



New Cases of Intergroup Violence Among Chimpanzees in Gombe National Park, Tanzania

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Despite considerable attention to chimpanzee intergroup violence, the number of observed cases remains small. We report 4 cases of intergroup violence that occurred in Gombe National Park, Tanzania, between 1993 and 2002. We observed (3 cases) or inferred (1 case) males from the Kasekela community to attack members of their 2 neighboring communities: Mitumba and Kalande. In 1993, Kasekela males killed and ate a female infant from Mitumba. In 1998, Kasekela males captured 2 infants (sex unknown) from Kalande, one of which escaped and the other was killed and eaten. Also in 1998, Kasekela males attacked an adolescent male from Kalande. The victim was alive but severely injured by the end of the attack. The intensity and duration of the attack are comparable to other attacks that resulted in fatal injuries. In 2002, observers found the body of an adolescent male from Mitumba following an incursion by Kasekela males into the area. The injuries inflicted on the Mitumba male together with circumstantial evidence suggest that Kasekela males killed him. The attacks support the view that intergroup violence is a persistent feature of chimpanzee societies and that the primary benefit attackers gain from them is reduced competition for resources.

KEY WORDS: chimpanzee, intergroup aggression, infanticide, coalitionary killing.

Male chimpanzees (*Pan troglodytes*) defend group territories, attacking and sometimes killing members of neighboring communities, including infants and weaned individuals of both sexes (Arcadi and Wrangham, 1999;

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Goodall, 1986; Newton-Fisher, 1999; Watts and Mitani, 2000; Wilson and Wrangham, 2003; Wrangham, 1999). Long-term studies of chimpanzees across Africa have revealed hostile intercommunity relations at all sites with neighboring communities (Boesch and Boesch-Achermann, 2000; Wilson and Wrangham, 2003). Intraspecific violence is one of the leading causes of mortality for chimpanzees (Goodall, 1986; Manson and Wrangham, 1991; Nishida *et al.*, 2003), and it has figured prominently in the ongoing debates on the evolution of human warfare (Alexander, 1989; Ferguson, 2001; Otterbein, 1997; van Hooff, 1990; van der Dennen, 1995; Wrangham and Peterson, 1996). Nevertheless, the sample of known or inferred intergroup killings remains small. Published descriptions of intergroup killings include 13 cases for infants and 9 cases for weaned individuals (Wilson and Wrangham, 2003). Additional cases of severe but nonfatal attacks have been reported by Nishida and Hiraiwa-Hasegawa (1985) and Goodall (1986).

The small number of observed cases of intergroup violence is not surprising, given that in a long-lived, slowly reproducing species such as the chimpanzee, lethal attacks are expected to occur infrequently. The fission-fusion nature of chimpanzee society probably results in a further reduction in the number of observations. Members of a chimpanzee community usually travel in numerous parties scattered across a large home range. Because observers rarely follow more than one party at a time, many events, including intergroup interactions, occur undetected.

While understandable, the limited sample size nonetheless complicates efforts to test hypotheses for why the attacks occur. Some have argued that intercommunity violence is not part of an evolved strategy, but is instead a rare and aberrant response to unusual circumstances, such as intensive provisioning (Power, 1991; Sussman, 1999). However, accumulating data from long-term studies have made it clear that intercommunity violence is widespread in chimpanzees, including at sites that were never provisioned (Wilson and Wrangham, 2003). The widespread occurrence of intercommunity attacks in chimpanzees suggests that such violence, like other forms of aggression, is a strategic option employed when assessment of expected costs and benefits indicates that attack will yield net benefits to the attackers (Archer, 1988; Huntingford and Turner, 1987).

Proposed explanations for intergroup violence in chimpanzees are focused on either the costs or benefits of attacks. The imbalance-of-power hypothesis (Manson and Wrangham, 1991; Wrangham, 1999) focuses on the costs, arguing that intergroup attacks occur because variation in party size creates opportunities for males from one community to kill rivals from another community at low cost to themselves. Playback experiments simulating intruders support the hypothesis, showing that males are more willing to call toward and to approach a lone male intruder when in parties containing ≥ 3 males than when in parties containing only 1–2 males (Wilson *et al.* 2001).

The specific benefits gained by attackers remain unclear (Boesch and Boesch-Achermann, 2000; Mitani *et al.* 2002; Wilson and Wrangham 2003). For example, there are ≥ 3 distinct explanations for the benefits obtained by intergroup infanticide, including (1) the sexual selection hypothesis, in which attackers increase their mating opportunities by inducing the victim's mother to immigrate to their community and/or mate with them in future intergroup encounters (Arcadi and Wrangham, 1999; Nishida *et al.* 1979); (2) the rival coalition reduction hypothesis, in which attackers reduce the future coalition strength of rival communities (Arcadi and Wrangham, 1999; Kutsukake and Matsusaka, 2002; Newton-Fisher, 1999; Nishida and Kawanaka 1985; Takahata 1985); and (3) the resource competition hypothesis, in which attackers either repel (Kutsukake and Matsusaka, 2002; Pusey 1978; Pusey 2001; Takahata 1985; Watts *et al.* 2002; Watts and Mitani 2000; Williams 1999; Williams and Pusey, submitted) or directly eliminate (Boone, 1991; Goodall, 1977; Watts *et al.* 2002; Watts and Mitani, 2000) competitors for food.

Although attacks on infants and weaned individuals are usually treated separately, only the sexual selection hypothesis applies specifically to infants. The other two explanations should apply equally to weaned individuals, with infants differing primarily in their greater vulnerability to attack.

The rival coalition reduction hypothesis (RCRH) and resource competition hypothesis (RCH) share the same basic assumptions: male chimpanzees compete over group territories to gain access to resources, and males seek to expand their territory by repelling members of rival groups during intergroup fights. The hypotheses differ in two respects: (1) the predicted sex of victims, and (2) whether victims should be killed. The RCRH argues that male chimpanzees seek out male victims, and that victims should be killed whenever the costs of killing are low (Nishida and Kawanaka, 1985; Takahata, 1985; Wrangham, 1999). By killing rival males, the attackers reduce the coalition strength of the rival community, thereby increasing their chances of success in future intergroup fights (Wrangham, 1999). In contrast, the RCH predicts that males should attack rivals of either sex, with the exception of adolescent females, which are potential mates (Wolf and Schulman, 1984). The RCH does not exclude the possibility of killing victims, as killing reduces the number of competitors for resources. However, killing is not necessary to gain the predicted benefits. Instead, attackers need only to repel rivals and/or inhibit rivals from making future visits to the region where the attack took place (Pusey, 2001).

In chimpanzees, intragroup infanticide appears largely consistent with the sexual selection hypothesis (Arcadi and Wrangham, 1999; Hamai *et al.*, 1992). Attacks tend to focus on infants whose paternity is in doubt, either because the mother is a recent immigrant (Nishida and Kawanaka, 1985) or has a peripheral range (Arcadi and Wrangham, 1999). After the attacks,

a mother mates more restrictively with the killer of her infant (Arcadi and Wrangham, 1999; Hamai *et al.*, 1992; Takasaki, 1985).

In contrast, intergroup infanticide has not been shown to meet these conditions. Obtaining relevant observations is difficult given that in most cases intergroup infanticide involves attacks on unhabituated females. In only one case—Wantendele of K-group, Mahale—might the mother of an infanticide victim have transferred to the community of her infant's killers (Takahata, 1985). In this case, the female did not transfer until 6 years after the suspected killing of her infant by M-group males (Nishida *et al.*, 1979, 1985). Wantendele remained in K-group until all of the adult males had disappeared (Nishida and Kawanaka, 1985), suggesting that, had the males survived, she would have remained in K-group and thus avoided the costs of transferring, which included the infanticidal killing of her first infant born in M-group (Takahata, 1985)).

Most recent studies have favored either the rival reduction or resource competition hypothesis (e.g., Kutsukake and Matsusaka 2002; Newton-Fisher, 1999; Watts *et al.*, 2002).

We report 4 cases of violent intergroup attacks that occurred in Gombe National Park, Tanzania, between 1993 and 2002 (Figure 1). Observers saw males from the Kasekela community capture 3 infants: one from the Mitumba community and 2 from Kalande. One of the Kalande infants escaped, while the other infants were killed and eaten. In 1998, observers saw and videotaped a brutal attack on an adolescent male from Kalande. In 2002, observers found the body of an adolescent male from Mitumba the day after a large party of Kasekela males spent 5 h in the Mitumba community's territory. The pattern of wounds and other evidence indicate that Kasekela males killed the Mitumba male. Together, the observations provide additional evidence that intergroup violence is a persistent feature of wild chimpanzee societies and help to clarify the specific benefits gained by attackers.

In addition to describing the attacks, we examined the ranging and feeding behavior of the attacking chimpanzees. Intergroup violence in chimpanzees has been described as the result of lethal raids into the overlap zone between neighboring communities (Manson and Wrangham, 1991), sometimes involving deep incursions, in which chimpanzees travel deep (≥ 1 km) into neighboring territory to conduct attacks (Wrangham, 1999). However, few studies have provided sufficient systematic data on ranging to determine the location of attacks relative to boundaries. Likewise, few data are available that would permit a test of whether such attacks were the goal of an incursion, or if chimpanzees happened to encounter neighbors while searching for food. Although it is impossible to know for certain the goals of attacking chimpanzees, we determined the location of the focal chimpanzee's feeding bouts in relation to the location of the attack and community boundaries.

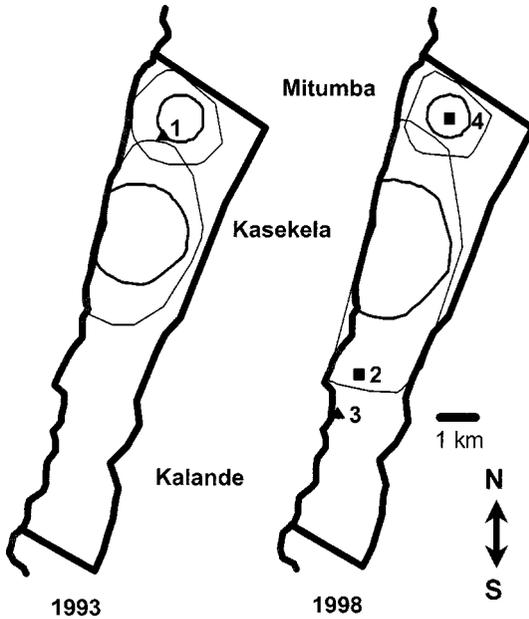


Fig. 1. Locations of attacks on infants (triangles) and adolescent males (squares) with respect to the ranges of the Mitumba and Kasekela communities in the (a) early and (b) late 1990s. Bold lines indicate the park boundary to the north, east and south and Lake Tanganyika to the west. The range of each community is indicated by 2 concentric polygons, enclosing 80% and 99% of locations used by each community. For the early 1990s, ranging data are from 1993 for Kasekela and 1994 for Mitumba (the earliest year for which systematic ranging data are available). For the late 1990s, ranging data are from 1998 for both communities.

METHODS

Study Population and Study Site

Gombe National Park is a narrow strip of land covering *ca.* 35 km², bounded on the west by Lake Tanganyika, on the east by a rift escarpment, and on the north and south by villages and cultivated land (Figure 1). It contains 3 chimpanzee communities, from north to south: Mitumba (20–25 individuals), Kasekela (45–55 individuals) and Kalande (20–30 individuals) (Greengrass, 2000), Fig. 1). Goodall initiated data collection on the Kasekela community in 1960, and data collection by a variety of field assistants and

students has been continuous since then (Goodall, 1986). The birth years of all individuals named in text are in Tables I and II.

Data Collection

Since 1973, observers have conducted all-day focal follows of specific individuals in the Kasekela community, recording party composition, reproductive state, feeding behavior and location at 15-min intervals. Habituation of the Mitumba chimpanzees began in 1986, with data collection becoming more systematic through the 1990s with the introduction of the same methods used in Kasekela. Each focal sample also includes a narrative account of the focal subject's submissive pant-grunts, pant-hoots, copulations, grooming, and displays, and major events among others in the party includ-

Table I. Selected Kasekela chimpanzees and whether they were present at known or inferred time of attack

Name	Sex	Birth year	30 March 93 (Mitumba infanticide)	29 Oct. 98 (Kalande infanticide)	14 Aug. 98 (Kalande adolescent)	26 June 02 (Mitumba adolescent)
Apollo	M	1979	X			X
Atlas	M	1967	X			
Beethoven	M	1969	X			X
Faustino	M	1989				X
Ferdinand	M	1992				X
Freud	M	1971	X			X
Frodo	M	1976	X	X	X	X
Gimble	M	1977	X			X
Goblin	M	1964	X	X		X
Jackson	M	1989				
Kris	M	1982			X	
Mel	M	1984	X			
Pax	M	1977	X	X	X	X
Prof	M	1971	X			
Sheldon	M	1983				X
Tubi	M	1977	X	X		
Wilkie	M	1972	X	X	X	X
Gigi	F	1954	X			
Hillary	F	1984	X			
Hope	F	1970	X			
Jiffy	F	1975				
Patti	F	1961	X			
Schweini	F	1991		X		
Skosha	F	1970	X			
Sparrow	F	1960		X		
Tanga	F	1989	X			
Tita	F	1984	X			
Trezia	F	1978	X			
Darbee	F	1984	X			

Table II. Selected Mitumba chimpanzees

Name	Sex	Birth year
Edgar	M	1989
Rudi	M	1986
Rusambo	M	1989–90
Vincent	M	1976
Konyagi	F	1981
Rafiki	F	1974
Rejea	F	1992

ing patrols, intercommunity encounters and attacks (Goodall, 1986). The narrative notes involve sampling *ad libitum*, which has well-known limitations (Altmann, 1974). The notes nonetheless provide a detailed and useful account of each day's events.

Tanzanian field assistants write narrative notes in Swahili. E. Collins, a Tanzanian fluent in both English and Swahili, has provided English translations of all notes for the Kasekela community dating back to 1993. For each report, we also examined the original Swahili, with help from B. Kissui.

Our study draws heavily on data collected by Tanzanian field assistants. They are hired only if they demonstrate honesty and accuracy during an apprenticeship process that lasts ≥ 6 mo. Before their data can be entered in the long-term record, they are required to learn the identity of all chimpanzees in the study community and the major food plants and local topography (Goodall, 1986, p. 603–608). The 6 field assistants whose reports we used had a median 15 years of experience before making the observations described here ($N = 11$ reports, range = 2 to 26 years experience at time of making the report). Our study also includes some observations from 3 observers at Mitumba who were recently recruited and had not completed training in data collection (D. Cyprian, S. Yohana and T. Paulo).

In addition to field assistant reports, for the 14 August 1998 attack, we had access to videotaped footage. W. R. Wallauer, who recorded the footage, also wrote a detailed report of the incident on the day it occurred. Wallauer has made video recordings *ad libitum* of chimpanzee behavior at Gombe since 1993.

During each focal follow, an observer marks the locations and draws the path of the focal chimpanzee on field maps that show the locations of streams and other landmarks. Since the mid 1990s, the maps have been generated from a basemap constructed via digitized 1:50,000 toposheets, a map of streams derived from stereo aerial photos, and Global Positioning System (GPS) control points.

Concern that the presence of researchers might embolden Kasekela chimpanzees to make deep incursions into neighboring communities re-

sulted in a temporary (2000–2002) moratorium on following them beyond their traditional borders. Despite this policy, Kasekela chimpanzees continued to make deep incursions, resulting in 19 interrupted follows in 2000 and 28 in 2001. To avoid further loss of data, researchers resumed follows into border regions in December 2002.

Range Analysis

We digitized hand-drawn locations of focal chimpanzees via digitizing tablets and Arc/Info (ESRI 1997). We found a median error of 109 m (range: 15–422 m, $N = 146$) between points digitized from hand-drawn locations and ones obtained simultaneously from GPS readings (JGI-CPS, unpublished data).

To estimate the location and extent of community ranges, we used the home range software Biotas (Ecological Software Solutions 2001) to calculate minimum convex polygons enclosing different percentages of observed locations (Jennrich and Turner, 1969). To estimate the total range used each year, we calculated polygons enclosing 99% of locations, thereby excluding overly influential outliers. We calculated 80% polygons to provide an (admittedly arbitrary) indication of where community members spent most of their time. This percentage corresponds to the definition of core by Wrangham (1979) and Wrangham and Smuts (1980), though other studies have defined core as 50% or 75% of locations (Herbinger *et al.* 2001).

To examine whether chimpanzees fed during their incursions into neighboring territories, we plotted the location of the target chimpanzee at the start of each feeding bout: the span of time during which the chimpanzee fed continuously on a particular species of food. Feeding bouts lasted a median 25 min (range: 1 to 156 min). We plotted a circle for each bout, with larger circles indicating longer bouts.

RESULTS

Infanticides

Mitumba

On 30 March 1993, Y. Almasi and C. Alberto followed a large party of Kasekela chimpanzees north into Mitumba (Figure 2). Almasi recorded narrative notes and Alberto recorded map locations and party composition. They conducted focal observations on Patti, an adult female with 2 depen-

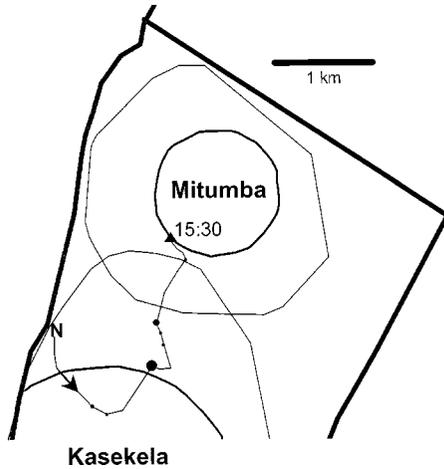


Fig. 2. Close-up of the Mitumba and Kasekela ranges in the early 1990s, with the location of the 1993 infanticide indicated by a triangle and the time of attack. The path of the Kasekela focal chimpanzee is shown by a solid line. The nesting site where the focal chimpanzee was located before dawn is indicated with an N. Arrows indicate the direction of travel. Dots indicate the location and duration of feeding bouts, with circle size proportional to feeding time (1–156 min).

dent female offspring, juvenile Tita and infant Tanga. The party contained 10 adult males, including the current alpha male (Freud), the recently deposed alpha male (Wilkie), and 8 others (Atlas, Beethoven, Frodo, Gimble, Goblin, Pax, Prof, Tubi), and 4 adult females (Hillary, Hope, Patti, and Skosha), a 14-year-old adolescent male (Apollo) and Patti's 2 daughters. Pax was effectively castrated as an infant, possibly during an intergroup attack by the Kalande community (Goodall, 1986, p. 100), and has never reached full adult size.

At 09:15 h, 3 females (Gigi, Darbee, Trezia) and a 9-year-old male (Mel) joined the party. The chimpanzees had nested in the northern part of their range, and soon after leaving their nests traveled further north. Until early afternoon they fed and traveled, producing 3 pant-hoot bouts on arrival at fruit trees, at 07:57 h, 08:35 h, and 12:10 h. After 12:10 h, however, they did not pant-hoot when arriving at fruit trees. At 12:45 h, they chimpanzees reached Rutanga Stream. Gimble's hair was erect as he approached the stream.

At 14:30 h, the party crossed the Rutanga footpath and continued traveling quietly to the north. By 15:15 h the party had reached Mitumba valley, with Goblin leading. At 15:20 h, they heard chimpanzee calls and stopped

to listen quietly. At 15:21 h, Darbee climbed a tree and vocalized, apparently having seen something. Soon thereafter, the other chimpanzees also saw something and they all produced waa-barks and pant-hoots. Many of the males gave roar pant-hoots, displayed and stamped their feet on the ground. The observers moved closer and saw an unfamiliar female sitting in the bushes, producing waa-barks. Based on subsequent consultation with observers familiar with Mitumba chimpanzees, researchers later concluded that she was probably Rafiki, carrying her 4-mo-old daughter, Rejea.

The males immediately surrounded Rafiki and attacked her, kicking her, beating her body and biting her on the head, ears, fingers and toes. Rafiki attempted to protect Rejea by holding her against her chest. Rafiki continued calling for some time, but her calls eventually faded out. The attackers threw Rafiki to the ground and tried to grab Rejea. Goblin kicked Apollo, Gimble and Tubi, which were attempting to take Rejea. After Goblin failed to separate the males from Rafiki, he displayed around the scene. The males continued to attack with their teeth.

At 15:43 h, while Rafiki still held Rejea, Prof killed the infant with a bite to the stomach. The Kasekela males continued to attack. Many of the males produced loud calls, stamped their feet on trees, slapped their hands on the ground, and circled around in the bushes. Freud, Prof, Pax and Goblin held Rafiki down.

At 15:52 h, Prof snatched Rejea from Rafiki. Patti, carrying Tanga ventrally, moved closer to Rafiki and gave waa-barks. When Frodo saw Patti move closer, he jumped up and kicked her 3 times. Patti screamed. Tanga dropped off of her mother's ventrum and climbed a tree. Patti screamed by herself for a short time, then carried Tanga ventrally and moved close to Prof. Patti grabbed Rejea and together with Prof beat the dead infant with her hands. By 15:54 h, Apollo held the dead infant. Prof ran down, beating on trees. The others continued to attack Rafiki, which by this time had stopped calling, leading observers to believe that the attack would be fatal for her.

At 16:15 h the males that were attacking Rafiki paused to display around the bushes, producing roar pant-hoots and waa-barks. Rafiki took advantage of this pause to escape, running to the north. When Prof, Frodo, Freud, Tubi, and Beethoven saw that Rafiki had left they chased after her for about 70 m. They failed to find her and came back producing waa-barks and roar pant-hoots and displaying. Frodo threw a stone weighing *ca.* 1.5 kg with his right hand toward one of the observers, narrowly missing his head. The other chimpanzees followed, carrying Rejea.

By 16:20 h the Kasekela chimpanzees were giving fewer pant-hoots and waa-barks. Goblin took Rejea from Apollo and began to eat her after climbing into a tree. Gimble, Tubi, Apollo and Tita climbed the tree and watched Goblin eat Rejea. The others rested.

At 16:30 h Freud, Frodo, Prof, Patti and Tanga began to travel back to the south. Apollo, Tita and Tubi climbed down and followed the others. Goblin and Gimble remained where they were. Hope and Trezia sat in a nearby tree, watching Goblin eat Rejea. At 16:37 h, Gimble begged by showing his hand to Goblin. Goblin tore off a small piece of meat with his teeth and handed it to Gimble, which ate it. Pax then climbed up the tree and sat close to Gimble and Goblin, watching them eat.

At 16:43 h, Goblin climbed down the tree with Rejea. Pax climbed down, following Gimble, and sat close to Goblin. Pax tore a piece of meat from Rejea's abdomen. Goblin then left the body and walked about 18 m away and sat down eating a little bit of meat. Pax tore off a piece that included skin and fingers. Gimble erected his hair, picked up Rejea's body and tossed it up and then knocked it down, displaying and beating it with his hands. At 16:45 h Gimble saw the rest of the party leaving and followed them, leaving Rejea. The entire party traveled toward the south. The observers stopped to examine the corpse. The attackers had eaten parts of the abdomen and the right arm, but left the rest of the body intact.

Observers from Mitumba next saw Rafiki on April 10th, 11 days after the attack. Her infant was missing and she suffered from facial cuts and a swollen left eye but otherwise appeared to be healthy. She resumed cycling by 29 April 1993 and gave birth on 15 Feb 1994, to an infant that survived only a week before being killed, apparently by other Mitumba females (A. E. Pusey, in prep). Rafiki continued to reside in the Mitumba community and gave birth to twins on 15 March 1995. She and her twins died during a respiratory epidemic in 1996 (Wallis and Lee, 1999).

Kalande

On October 29, 1998 at 06:20 h, S. Yahaya and H. Mkono reached the night nests of Kasekela chimpanzees that had nested deep in the south of their range (Figure 3). They chose Tubi as the focal target, with Yahaya recording narrative notes and Mkono recording map locations and party composition. Four other adult males accompanied Tubi: Goblin, Pax, Wilkie, and Frodo, which gained alpha status in 1997 and remained alpha through the end of 2002. One adult female (Sparrow), and her juvenile daughter (Schweini) were also present. By 06:31 h, they had left their nests and traveled cautiously and quietly south in a patrol.

At 07:00 h they reached a rocky area with trees of *Garcinia huillensis*. For 2 min they watched the trees, their body hair erect. At 07:02 h they saw alien chimpanzees in the trees and ran toward them. A male chimpanzee climbed down very fast, jumped and ran away. When Tubi and the

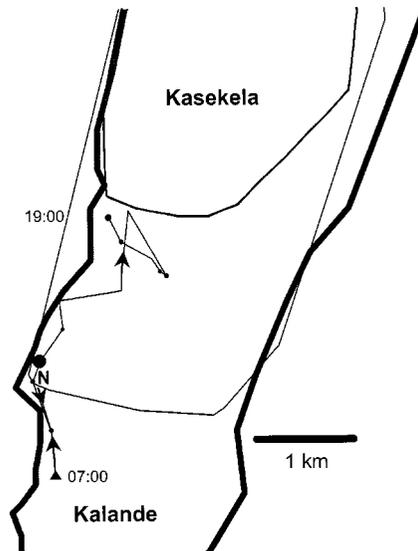


Fig. 3. Location of the 1998 infanticide (triangle) and the path of the Kasekela focal chimpanzee that day, with nesting and feeding sites indicated as in Fig. 2. Much of the southern expansion of the 99% polygon in 1998 is the result of a small number of incursions to the south, including this infanticide and the August 1998 attack on the adolescent male.

others arrived at the trees, they found a mother with a *ca.* 1-year-old infant and another mother with a *ca.* 2-year-old infant. The observers did not record the sex of either infant. When interviewed in 2002, they recalled that the sex of the 2-year old was unknown, but the 1-year old appeared to be female.

After seeing the Kasekela males, the strangers gave loud waa-barks and began to climb down. At 07:03 h, Frodo, Goblin and Wilkie climbed up the trees and intercepted them. The males attacked the strangers, kicking and biting them. The strangers cried out loudly. The males continued to attack the strangers after they were on the ground. Goblin and Frodo each grabbed an infant from 1 of the strangers. Goblin took the 1-year-old and Frodo took the 2-year-old. Both infants cried. The males kicked the mothers whenever they tried to retrieve them. At 07:04 h, Frodo dragged the 2-year-old and threw it approximately 7 m. The mother raced to her infant and ran off with it, disappearing into the undergrowth. Tubi and Wilkie displayed, charging toward them but did not find them.

At 07:05 h, the mother of the younger infant tried repeatedly to grab it from Goblin, but Frodo prevented her by attacking and kicking her. Goblin carried the infant up a tree and killed it with a bite to the abdomen. The mother waa-barked loudly but was surrounded by Frodo, Tubi and Wilkie. At 07:08 h, she climbed the tree and looked at Goblin, which was feeding on her infant. She was shaking. Frodo followed her up the tree and groomed her. At 07:10 h, Frodo stopped grooming her, climbed down, and climbed another tree 10 m away to feed on fruits of *Garcinia huillensis*. The mother climbed down slowly and walked away. No Kasekela chimpanzee followed her.

Goblin continued to feed on the infant and the others begged for pieces of meat, just as they might after a monkey hunt. Goblin allowed both Sparrow and Pax to pull some meat off for themselves, and Sparrow then allowed her daughter Schweini to share. At 09:02 h, Goblin allowed Pax to take a large part of the upper body and head. At 09:04 h, Frodo led a pant-hoot chorus, the first pant-hoot of the day, which was joined by Tubi, Goblin, Sparrow and Schweini. Tubi, Frodo and Wilkie displayed and drummed with their feet on tree buttresses. No reply was audible. Tubi, Wilkie and Frodo pant-hooted again at 09:06 h and listened, as if anticipating a reply from strangers, but none was audible. Frodo begged for meat from Pax at 09:07 h. Pax gave a submissive pant-grunt call to Frodo and they divided the carcass, with Frodo taking the chest and ribs, and Pax remaining with the neck and head. Tubi and Wilkie did not beg for meat and did not receive any. Goblin finished eating his portion of the carcass by 09:15 h, and at 09:25 h began to travel north with Tubi and Wilkie, backtracking along the path they had taken earlier that morning. Frodo and others remained behind feeding on meat until $\geq 10:20$ h. They did not resume feeding on plant foods until 10:45 h, when they were 1 km north of the attack site. After feeding, they continued to move north until 14:30 h and eventually nested 2.7 km north of the attack site.

Attacks on Young Males

Kalande

On 14 August 1998, 4 Kasekela males conducted a patrol to the far south of their range (Figure 4). Three observers were present: C. Alberto and J. Mazogo, and videographer W. R. Wallauer. The party consisted of Frodo, the current alpha male; Wilkie, a high-ranking male that was alpha from 1989–93; Kris, a healthy young male; and Pax. They had nested the night before with 2 other adult males, Freud and Goblin, an adult female, Jiffy, and her adolescent son, Jackson. Alberto followed Kris and Mazogo

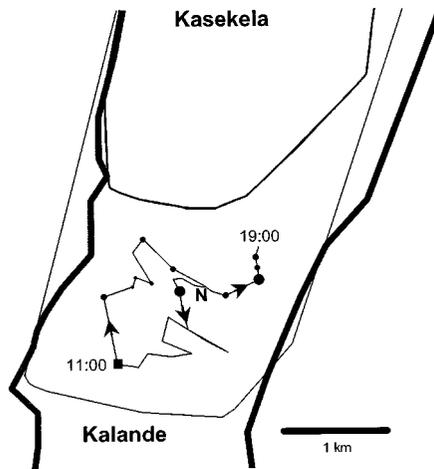


Fig. 4. Location of the 1998 attack on the adolescent male (square) and the path, nesting and feeding sites of the Kasekela focal chimpanzee that day.

followed Wilkie. The focal subjects traveled together for most of the day, providing 2 narrative records for the day's events.

At 06:55 h, Frodo, Kris, Pax and Wilkie left the others behind and traveled to the southeast. At 07:40 h, those left behind pant-hooted, to which Frodo and others responded with grunts. The 4 males then remained silent until the time of the attack, 3 h and 20 min later. At 07:54 h, they stopped to feed on fruits of *Uapaca nitida* but they did not pant-hoot on arrival at the fruit tree. Just before 09:00 h they changed travel direction, returning to the west, moving quietly. While they were foraging, they appeared to be uneasy. They were all very quiet and seemed to be alert and cautious, as if they had recently encountered signs of neighboring chimpanzees. As they traveled south, they stopped often to stare into Nyasanga Valley. They spent long periods looking up and down the valley and listening for calls. More than once, one of them erected his body hair and they reached for one another as if for reassurance. For many min at a time, they sat motionless, staring one way then another. Pax seemed the most eager to continue. He often moved well ahead of the others, and then waited, looking back. The males spotted a group of red colobus but continued patrolling instead of stopping to hunt.

As they descended into the valley bottom, they quickened their pace. On reaching the stream at 10:54 h, Frodo, Wilkie, and Kris had their body hair erect and seemed tense and excited. Just before 11:00 h, Pax spotted a freshly

constructed nest high in the canopy. All changed direction, then stopped and looked into the treetops. Kris stood bipedally and embraced Frodo. At 11:00 h, one of the males waa-barked and plunged into thick vegetation, with a burst of screams and waa-barks following soon after. Kris and Wilkie gave frenzied displays. In the thick vegetation, Frodo sat over the top of a small chimpanzee, *ca.* 10 yr old. The observers initially thought the individual was female, but frame-by-frame analysis of the videotape revealed a clear view of the scrotum and testes. Frodo pounded on the victim with feet and fists while the other males made intermittent waa-barks and roars. Frodo then dragged him into a clearing and sat over him roaring. While the other males emerged from the bushes, Frodo jumped up and down on the victim.

During the next 14 min, Frodo continued his attack, repeatedly beating and stomping on the victim, slamming him to the ground, dragging him during displays, and biting his back, abdomen and groin. Frodo punctuated his attack with ≥ 11 bouts of intense stomping and pounding, usually at the climax of pant-hoots and charge displays. Intermittently, Frodo usually rested, holding the victim by the scruff of the neck, but sometimes continued to crouch over him, biting. Throughout the attack, the victim screamed and whimpered. He occasionally tried to fend off the attackers with his hands and teeth, but in general appeared unable to offer much resistance, perhaps being too badly stunned and injured by the initial beatings. Throughout the attack the chimpanzees appeared to ignore the observers, except on 2 occasions. At 11:02 h, Kris approached the videographer and roared directly into the camera, and at 11:05 h Wilkie charged at and hit the videographer.

While Frodo attacked, Pax sat close by, occasionally hitting or biting the victim. The other males gave frequent charge displays, waa-barks and pant-hoots and sometimes hit or bit the victim but generally kept their distance from Frodo.

About 3 min into the attack, an unusual incident occurred involving competition over access to the victim. Kris approached and shoved Pax away from the victim. Wilkie also approached while Kris chased Pax further from the victim. Wilkie pounded briefly on him then charged away. Kris screamed toward the victim with an open-faced grin. Kris approached the victim again, hit him once with his right hand then crouched down to bite. Frodo still crouched over the victim, biting the back of his neck. Frodo then rose up and displayed at Kris, which backed away with a fear grimace. Pax sat quietly, watching. Kris fled about 1.5 m up a tree trunk while Frodo charged away, dragging the victim. Once Frodo had left, Kris leapt down from the tree and chased Pax. Kris and Pax squabbled again at 11:06 h, when Pax reached out to the victim. Kris approached and sat next to Pax, swiping a hand at Pax, which gave a fear grimace to Kris. Pax moved away, apparently in fear of Kris, which followed him. Frodo continued to bite victim on the

leg. Wilkie and Kris did not join in any further attacks, and by 11:10 h had left, walking back to the north.

Frodo continued to attack the victim for several min, with Pax staying close. At about 11:14 h, Frodo ended his attack and walked away.

Only Pax remained with the victim, which was only slightly smaller than Pax, but so badly wounded by this point that he put up little resistance. At 11:15 h, Pax charged toward victim, thrashing vegetation, then grabbed him and began beating him. The victim screamed as Pax dragged him along the ground. He tried to fend off Pax with his hands as Pax crouched to bite. Pax chewed on the victim's right wrist. Pax then paused and released him. He cried out and moved just a few cm away. He then slowly walked away from Pax and climbed up a tree, finally resting in a crook perhaps 5 m up. Pax climbed a nearby sapling in pursuit. Pax then leapt into the victim's tree and reached out to grab him. The victim screamed. At 11:16 h, Pax pulled the victim down to the ground and immediately resumed beating him.

Soon after, Pax and the victim sat by the stream, 30-40 cm apart. The victim sat quietly, his breathing labored, and looked at Pax. Pax beat the victim again, and stomped on him with both feet. He screamed and bit at Pax's wrist. At 11:18 h, Pax again stomped on and hit him repeatedly, then walked off and sat 0.5 m away. The victim barked and grunted at Pax and briefly leaned toward his attacker. Pax then walked away, leaving him alone.

The victim clutched a branch with his left hand, which was torn and bloodied; a large gash across the palm bled profusely. He walked slowly toward stream, his back and hindquarters matted with blood. He had a bloody gash on his lower left leg and moved gingerly, stumbling on a rock as he crossed the stream. He then concealed himself in thick vegetation.

At about 11:20 h Pax returned, but after a brief look around, he traveled north in the direction the other males had traveled. The observers followed the attackers, rather than staying to assess the victim's wounds, to avoid providing any unintended aid to the attackers in finding him again. Nevertheless, they could clearly see that the victim had many bleeding wounds, and likely also suffered massive internal damage.

Whether they wounds proved fatal remains unknown, though the observers agreed that the victim was unlikely to survive. The attack was comparable in duration and intensity to fatal attacks on members of the Kahama community during the 1970s (Goodall, 1986). Nonetheless, some caution is warranted, as chimpanzees have shown remarkable resilience. For example, in the Mitumba infanticide case described above, Rafiki survived the prolonged and brutal attack with relatively minor wounds and lived for another 3 years.

By 11:40 h, the observers caught up to Frodo, which was traveling northwest. Kris and Wilkie joined a short time later. Within the hour, all were calm

and relaxed, behaving as if nothing out of the ordinary had happened. Pax did not rejoin them that day.

Mitumba

On 27 June 2002, researchers following Mitumba chimpanzees found the body of Rusambo, an adolescent male *ca.* 12–14 years old, which had apparently died the previous day.

Sequence of Events

24 June: Rusambo briefly joined a party of Mitumba chimpanzees (observer: G. Paulo) *ca.* 500 m east of where his body was later found.

26 June: G. Paulo and T. Paulo followed adult female Darbee, which had transferred to Mitumba from Kasekela in 1999. Darbee traveled with Mitumba's 2 remaining adult males, Rudi and Vincent, adolescent male Edgar, and adult female Konyagi. The party traveled to the northwest of Mitumba's range (Figure 5).

09:00 h C. Alberto and I. Issa followed a large party of Kasekela chimpanzees to the Rutanga footpath, 1.0 km south of the site of Rusambo's death (Figure 5). The party comprised 9 adult males (Apollo, Beethoven, Freud, Frodo, Gimble, Goblin, Pax, Sheldon, and Wilkie) and 2 adolescent males (Faustino and Ferdinand). They traveled quietly. The observers remained behind to avoid influencing intergroup interactions. They located the Kasekela males returning to the south the same day at 14:00 h.

10:40 h Heavy rainfall began and lasted until 11:10 h. After the rainfall, Mitumba field assistant G. Paulo entered the forest looking for the researchers following Darbee. At *ca.* 13:00 h, Paulo found a trail of trampled vegetation, *ca.* 40 m from where Rusambo's body was found the next day. Paulo continued searching the area but did not find chimpanzees. At the time of the rainfall, Vincent and the other Mitumba chimpanzees were 1.4 km to the northwest of Rusambo's death site, on the other side of a steep ridge.

27 June D. Cyprian, S. Yohana and T. Paulo followed adult female Konyagi and several other Mitumba chimpanzees. At 13:40 h, Konyagi found Rusambo's body. She looked at the body briefly but made no calls. The other chimpanzees did not appear to see the corpse.

Rusambo lay on his stomach, his right arm outstretched, his face lying on his left arm. Both his legs were stretched and bent backward. The observers initially reported that the eyes had been removed, but post mortem revealed

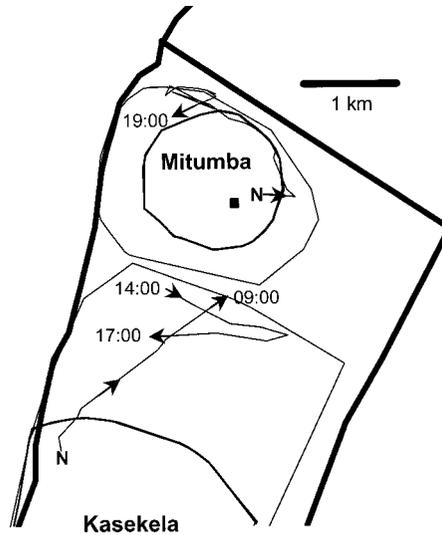


Fig. 5. The paths traveled by focal chimpanzees in Mitumba (northern path) and Kasekela (southern path) chimpanzees on the day Rusambo appears to have been killed: 26 June 2002. The square is where Rusambo's body was found the next day. Ranges are based on data from 2001 for both Kasekela and Mitumba. In 2001-2002, a temporary policy limited follows of Kasekela chimpanzees beyond their traditional boundaries. Accordingly, the Kasekela polygon underestimates the extent of the overlap with Mitumba. Observers in Mitumba occasionally saw Kasekela chimpanzees ranging deep into Mitumba in both 2001 and 2002.

that both eyes were intact, suggesting they had been swollen shut at time of discovery. Observers noted a large wound on the right arm between the shoulder and elbow, and another wound extending from the left shoulder to the neck. Many small wounds and bruises covered the body and hands. The penis, testes and approximately 70% of the scrotum had been removed and were not found near the body. The serrated edges of the wound indicated the scrotum had been torn off. A wound in the tarsus of the right foot penetrated to the bone.

The field assistants returned to the site later that day and carried Rusambo's body back to camp.

28 June: G. Paulo returned to the dragging site and followed the trail of trampled vegetation to an *Albizia glaberrima* tree, 140 m due north from the site of Rusambo's body (measured by GPS). The tree had many vines,

some of which were pulled and torn from the tree, suggesting Rusambo was attacked there and dragged to the death site. By this time Rusambo's body had begun to decompose, so researchers enclosed it in a plastic bag and buried it.

29 June: Researchers exhumed Rusambo's body for examination post-mortem by resident veterinarian Magdalena Lukasik. The following description is based upon her report (Lukasik, 2002). The exhumed body was partly decomposed and covered with maggots. It was nonetheless clear that Rusambo had been in good general health at time of death: well-muscled with considerable subcutaneous fat; teeth, coat and skin in good condition; and stomach full of fruit, seeds and a species of ant commonly eaten by chimpanzees. Rusambo clearly died from extensive traumata rather than disease. An area of 12 by 15 cm on the upper part of throat was dark blue from extensive bleeding in subcutaneous tissue, with no swelling apparent. Most of the damage was to the right side of the throat. Three penetrating wounds surrounded the damaged area (2 on the right and one on the left side), with each wound *ca.* 2 cm deep and 0.5 cm wide. The jugular vein was intact, suggesting that the bleeding had come from smaller subcutaneous vessels. The fingers and toes appeared to be complete. Internal organs including heart, lungs and intestines were intact.

What Killed Rusambo?

The examination post mortem indicated that Rusambo died from wounds, and was otherwise healthy and well fed at the time of death. The only predators at Gombe capable of killing an adolescent male chimpanzee are humans, leopards, and other chimpanzees. None of Rusambo's wounds appeared to have been inflicted by human weapons such as spear or machete, making chimpanzees or leopard the only likely suspects.

Researchers initially considered a leopard the most likely attacker. They sometimes prey on chimpanzees and are capable of killing adult males (Boesch, 1991). No definitive evidence exists for leopards attacking chimpanzees at Gombe in the past 42 years, but recent leopard sightings and other signs indicate that one or more leopards remain active in the park.

Although leopard attack is not implausible, ≥ 4 lines of evidence point to attack by chimpanzees rather than a leopard: (1) wounding patterns, (2) uneaten carcass, (3) dragging and final location of carcass, and (4) known incursion by hostile chimpanzees at the likely time of death.

First, although a precise determination is impossible to make, the overall pattern of wounds appears more similar to ones inflicted by chimpanzees than by leopards. Like other cats, leopards generally kill large prey with a

suffocating bite to the throat (Ewer, 1973; Kingdon, 1977). In contrast, chimpanzees killed by other chimpanzees have suffered numerous canine bite marks, strips of flesh torn from the body, bruises from beating, genital removal, and ripped out trachea (de Waal, 1989; Goodall, 1986; Muller, 2002). Consistent with chimpanzee, but not leopard attack, Rusambo suffered numerous small canine wounds and bruises and had his genitalia removed. The trauma to Rusambo's throat bears some resemblance to wounds expected by leopard attack. However, chimpanzees, can inflict massive damage to the throat of a victim (Muller, 2002). Chimpanzees killed or wounded by leopards have suffered numerous claw marks, including parallel scratches (Boesch, 1991). For example, a 9-year old female killed by a leopard "presented 23 claw cuts all over her body, one cutting the skin of her belly and partly exposing the viscera, two others on the left side perforating her lungs" (Boesch, 1991, p. 226). Contrarily Rusambo's wounds included no obvious claw mark.

Second, leopards routinely eat what they have killed, starting with the soft parts of the prey's belly and chest (Brain, 1981; Pickering 2001; Smith 1977). In contrast to what would be expected from a leopard attack, Rusambo's body appears to have lain undisturbed and uneaten overnight, with only his penis and testes removed. Even if a leopard had been frightened off its kill, it seems likely that it would have returned during the night to feed.

Third, while leopards often transport their prey, the pattern of dragging appears opposite of what would be expected from leopard attack. Leopards typically either take their prey up a tree or drag it ≤ 1600 m to a secluded place (Brain, 1981; Pickering, 2001; Smith, 1977). Instead of being in a tree or in a secluded area, Rusambo's corpse was in an open area: a dry streambed near a trail. He appeared to have been dragged downhill from a vine-tangled tree 140 m away. The pattern of dragging is similar to that in the Kalande attack, and the extensive trampling of vegetation is similar to that surrounding a chimpanzee killed by chimpanzees in Kibale National Park (Muller, 2002, M. L. Wilson, personal observation).

Fourth, a large party of hostile male chimpanzees was within 1 km of Rusambo's death site at the likely time of his death. The party included many of the males that had attacked members of neighboring communities. Rusambo died well within the part of Mitumba visited by Kasekela males in recent months. In contrast, observers reported no sign of leopards—footprints or calls—despite a thorough search of the area.

Observed intercommunity killings have included many loud vocalizations including screams, pant-hoots, roars and waa-barks. Neither the researchers following Darbee nor the researchers waiting for the Kasekela

males reported hearing any such loud calls. All observers were ≥ 1 km from Rusambo's death site and the rugged terrain in the region limits transmission distance of calls. Moreover, a heavy rainfall lasted from 10:40 to 11:10 h; if the attack occurred during the rains, researchers would have had great difficulty hearing any distant chimpanzee call. No blood was near Rusambo's body, suggesting he was killed before or during the rain.

Summary of Ranging and Feeding Behavior

All 4 attacks took place in areas rarely used by the Kasekela community, considering the polygons enclosing either 80% (median: 2105 m; range: 1370–2850 m outside the polygon) or 99% of locations (median: 495 m outside the polygon; range: 410 m inside to 960 m outside the polygon). Only the August 1998 attack occurred within the 99% polygon, and this attack took place along an expanding frontier; the site was only 40 m inside the edge of the previous year's 99% polygon and far beyond any previous year's range.

Chimpanzees spent little time eating plant foods immediately before or after the attacks. On the day of the 1993 infanticide, most of the focal chimpanzee feeding took place before approaching the zone of overlap with the Mitumba community (Figure 2). Only 15 min of feeding occurred within the Mitumba community's range before the attack, and feeding on plants was not observed after the attack. Observations continued until 17:00 h, 1.5 h after the start of the attack. The 1998 infanticide took place early in the morning. The focal chimpanzee ate fruit soon after descending from his night nest (06:35–06:50). The party then traveled further south. They encountered the mothers at 07:00 h and attacked their infants, then returned north, not stopping to feed again until 10:45 h (Figure 3). On the day of the 1998 attack on the young male, the focal chimpanzee fed early in the morning (7:45 h), then proceeded south without feeding. After the attack at 11:00 h, he returned north with the others and didn't feed again until 11:30 h (Figure 4).

DISCUSSION

From 1993 to 2002, observers saw Kasekela males kill and eat 2 infants and severely attacked 1 young male, and the males almost certainly killed a second young male. The attacks share some important similarities. Each of them was unprovoked, and killing or inflicting harm appeared to be the goal of the attackers. In all cases, the attacks took place in areas rarely visited by the attackers. The Mitumba attacks in particular occurred well within the

range of the Mitumba community. In the observed cases, the attackers had overwhelming numerical superiority, with parties containing ≥ 4 adult males attacking victims that were either alone or limited to mothers and infants. The attackers suffered no more than superficial injuries in any case. The attackers spent little time feeding in the border regions, suggesting they traveled to border regions to search for neighbors rather than to feed. The features shared by the attacks are thus broadly consistent with previous descriptions of lethal raiding in chimpanzees (Manson and Wrangham, 1991).

Most or all males present, and to some extent the females, participated in the attacks, indicating that they were not the outcome of individual idiosyncrasy or pathology. Nonetheless, males varied in the frequency with which they were present for attacks, with 3 specific males known or inferred to be present in all 4 cases (Frodo, Pax and Wilkie; Table I). Another 6 males were present for ≥ 2 attacks (Apollo, Beethoven, Freud, Gimble, Goblin and Tubi).

Although the sample of observed intergroup attacks remains sufficiently small and diverse to preclude definitive hypothesis testing, the observations help to clarify which of 3 proposed hypothesis—sexual selection, rival coalition reduction, and resource competition—best explains the benefits gained by attackers.

First, the sexual selection hypothesis predicts that, in the case of intergroup infanticide, the mothers of the infanticide victims should be more likely to mate with the attackers in the future. Neither of the infanticides was followed by observed mating between the mother and the killers of the infant, but only in the case of the Mitumba female Rafiki was the mother known and sufficiently habituated to make strong inference about her mating behavior. Following the 1998 infanticide, 3 females without dependent offspring immigrated to Kasekela, presumably from Kalande (Sifa and Nasa in September and October of 2000, respectively, and Malaika in September 2001). Their ages are uncertain, though Malaika and Nasa appeared to be young adolescents that might have immigrated in any case, rather than mothers of infanticide victims.

Second, the rival coalition reduction hypothesis predicts that intergroup attacks on both infants and adults should be biased toward males. The intergroup killing of Rejea undermines the previously reported male bias in infanticide victims. Determining the sex of an infant victim during the frenzy of an intergroup encounter is difficult. Wilson and Wrangham (2003) found that the sex of 8 of 15 intergroup infanticide victims is unknown. For the 7 victims whose sex was determined, 5 were male and 2 were female, a proportion not statistically different from the expected proportion of 50% (binomial test, NS), which suggests that the apparent male bias is a result of small sample size, much as has been found for intracommunity infanti-

cide in chimpanzees (Hamai *et al.*, 1992). Nonetheless, the costs of making a mistake in identifying the sex of the victim might be low: adult males are unlikely to live the additional 10–15 yr that it would take for female infants to mature and potentially mate with them (Hill *et al.*, 2001). However, attacks on weaned individuals, support the rival coalition reduction hypothesis, in that all but one of 11 weaned victims were males (binomial test, $P < 0.01$).

Third, the resource competition hypothesis does not require the killing of rivals. In support of this view, in most cases of intergroup attacks on weaned individuals, the attackers left while the victim was still alive, even if the victim was known or suspected to have died as a result of the attack (Goodall, 1986; Wilson and Wrangham, 2003). For example, in the observed attack on the Kalande juvenile, the attackers left before killing him, even though they easily could have done so.

A conclusive test of whether chimpanzees intend to kill may be impossible. Moreover, ≥ 3 alternative explanations exist for the failure to kill victims. First, attackers may leave the victim before ensuring its death to reduce the risk of counter-attack by members its community. Second, attackers may accurately assess that they have inflicted sufficient damage to kill the victim, and refrain from wasting additional energy once it is mortally wounded. Third, chimpanzees may fail to kill victims because of cognitive limitations. Chimpanzees have a drastically limited understanding of the concept of death (Boehm, 1992). Like other primates, chimpanzees sometimes carry infants for many days after they have died. When hunting, chimpanzees frequently begin eating prey that is still alive, killing the prey only if necessary to subdue large and dangerous animals such as adult red colobus (Goodall, 1986, p. 290–291).

In conclusion, the cases, together with more recent observations at other sites, indicate that intergroup violence is not limited to the few instances at Gombe in the 1970s and is therefore unlikely to be related to unique factors such as the changes in provisioning intensity in the late 1960s. Second, regarding the costs faced by attackers, in all cases the attackers greatly outnumbered the victim(s), supporting the imbalance of power hypothesis. Third, though the sample remains small, the cases support the view that intergroup violence directed at infants and weaned individuals serves a similar function, though distinguishing the rival coalition reduction hypothesis from the resource competition hypothesis remains difficult. Kills of female infants suggest that the attacks are not simply to eliminate future coalition members, though the cost of making mistakes could be low. The male bias in fatal attacks on weaned individuals supports the rival coalition reduction hypothesis, but the failure to ensure the death of male victims in some cases favors the resource competition hypothesis.



Fig. 6. Torso and lower limbs of Rusambo at the time of post-mortem. Note injuries to the groin area, including removal of genitalia.

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