounds appeared fatal, despite their severity, and he probably succumbed to internal injuries.

Case 2: Attack by Ngogo Males on an Adult Wantabu Male, 23 November 2002

On the morning of 22 November, most of the Ngogo males and many females with associated dependent young had gathered in the north-central part of their range to eat *Uvariopsis congensis* fruit. Eight adult males and one adolescent male went east on a boundary patrol at 1000 hr, but the other chimpanzees stayed in the same general area until mid-afternoon, when they moved west and then back to the south to eat *Monodora myristica* fruit. Many chimpanzees nested

TABLE 2. Wounds on Adult Male Victims of Lethal Coalitionarv Aggression at Ngogo and Kanvawara

Body Part	Case 1	Case 2	Case 3	Case 4
Head and face	Multiple bites to lips, eyes, ears, mandible	Multiple bites to brow ridges, ears; deep, 5 cm puncture/ slash along mandibular symphysis; shallower vertical slash in mandible	L ear torn off, R ear torn for half of length; multiple punctures and slashes on brow and top of head; lower lip torn	R Ear torn, nasal septum torn, large gash from R nostril to upper lip, 5 cm gash on lower gum, multiple bites on head and browridge 4 cm gash under mandible
Neck	1 dorsal puncture	Wide, 5 cm horizontal stash on ventral side	Multiple bites on back of neck	Severed trachea
Arms	Deep gash to bone on L humerus, 3 bites on left ulna 1 on R ulna	Multiple large puncture/ slashes in both axillary regions; multiple 3–6 cm puncture/slashes on both upper arms; punctures in shoulders	Multiple bites on both arms	L arm: 3 wounds ventral surface, 12 cm × 6cm patch or skin torn from upper arm; R arm: 6 bites on ventral surface
Hands		Multiple bites to both hands	Multiple bites to both hands	Nails torn from 4 fingers on L hand and I on R; multiple bite wounds on born hands, 3 fingers on R hand almost severed
Thorax and abdomen	1 deep puncture wound on L thorax, 7 bites on abdomen	Deep, gaping 8 cm slash in R inguinal region; deep, 6 cm slash 6 cm slash to R thorax; multiple smaller slashes both sides thorax		Compound fractures in 4 L ribs, 18 punctures & lacerations on abdomen
Back			Long slash	
Genitals	Both testes ripped from scrotum	1 testis ripped from scrotum	Testes intact	Both testes ripped from scrotum
Anus	1 bite			
Legs	2 deep punctures and 2 smaller bites on L thigh; 2 bites on R thigh	Multiple deep, gaping puncture/slashes on both sides of groin and on surfaces of thighs		
Feet		Multiple punctures, slashes both feet	Multiple punctures, slashes both feet	1 nail torn from R foot; 2 punctures R foot, two deep gashes on L foot

about 1.5 km west-northwest of the Ngogo camp that night. They scattered into smaller parties early the next morning to eat more *M. myristica* fruit, but maintained vocal contact and generally moved west. By late morning, 17 adult and nine adolescent males, including all but one male (adult TY) that had gone on the boundary patrol the previous day (Table I), were scattered along both sides of an extensive valley in the northwest part of their range, along with at least 12 adult females with seven associated juveniles and 10 infants, and at least two adolescent females. Most of the females were on the west side of the valley, and most of the males were on the east side. At 1245 hr, the males crossed the valley at several locations. As they reached the females, the males started to charge at them and at each other. This continued for about 20 min, with most of the females moving farther northwest to avoid the males.

The chimpanzees then rested briefly in several clusters along the side of another valley. They started to sweep north from there at 1345 hr. They were now in an area in which their range overlaps that of at least one other community, and were moving farther into those neighbors' range. They seemed to be on a hunting patrol to search for red colobus, as indicated by the presence of many females and immatures, and the fact that the chimpanzees divided into two columns that moved north in parallel, out of each other's sight. Also, the chimpanzees that stayed to the east stopped to sit quietly and listen above a large swampy valley, then excitedly ran to join the others farther to the west when those others encountered a red colobus group at 1425 hr and gave ''hunting calls'' or barks [Crockford & Boesch, 2003; Mitani & Watts, 1999]. Finally, the chimpanzees were extremely noisy when they converged on the red colobus group, and the males again started to display. During boundary patrols, they usually bypass red colobus, but when they do hunt them they do so silently.

The red colobus were in several large trees close to young forest with a low and open canopy, where they would have been highly vulnerable to the chimpanzees [Watts & Mitani, 2002]. Given the large number of male chimpanzees that were present, observers D. Watts, Adolph Magoba, and Alfred Tumusiime expected them to hunt. However, only a few males climbed toward the red colobus, and they descended by 1450 hr without having pursued the monkeys. Several others on the ground repeatedly gave charging displays. They briefly quieted and watched the red colobus, but at 1455 hr at least four adult males resumed displaying. Adult male PA charged repeatedly at male MW, with which he was then in the process of reversing rank, and a coalition of several males attacked low-ranking adult male PI. Display outbursts punctuated by periods when males sat calmly continued for about 30 min.

The chimpanzees were extremely noisy during much of this time. The females drifted away, perhaps to avoid being targeted in displays. Chimpanzees from a neighboring community (presumably the Wantabu community, to the north of Ngogo) were nearby and made no attempt to avoid the Ngogo chimpanzees, despite their vocalizations. However, the other chimpanzees may have approached from the opposite side of the nearby Wantabu stream and failed to hear the Ngogo chimpanzees because of the loud noise of the rushing water (the stream was flowing at high volume and observers could hear it clearly from several hundred meters away). At 1528 hr, loud, sharp screams came from the direction of the Wantabu, on the Ngogo side of the stream and west of the Ngogo males and the red colobus. The observers initially assumed that the screams came from Ngogo females, but soon realized that they might have come from Wantabu chimpanzees. All of the Ngogo males immediately ran in that direction. The observers followed them for about 150 m and then found several chimpanzees

(including MW and MO) attacking a screaming adult female chimpanzee that crouched as if protecting an infant. Within 10 sec, the males left her to run toward many more chimpanzees that were screaming and giving ''waah'' barks farther southwest.

The observers lost sight of the chimpanzees for a few seconds, and then at 1531 hr they found many males surrounding a single adult male chimpanzee that was about 10 m up a small tree. Within 30 sec, several Ngogo males started to climb the tree, at which point the trapped male climbed farther out and tried to bridge into another tree. However, the first tree collapsed under the combined mass of several chimpanzees, and he crashed to the ground and ran. Within seconds, the Ngogo males grabbed and attacked him. The observers could not see which animal first made physical contact with the male, but he was quickly surrounded by at least 16 adult and three adolescent males (Table I), all of which apparently made at least some contact with him and quickly immobilized him.

Even with the video record, it was impossible to ascertain exactly which individual did what throughout the entire attack. Too often the attackers moved fast, with their faces not visible, or were obscured by vegetation. At least two or three Ngogo adults held the Wantabu male's arms for about the first 2.5 min of the attack, while others jumped on, hit, and bit him. He sat on the ground, unable to move, during this time. Adult males BE, BF, BS, BT, DO, EL, HA, MG, MI, MO, MW, OR, PA, and PI were most prominently involved in the initial attack. All repeatedly hit, bit, and/or stomped on the Wantabu male, and most held him by the arms, legs, or shoulders at some point. ST, a small, low-ranking adult male, participated in the initial attack but appeared to make only brief physical contact with the Wantabu male. Most of the bite wounds inflicted in the first few minutes were to his shoulders, arms, and hands (Table II). He also received multiple bites on his upper back and on the back of his head when several males attacked him from behind. They did this while the male sat with legs extended, and two other males pulled his arms forward and forced his trunk to flex ventrally at the hips. MOR and RAH were the largest and presumably the oldest of the adolescent males present. Both joined in the initial attack and at least MOR probably bit the male, but both retreated to the edge of the pile of males around and on the victim within about 1 min after the start of the attack. Younger adolescent male ROL was initially on the edge of the cluster of males attacking the Wantabu male, and probably touched him. After about 1 min he jumped about 1 m up a small tree above the attackers. When adult DO briefly broke away from the attack, charged toward ROL, and grabbed at him, ROL fled. He did not rejoin the cluster of attackers.

After about 2.5 min, enough Ngogo males had released their holds for the Wantabu male to move, and he managed to struggle for a distance of about 2 m. Several Ngogo males then grabbed him again, and adult male DO pounded him on the back, jumped on and then over him, grabbed one of his legs and pulled it hard and twisted it, and bit his foot.This ended any possibility that he could move. The attack continued for another 2 min at the spot where he was now again immobilized. During this initial phase of the attack, no single Ngogo male maintained uninterrupted contact with the victim. Instead, individuals repeatedly joined in to hold, bite, and/or hit or jump on him, then broke contact to display at or to embrace each other, or just to watch excitedly. For example, EL moved in and out of the pile in contact with the male at least five times. He attacked the male by twisting his leg, biting him, and/or drumming hard on his back each time he rejoined the pile. MW and DO embraced each other, as did several other pairs of males, and BT (the alpha male), PA, and BS each displayed

toward others on the edge of the pile. At moments, EL, OR, MW, PA, and others climbed over other Ngogo males to get to the center of the pile, where they bit or stomped on the male.

At about 1537 hr, several Ngogo males dragged the Wantabu male about 15 m downhill, where they and others resumed the attack. From that point on, the Ngogo males were no longer in constant physical contact with him, but he was too weak to do more than sit up, and by 1541 hr he simply lay on the ground with his limbs twitching spasmodically. A few males drifted away, but BE, BF, BS, DO, EL, HA, MG, MI, MW, and PI, and adolescents MOR and RAH continued to hit and bite him intermittently. MW and another male (MI?) also jumped on him hard. At one point when the Ngogo males had broken contact with the victim and he lay on the ground, adult male BE grabbed his left leg and bit into it deeply, then dragged him 2 m by that leg. Several others also dragged him again while he was still alive. Because he was supine or lying on his side during this part of the attack, most of the wounds were to the ventral side of his chest and his abdomen, groin, legs, and feet (Table II). At some point, probably during this part of the attack, the attackers tore one of his testicles from his scrotum.

The Wantabu male died within 10 min of when the Ngogo males first grabbed him. After he died, BS, PI, RAH, and one other male that the observers could not identify each dragged his body for a short distance. As PI started to drag him, BS drummed repeatedly with his full strength on the male's abdomen. BS and RAH were the last males to leave the body, at 1548 hr.

By then, the other Ngogo males had moved 50–100 m east of the body. The Ngogo females and their dependent offspring were not evident and had probably already moved back south. The males were still highly excited, but did not display or call. They quickly moved south-southeast in several groups when a severe thunderstorm started at 1600 hr. The observers eventually lost them in the downpour when they were well back toward the center of their range. They located 11 of the adult males and two of the adolescents together in the west-central part of the Ngogo range on the next day, and had seen all of the attackers in this area or farther east by November 26.

The way the males moved in and out of the attacking pile was particularly notable and was a consequence of the large number of males present. The attackers could not all have maintained continuous contact with their victim, and when individuals momentarily broke off their assaults, they gave others the opportunity to join in. Males could jump in and out of the fray without putting others at risk because the combined force of the attackers was so overwhelming. The Wantabu male appeared completely unable to resist the attackers, and none of them had visible wounds afterwards.

Case 3: Attack on an Adult Male by Ngogo Males, 1 August 2004

On the morning of 1 August 2004, D. Watts, J. Mitani, S. Amsler, and M. Muller found at least 30 Ngogo chimpanzees in the northeastern part of the territory. These included 15 adult males, five adolescent males, two females with sexual swellings (both with juveniles), and several other females and immature individuals. One of the swollen females (ME) was the subject of intense interest (some of the males had been following her for the previous week), although she was stationary in the top of the canopy and most of the males had spread out to feed. At 0815 hr, those males converged on the ground under ME along with the other males that had not left her.

At 0832 hr, chimpanzee pant hoots were audible from the NNW, perhaps 1 km away. Most of the Ngogo males excitedly rushed about 50 m in that direction, and then sat and listened. More calls came at 0842 hr, in response to which the Ngogo males gave a chorus of pant hoots. At 0847 hr, nine fully adult males, three large adolescent males, and one old and apparently post-reproductive female (Table I) started to move rapidly NNW. Six other adult males and three adolescent males stayed behind, and adolescent male DX stopped after he went a short distance and returned to female ME. At 0852 hr, the 11 males and one female stopped for 10 min to listen while they looked northward, and then moved steadily and silently in that direction.

The chimpanzees moved steadily northward and slightly west for the next hour. They crossed several valleys and stopped once to sniff the ground and once to sniff a *Pterygota mildbraedii* sapling from which a chimpanzee apparently had eaten leaves. At 0952 hr, they stopped to listen for 11 min at a point 2 km from where they had first heard the other chimpanzees, which also must have gone northward. At 1003 hr, most of the Ngogo chimpanzees resumed moving northward, but adult males HO and PA turned and started back south.

At 1009 hr, a juvenile or infant chimpanzee screamed from about 200 m farther north. The Ngogo chimpanzees excitedly but silently gathered in a cluster and several embraced each other. Males HO and PA ran back and rejoined them, and all then moved swiftly and silently toward the screams. As they were moving along the side of a narrow valley at 1022 hr, they again heard screams from a nearby immature chimpanzee. After another excited flurry of embraces (e.g., adult male BS embraced BE as BE embraced HO) and other reassuring gestures, the Ngogo chimpanzees ran toward the sound and encountered at least five adult female chimpanzees, accompanied by several infants and juveniles, feeding in the canopy of a *Ficus mucuso* tree.

The Ngogo males, no longer silent, charged around and displayed under the tree while the stranger females screamed and retreated to peripheral branches in the top of the fig or at the edge of the canopy of an adjacent tree. Several males, including adults BS, HO, and OR, climbed toward the females and at least two of them got close enough to hit females, but the females and associated immatures escaped a more serious attack because the males could not maneuver easily or safely in the terminal branches of the two trees. Displays, waahs, and screams continued for several minutes. At some point, several Ngogo chimpanzees realized that one or more other members of the other community were nearby to the east, and ran in that direction. The observers did not notice when the first chimpanzees did this, but eventually realized that waahs and screams like those that occur during lethal coalitionary attacks were coming from the east, and followed adult male OR as he ran to join the others that had gone that way.

At about 1028 hr, the observers found that eight of the Ngogo males were attacking a single male from the neighboring community. They did not see adult males BE, BT, and PA, which apparently had started back to the south after the attack on the females. Ngogo female MA was present but did not directly participate in the attack on the male. Adult males MO, BS, and, especially HO and OR were prominent participants. MOR, a young adult male, contacted the stranger male several times, and large adolescents TA and WB also both hit and bit him. The Ngogo males repeatedly bit, stomped on, pummeled, and kicked the male for about 5–6 min. One or more held and immobilized him for some of this time, and he was quicky unable to do more than push weakly at his attackers and did not engage in serious counteraggression. The Ngogo males paused at least four times during the attack to sit and listen as other chimpanzees called nearby.

They did not restrain the male during these pauses, and he ran a few meters away during the first pause. However, the Ngogo males quickly surrounded him; HO pounded on his back and then stomped on him as he collapsed, and others also resumed the attack. The third pause lasted 15 sec, but by then the male could no longer flee. The observers thought that the callers included one or more males, and since the calls were from farther north, the voices would not have been those of BE, BT, or PA, who had gone south. The Ngogo males fell silent and appeared nervous as they listened. However, they resumed the attack after each pause, although only briefly after the third as they started to leave. Adult male BS delivered a few last blows to the male at 1034 hr, after which all of the Ngogo males left.

The stranger sat at the attack site for a few more seconds and then staggered weakly off to the north. His left ear had been torn off and his right ear had a large gash; he had a long canine slash along his back and multiple gashes and punctures on his hands, feet, brow, head, and the back of his neck. His lower lip was ripped open, and he undoubtedly had suffered internal injuries from the pounding and stomping (Table II). The observers did not try to follow him and were uncertain about his fate. However, one of us (D.P.W.) thought that his bite wounds were at least as bad as those inflicted on an Ngogo adult male during a fatal within-community attack in 2002 [Watts, 2004], and in that earlier attack the attackers did not also pummel and stomp on their victim. The Ngogo male survived the initial attack in 2002, but died from his wounds within several days [Watts, 2004]. Thus, we consider it highly unlikely that the stranger survived.

The Ngogo males swiftly moved about 1 km south before any of them stopped. They did not all stay together, but some called several times. The observers followed adult males HA and MO to a patch of *Ilygera pentandra* vines, where they rejoined adult males HO, BE, and PA, and female MA to eat seeds. They resumed moving south at 1220 hr and increased their pace when they heard calls from other Ngogo chimpanzees farther SSE at 1225 hr. At 1242 hr, they rejoined estrous female ME and most of the other males where they had left ME that morning. Four participants in the attack (BS, MOR, OR, and TA) continued farther south instead of rejoining the others.

Case 4: Attack at Kanyawara, 25 August 1998

A fourth fatal attack on an adult male occurred at Kanyawara on 25 August 1998, as previously described by Muller [2002]. Field assistant Francis Mugurusi followed 10 adult males from the Kanyawara community (BB, MS, AJ, LB, LK, SL, SY, ST, TU, and YB) on a boundary patrol near the northern border of their territory on that day, but lost them before they made contact with neighboring chimpanzees. At 1040 hr the next morning, M. Muller and Field Assistant Christopher Katongole located all 10 of the males with the body of a dead adult male from the neighboring Sebitoli community, which lay in a 7×12 m patch of trampled vegetation at the base of a steep slope. At least two individuals were pounding on the corpse with their hands. At 1045 hr, three males from the Sebitoli community gave alarm calls and displayed near the scene of the attack. The Kanyawara males exchanged aggressive vocalizations with the strangers, slapped the ground, and performed charging displays. At 1115 hr they moved silently toward the strangers en masse, and the strangers ceased vocalizing and apparently left. The observers were then able to examine the dead male closely before the Kanyawara males returned at 1133 hr. Rigor mortis had set in, suggesting that he had been killed the previous evening. Disturbance to

vegetation at the site, and wounds on the male's body showed that he had experienced a protracted and intense assault (Table II). His arms and legs were fully extended, as if some individuals had immobilized him while others attacked. The immediate cause of death appeared to be massive trauma to the throat, including a severed trachea. The number, severity, and variety of his wounds indicate that only chimpanzees could have inflicted them. Leopards apparently are no longer present in Kibale (nor would a leopard have inflicted injuries like the rib fractures), and the body bore no signs of predation. Its position in a patch of trampled vegetation at the base of a steep hill is consistent with other observations of chimpanzees killed by coalitions of conspecfics [Wrangham & Peterson, 1996] (cases 1, 2, and 5, this paper). Given that the Kanyawara males had patrolled near the attack site on the evening of the 25th, they were most likely responsible for the death.

Case 5: Attack on a Juvenile Male by Ngogo Males, 9 August 2002

At 0710 hr on 9 August 2002, D. Watts and Ngogo field assistants Alfred Tumusiime and Adolph Magoba found a party that included five adult males, one adolescent male, one adult female with a juvenile, and two adolescent females eating *Cordia millenii* fruit about 1 km southeast of the Ngogo camp. A sixth adult male joined them at 0800 hr. At 0835 hr, the chimpanzees went about 400 m south to a *Ficus mucuso* tree that had a large crop of ripe figs. Other chimpanzees were already feeding there, and more arrived over the next 2 hr. By 1035 hr, when most of the chimpanzees stopped feeding and descended, the party included 14 adult and six adolescent males, six adult and two adolescent females, three infants, and three juveniles.

After resting near the fig, most of these chimpanzees excitedly moved east at 1200 hr, raided a beehive, and obtained a small amount of honey. At 1220 hr they swept north along a route that Ngogo chimpanzees often follow when they begin to patrol along the northern and northeastern boundaries of their territory, and also sometimes follow when searching for red colobus monkeys to hunt. This route goes up a tongue of forest that extends into grassland, and then through a short stretch of grassland to forest on the north side of the road to the Ngogo camp. Several individuals, including one adult and one adolescent male, one adult female with an infant, and one adolescent female, stayed behind. The presence of the other females with their dependent offspring led observers to think that the chimpanzees were searching for red colobus. At 1244 hr the chimpanzees encountered a small red colobus group in a valley just south of Ngogo road. They paused briefly but did not hunt; instead, they crossed the road and moved east along the edge of the forest north of the road.

Several females soon fell behind the males, and one female called at 1306 hr. This prompted a chorus of pant hoots from a swampy valley north-northeast of the males. In response, the Ngogo males stopped and excitedly but silently clustered together; all were piloerect and many embraced each other. After a brief pause the males moved northeast again; they were silent, tense, and in close proximity, as on boundary patrols. None of the females stayed with the males, which now numbered 13 adults and five adolescents, although the observers later realized that several had stayed in the area. The males went slowly, and rather than moving directly toward the spot from which the calls had come, they stayed near the top of a hill above the valley. More calls came from the north at 1316 hr, and the callers seemed to be moving away. The Ngogo males paused until 1321 hr, then continued northeast, still staying on the hillside.

At 1326 hr, a chimpanzee broke a branch in the bottom of the valley, about 100 m north and directly below the Ngogo males. The males, which were all close together, engaged in a flurry of embraces and reassurance gestures, then charged downhill to attack the other chimpanzees. The observers followed, only to realize that at least some of the other chimpanzees had fled back up the hill somewhat to the east, and that the Ngogo males were chasing them. By the time the observers caught up with the males, all adults from the other community had escaped. Their calls were audible as they fled to the north. However, the Ngogo males had caught a juvenile male that was probably about 6 years old, and many were hitting, biting, and stomping on him. This attack lasted about 1.5 min before an adult male dragged the juvenile downhill. This action occurred too quickly for observers to be certain who dragged the juvenile, but whoever it was released him when he reached the valley bottom, where the juvenile, dazed and bleeding from multiple bite wounds, was slowly walking, surrounded by Ngogo males. Over the next 5 min, Ngogo males attacked the juvenile three more times. All of the attacks were briefer than the initial attack, and at least two involved multiple attackers, but the vegetation in the swamp was too dense, and the chimpanzees were moving too fast as they again grabbed and dragged the juvenile, for the observers to be certain of who participated.

The last of these attacks occurred at 1335 hr. After this, the juvenile sat in the swamp, bleeding from a puncture wound in the middle of his forehead and from multiple bite wounds (some of them deep punctures) on his ears, neck, shoulders, hands, and feet. He started to walk weakly through the swamp, with the Ngogo males following but not touching him, and crawled into a dense thicket, where he lay down at 1340 hr. Several Ngogo males looked into the thicket between then and 1350 hr, but did not enter it. The observers did not try to get close enough to the juvenile to see the full extent of his wounds.

Several of the Ngogo males moved back south as the attack ended, but did not go far. Eight adults and two adolescents stayed at the attack site until 1505 hr, although they initially moved about 40 m north of the juvenile. Between 1350 and 1410 hr, several outbreaks of calls and screams came from the north, where the chimpanzees of the other community had fled, and the Ngogo males called in response; some of the Ngogo males that had moved south also called. At 1412 hr, adolescent male GZ returned to the juvenile and apparently approached him closely. The juvenile screamed, and the eight nearby adults and the second adolescent rushed back to the juvenile also. Adult MG entered the thicket but apparently did not attack the juvenile, which gave a ''pant bark'' [Goodall, 1986] and then whimpered. MG rejoined the other males, which lay down near the thicket. They were still highly alert, but did not respond when more calls (now farther away) came from the north at 1418 hr.

However, the next calls from the north, at 1454 hr, seemed to include several adult males, and it brought the Ngogo males to their feet. Several moved 10–15 m in that direction, then sat and listened. The males called again from the north at 1457 and 1459 hr. The Ngogo males gave several pant-hoot choruses and charging displays in response to the last of these calls, and many charged near the juvenile, although they did not attack him; other Ngogo males also called from the south. At 1505 hr, the Ngogo males gave one last outbreak of calls and displays, then started to move south. As they did, adult males MG and BA charged into the thicket and stomped on the juvenile. At 1518 hr, the males encountered two Ngogo females, each with an infant and juvenile, and at 1615 hr, as they ate *Pterygota mildbraedii* leaves in forest just north of Ngogo road, they rejoined the males that had left the attack site about 2 hr previously. Calls from chimpanzees

from the other community were audible far to the north at 1537 and 1542 hr. The Ngogo males did not respond to these calls.

The juvenile was apparently alive when the Ngogo males left him, but because observers followed the Ngogo males and did not see him again, we did not know his fate. However, given the number and severity of the bite wounds, the severity of the other aggression, and the fact that he had not moved for over an hour (during which time the other chimpanzees from his community moved far away), he probably did not survive. D. Watts's impression was that, as in case 3 (above), the juvenile's wounds were about as severe as those inflicted on an adult male at Ngogo during the fatal intracommunity attack in October 2002 [Watts, 2004].

Other Intercommunity Attacks at Ngogo

As of mid-August 2004, we had documented direct physical aggression during 12 of 95 boundary patrols and eight of 68 other encounters with neighboring communities at Ngogo (Table III) [cf., Mitani & Watts, 1999]. These included four infanticides described in Watts and Mitani [2000] and Watts et al. [2002], and a nonfatal gang attack by males on an unidentified stranger during the boundary patrol that led to the first infanticide [Watts & Mitani, 2000]. In October and November 2004, researchers at Ngogo documented three more lethal attacks on members of other communities during separate intergroup encounters: two infanticides and a fourth lethal coalitionary attack on an adult male. Another infanticide may have occurred during one of these encounters. During another encounter, they saw another serious attack on an adult female and a fight between Ngogo males and stranger males (H. Sherrow, personal communication). The targets of observed attacks have thus included adult males, adult females, juveniles, and infants. At least one of the adult female targets was clutching an infant to her ventrum (attack of 25 June 2003; Table III), and this may have been true in some or all of the other attacks on females. Regardless of whether the males were unsuccessfully trying to grab infants in these cases, they bit the females repeatedly and hit, stomped on, and dragged them. The resulting injuries were probably severe and may have been fatal, but the females were unhabituated and their fates are unknown.

DISCUSSION

Male chimpanzees at Ngogo and Kanyawara patrol territorial boundaries and make incursions into neighboring territories, and patrol frequency is relatively high at Ngogo [Mitani & Watts, 2005; Watts & Mitani, 2001]. They sometimes encounter neighbors during patrols and occasionally encounter them in other contexts. They do not always respond overtly to vocalizations from neighbors, and small parties may move away from even distant callers, but large parties routinely call and display in response, sometimes approach, and may attack the neighbors (this study) [Watts & Mitani, 2001; Wilson et al., 2001]. Observers have repeatedly seen attacks involving physical contact during patrols at Ngogo and have also seen such attacks during other encounters. The targets included adult males, nonswollen adult females, juveniles, and infants, and the attacks led to nine definite fatalities (including cases 1 and 2 above), almost certainly two others (cases 3 and 5), and perhaps more. Two fatalities at Kanyawara are known (case 4 above) [Wrangham & Peterson, 1996].

TABLE 3. Attacks With Physical Contact During Inter-Community Encounters at Ngogo*

Date	Context	Description
Nov. 28, 1998	Patrol	Males attack party of females with juveniles and infants
Feb. 27, 1999	Patrol	Males attack party of females with juveniles and infants
April 3, 1999	Patrol	Males attack unidentified individual (escapes)
April 3, 1999	Patrol	Same males attack lone female, seize infant; infanticide
June 16, 1999	Patrol	Males attack medium-sized party; charges and counter charges, some physical contact
June 28, 1999	Patrol	Males attack lone female; infanticide
July 5, 2000	Patrol	Males attack small party; two infanticides
July 19, 2001	Patrol	Males attack female and juvenile
Aug. 11, 2001	Foraging	Males and females encounter large party charges and counter-charges, at least one male bitten
June 3, 2002	Patrol	Males attack small party, kill adult male (Case 1, this paper).
Aug. 9, 2002	Foraging	Males attack fairly large party; prolonged, probably fatal attack on juvenile (Case 4, this paper).
Sept. 4, 2002	Foraging	Males and females encounter large party; charges and counter-charges, at least one male briefly seized and bitten
Sept. 25, 2002	Foraging	Males and females encounter large party; males attack; at least one adult female seized, bitten, and pummeled in prolonged attack
Nov. 9, 2002	Foraging	Males and females encounter large party; charges and counter-charges by males, at least one male bitten
Nov. 23, 2002	Foraging	Males attack small party; kill adult male (Case 2, this paper)
Dec. 4, 2002	Patrol	Males encounter small party; prolonged gang attack on adult female (attempted infanticide?)
June 25, 2003	Patrol	Attack fairly large party; prolonged gang attack on adult female (attempted infanticide?)
July 4, 2003	Foraging	Males and females encounter party feeding in *Ficus mucuso* in overlap area; males attack; blood on vegetation
Aug. 1, 2004	Patrol	Males and one female encounter party of females and young feeding in *Ficus mucuso*; attack, but no serious injuries; most of same males then make gang attack on adult male and inflict massive, probably fatal injuries (Case 3, this paper)
Aug. 6, 2004	Foraging	Eleven adult males and seven adolescent males approach large party containing multiple males from community to south after hearing calls; meet in overlap area; charges and chases for five minutes with some physical contact but no serious wounds, calls and some displays for another 10 minutes as parties move apart.

*Data comes from late May to mid-August in 1997, 2000, 2001, and 2003; February, 1998 to August, 1999; and late May to mid-December, 2002.

Our observations are consistent with descriptions of territorial defense and intercommunity antagonism, including serious attacks that sometimes lead to fatalities, at other sites (Taï [Boesch & Boesch-Achermann, 2000; Herbinger et al., 2001], Gombe [Goodall, 1986; Goodall et al., 1979; Wilson et al., 2004], Mahale [Nishida et al., 1985], and Budongo [Newton-Fisher, 1999]). Overall, this evidence supports the argument that relations between chimpanzee communities are antagonistic, and that coalitionary aggression against outsiders is part of the evolved behavioral repertoire of male chimpanzees [Wrangham, 1999; Wilson & Wrangham, 2003]. The slow life histories of chimpanzees make it difficult to test proposed functional explanations for lethal coalitionary aggression. The relevant

hypotheses are not mutually exclusive, partly because different hypotheses could apply to attacks on members of different age/sex classes. The attacks on adult males described here and that on the juvenile male are consistent with the ''rival coalition reduction'' hypothesis, as are similar attacks at Gombe [Wilson & Wrangham, 2003; Wilson et al., 2004]. This hypothesis can not directly explain attacks on females–at least in populations like those at Kibale and Gombe, where females do not participate prominently in between-group attacks, although reducing the number of males in a community increases the vulnerability of its females. Long-term Gombe data support the ''resource defense'' hypothesis, which holds that female reproductive success depends on how successful males are at defending or even increasing access to food [Williams et al., 2004]. Assessing how consistent the Kibale data are with this hypothesis will require much longer-term data on demography and individual habitat use than we currently possess, in addition to models of population dynamics based on these data. However, we note that most observed intercommunity encounters at Ngogo occurred in the western, northwestern, and northern areas of the Ngogo territory when one or more of several important food species that are highly abundant in these areas were fruiting. Most of the patrols in our sample (63/95) were to the north, northeast, and/or northwest, in the general areas of the attacks described above [cf., Watts & Mitani, 2001; Watts et al., 2002], and the Ngogo community appears to have expanded its range to the north in recent years. Also, patrol frequency varies positively with ripe fruit availability [Mitani & Watts, in press], which is consistent with the food defense hypothesis.

Serious attacks on adult females are not expected if intergroup aggression functions to attract mates [Williams et al., 2004; Wilson & Wrangham, 2003; Wrangham, 1999]. Likewise, the sexual selection hypothesis, which is broadly supported by data on other nonhuman primate species [van Schaik, 2000], does not obviously apply to intercommunity infanticide in chimpanzees, given the apparent rarity of transfer by parous females [Williams et al., 2004; Wrangham, 1999]. Whether any of the females that were attacked by the Ngogo males and/or whose infants were killed subsequently joined the Ngogo community is unknown, but this seems unlikely. The food defense hypothesis can also explain attacks on females and infants if these induce females to shift or contract their ranges and allow territory expansion by the attacking community [Williams et al., 2004; Wilson & Wrangham, 2003; Wrangham, 1999]. Again, the Kibale data appear to be consistent with this hypothesis, but we cannot as yet test this.

The attacks described here, and earlier infanticides at Ngogo are consistent with the imbalance of power hypothesis. The attackers outnumbered their targets and faced no serious opposition. The Ngogo males immobilized their adult male victims until they were incapable of retaliating. The Kanyawara males apparently also immobilized their victim. No attackers were wounded. Only three of the attacks occurred during boundary patrols, but the hypothesis also predicts that chimpanzees make opportunistic attacks in other contexts when costs are sufficiently low. The Wantabu male apparently was in a small party, and the observers had no indication that other males from his community were nearby. Any males that were in the juvenile's party fled at the start of the case 5 attack. Females present at the start of the attacks in cases 2, 3, and 5 either immediately fled or posed no serious threat to the attackers. The 12 boundary patrols listed in Table III that led to the attacks represent 40% of the 30 patrols during which patrollers contacted neighbors. In 18 other cases, patrollers either heard distant neighbors or retreated when they heard relatively large parties that contained adult males [cf., Watts & Mitani, 2001]. Many of the 68 intercommunity

encounters in other contexts involved only auditory contact between parties separated by at least several hundred meters. The fatal and nonfatal attacks listed in Table III come from a subset of close encounters, during some of which the males surprised smaller parties of neighbors and caught one or more, or engaged neighboring males in back and forth chases without prolonged gang attacks like those described above (Watts and Mitani, unpublished data).

Functional explanations of lethal between-group coalitionary aggression in chimpanzees are controversial, and some critics have argued that human interference is the primary or even the only cause [Ferguson, 1999; Marks, 2002; Power, 1991]. The Kibale data, along with other evidence reviewed by Wilson and Wrangham [2003], make this unlikely. Neither of the study communities has been provisioned. Although Kibale is not a ''pristine'' habitat, it has not suffered encroachment during the history of the research projects from which our data are derived. The Ngogo chimpanzees in particular have no regular contact with humans other than researchers and field assistants. Ghiglieri [1984] did not observe boundary patrolling or coalitionary intergroup aggression at Ngogo, nor did he witness hunts by the chimpanzees. Power [1991] cited Ghiglieri to support her claim that such behavior was absent in unprovisioned populations [cf., Ferguson, 1999]. However, the chimpanzees were only semihabituated, which prevented Ghiglieri from systematically following them when they left trees where they had been feeding, and would certainly have prevented him from following silent chimpanzees on a patrol. Once the Ngogo chimpanzees were habituated, researchers started to follow them routinely wherever they went, and to document extensive hunting along with the kind of intergroup aggression described here [Mitani & Watts, 1999; Watts & Mitani, 2000, 2001; Watts et al., 2002].

We cannot claim to have resolved the question of why lethal coalitionary aggression occurs in chimpanzees. Nevertheless, we concur with Wilson and Wrangham [2003] that aggression, whether between individuals or groups, is a conditional tactic that can facilitate the attainment of strategic goals. Chimpanzees, like other primates, use aggression strategically in response to appropriate environmental circumstances. They exploit and sometimes seek imbalances of power but try to avoid confrontations in which they would face high risks, and whether responses to neighbors are aggressive depends on the relative size of the parties involved [Watts & Mitani, 2001; Wilson & Wrangham, 2003; Wilson et al., 2001; Wrangham, 1999]. Because chimpanzee behavior is highly flexible and the costs and benefits of between-group aggression can vary in response to many factors, we should expect variation in the frequency, quality, and consequences of intercommunity encounters within and across populations in response to variation in the community size, number of adult males per community, mean party size, home-range size, population density, and other factors [Wilson & Wrangham, 2003]. For example, chimpanzees at Taï spend more time in relatively large parties than those in at least some eastern populations [Boesch & Boesch-Achermann, 2000]. This could help to explain why, despite territorial defense and occasional severe attacks during intercommunity encounters there [Boesch & Boesch-Achermann, 2000; Herbinger et al., 2001], fatal attacks on individuals older than infants have not been seen. The balance of power during most encounters may make such prolonged attacks prohibitively costly. Likewise, males in one community at Taï stopped patrolling and avoided neighbors when all but four of the males had died [Boesch & Boesch Achermann, 2000], whereas the large number of males at Ngogo facilitates a relatively high rate of patrolling. Nor is implacable hostility between adult male chimpanzees with no history

of association in the same group inevitable. Male strangers that are carefully introduced to each other in captivity can develop social relationships similar to those of males that have resided together since birth in the wild, including the strategic use of aggression and mechanisms for conflict resolution [de Waal, 1982].

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