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Intracommunity Coalitionary Killing of an Adult Male Chimpanzee at Ngogo, Kibale National Park, Uganda

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Intercommunity coalitionary killing of adult and adolescent males has been documented in two chimpanzee communities in the wild, and it was strongly suspected in a third. It may increase survivorship for the attackers, their mates, and their offspring by reducing the combined strength of hostile neighbors and/or by increasing territory size and food availability, and it may help the attackers to attract mates. Lethal coalitionary attacks by males on other male members of their own communities would not provide these benefits and are not expected, given the importance of cooperation among male community members in contests for dominance rank and in both defense and offense against neighboring males. Nevertheless, intracommunity coalitionary killings associated with struggles for alpha rank occur in the wild and in captivity, and observers have seen serious gang attacks on maturing adolescent and young adult males at Mahale and Budongo: the victim in the Budongo case was killed (Fawcett and Muhumuza, 2000). I describe a lethal attack on a young adult male by a large coalition of males from his community at Ngogo, Kibale National Park, Uganda. The Ngogo community is the largest known for chimpanzees and has an unusually large number of males. The attack was not related to a struggle for alpha rank: the victim was low-ranking and the community had a well-established alpha at the time. However, the victim had risen substantially in the male hierarchy over the past few years and might have appeared threatening to many higher-ranking males. Simultaneously, he associated relatively little with most other adult males, had relatively few grooming partners and was not well integrated into the male grooming network, and had no influential allies. The combination of these social factors with the unusual

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demographic circumstances – which presumably meant that mating competition was relatively high and the cost of losing one male relatively low – might have triggered the attack.

KEY WORDS: Chimpanzees; intergroup aggression; males; conspecific killing

INTRODUCTION

Fatal wounding during contests between adult individuals is fairly widespread in mammals (red deer, *Cervus elaphus*: Clutton-Brock *et al.*, 1982; pronghorn, *Antilocapra americana*: Byers, 1997), but killing of adult conspecifics by coalitions of multiple individuals is known only in a few species of social carnivores and primates, including chimpanzees (*Pan troglodytes*; Wrangham, 1999). Researchers have documented coalitionary killing of adolescent and adult conspecifics in chimpanzee populations in Budongo (Fawcett and Muhumuza, 2000), Gombe (Goodall, 1986; Goodall *et al.*, 1979;), and Kibale (Wrangham and Peterson, 1996) and at the Arnhem Zoo (de Waal, 1986) and strongly suspected that similar killings occurred at Mahale (Nishida, 1996; Nishida *et al.*, 1985, and Wilson and Wrangham, 2003; Wrangham, 1999). Adult males have been the main or sole participants, and adult or adolescent males the main targets, in witnessed attacks (Goodall, 1986; Wilson and Wrangham, 2003; Wrangham, 1999). Attacks have usually, but not exclusively, occurred during boundary patrols by groups of males from one community: patrolling males may attack members of neighboring communities if they outnumber their targets sufficiently that the risk of damaging retaliatory aggression is negligible (Wrangham, 1999).

Several proposed functional explanations for lethal coalitionary aggression between communities exist. Whether any of them apply is disputed (Ferguson, 1999; Marks, 2002). However, long-term Gombe data that show a positive relationship between female reproductive success and territory size (Pusey, 2001; Williams *et al.*, 2004) support 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 (Pusey, 2001; Wrangham, 1999; cf. Watts and Mitani, 2001; Williams *at al.*, 2004). Similar logic may apply to intercommunity infanticide in chimpanzees (Pusey, 2001; Watts *et al.*, 2002; Wilson *et al.*, 2004). Also, territory expansion and elimination of neighboring males can lead to incorporation of more females into a community and thus directly increase male mating opportunities (Wrangham, 1999), as apparently happened at Mahale (Nishida *et al.*, 1985), though females may alter their movement patterns rather than associate with neighboring males (Gombe: Pusey, 2001;

Williams *et al.*, in press). Finally, given the existence of potentially lethal aggression, killing dangerous neighboring males can improve survivorship for all community members (Wrangham, 1999).

Because males that belong to the same community depend crucially on mutual support against outside males, and because cooperation between allies in intracommunity competition for dominance rank can provide males with more mating opportunities (de Waal, 1982; Goodall, 1986; Nishida, 1983; Watts, 1998), males are less likely to benefit from lethal coalitionary aggression against other males in their own communities. Nevertheless, several intracommunity coalitionary killings of weaned individuals are documented and others strongly suspected. Fawcett and Muhumuza (2000) described an attack in which multiple males in the Sonso community at Budongo killed a young, low-ranking adult male. They attributed this event to unusually intense mating competition—the community had a socionomic sex ratio close to unity—combined with the male's failure to show sufficient deference to high-ranking males. An ex-alpha male of the Mahale M-Group died of wounds inflicted by chimpanzees, and researchers inferred that he was the victim of an intracommunity attack (Nishida, 1996). They had previously witnessed a severe attack on him after he had been deposed from the alpha position. De Waal (1986) documented a fatal coalitionary attack on an adult male that marked the culmination of a struggle for the alpha position in the Arnhem Zoo chimpanzee community. Mahale researchers also saw a severe attack by 5 adult males, 2 adult females, and one adolescent male on a young, low-ranking adult male that, while not fatal, led to his prolonged ostracism (Nishida *et al.*, 1995). They speculated that the attack also resulted from the male's failure to show sufficient deference to higher-ranking males.

I witnessed an attack in which many adult males in the chimpanzee community at Ngogo, Kibale National Park, Uganda, fatally wounded another adult male member of their community. Like the fatal attack at Budongo and the non-fatal attack at Mahale, the killing was not associated with a struggle for alpha rank in the community. However, the victim was both ambitious and socially peripheral, a combination of characteristics that might have led other males to target him in response to elevated male-male competition in the extremely large Ngogo community.

METHODS

Kibale National Park is located in western Uganda between 0° 13' and 0° 41' N and 30° 19' and 30° 32' E. Ngogo is in the center of the park. Butynski (1990), Struhsaker (1997), and Lwanga *et al.* (2000) provided

detailed descriptions of the study area, which comprises a mix of mid-altitude mature forest, forest at various stages of regeneration from past disturbance, *Pennisetum purpureum* grassland, and other, less extensive vegetation types. The Ngogo community has been under continuous observation since 1993 and is the largest ever documented in the wild (Mitani and Amsler, 2003, Watts, 1998, 2000; Watts and Mitani, 2001). At the time of the attack (October 29, 2002), it had 23 fully adult and 16 adolescent males and a total of about 150 members. Several of the adolescent males, though not yet fully grown, outranked the lowest-ranking adult males.

Starting in early June, I had observed chimpanzees for >1,300 h in 132 days in 2002 before to October 29. Mostly this involved focal samples of adult males and estrous females, but I also collected all-occurrences and *ad libitum* data on events that are particularly informative about social dynamics or relatively infrequent—pant grunts, hunts, boundary patrols, male charging displays—or both. All Ngogo males and many of the females and their dependent offspring are well habituated, and males typically tolerate human observers within 5–10 m. The attack took place in mature forest with an open understory, and field assistant Adolph Magoba, filmmaker Bill Wallauer, his assistant James Mukera and I saw it from only a few meters. I videotaped most of the attack and filmed the victim for most of a half-hour period after he managed to escape his attackers and took refuge in a tree. The description here is based on notes I took at the time and on analysis of the video record.

RESULTS

Immediate Background to the Attack

The target was a young, but fully mature, adult male, GRA, first identified as an adolescent in 1995. GRA was low ranking – he ranked 16th in the male dominance hierarchy, tied with one other adult and above 6 adults and all adolescents (Watts, unpubl. data) – but had risen substantially in the previous several years, during which he reached full adult size. GRA had belonged to the western subgroup among the Ngogo males (Mitani and Amsler, 2003) and spent relatively large amounts of time apart from other adult males, with the exception of OR, another young male, also ranked 16th, which was his closest associate. Observers had last seen GRA on October 14. He traveled for several days with a large party that included most of the top-ranking males. On October 14th, he accompanied 13 other adult males on a boundary patrol that fit the description of a deep incursion (*sensu* Goodall, 1986; cf. Wrangham, 1999): the males traveled quickly and silently

to the eastern periphery of their range; entered areas where observers had previously known them to hear or to meet members of another community; continued to travel east, then south, for several hours and, alternately, to sit and listen intently; and maintained high vigilance. They did not encounter extra-community chimpanzees, and they scattered after returning to the west and re-entering the central part of their territory. Between then and October 29th, observers saw all adult males in the community except GRA and OR on ≥2 days. OR was also not seen between the 14th and the 29th, and we assumed that he and GRA were together much or all of that time.

Many chimpanzees congregated south and slightly southwest of Ngogo camp on the afternoon and evening of October 28th. They scattered early in the morning of the 29th, and many moved rapidly to the west and southwest singly or in small parties. At 0810 h, adult males BS, DZ, and MO and adolescent males COR and GTZ arrived at a *Ficus mucuso* in the west-central part of the study area that contained a large amount of ripe fruit. They met 5 other adult males (BF, HA, MI, MW, ST) and two adolescents (MOR, RAH), which were already feeding in the tree. By 0920 h, 6 other adult males (alpha male BT, DO, GA, HO, PA, PI), one adolescent male (DX), and 2 estrous females (FL, SE), one with an infant, also arrived at the tree. Between then and 0950 h, the males fed, groomed, rested, and mated with both females.

Of the 14 adult males that fed at the fig, all except PA had associated with GRA on October 14. Of those with which he had associated on the 14th, all but BS had accompanied him on the boundary patrol that day. Adolescent MOR, which was nearly fully grown, had also been on the boundary patrol.

At 0950 h the chimpanzees suddenly moved west from the fig tree. The males did not all stay together, but kept in vocal contact. Adult males BT, BF, GA, HO, MW, PI and adolescents COR, DX, GTZ stopped to rest and groom at 1000 h. GA and COR were somewhat apart from the others, which formed a single cluster. Many other chimpanzees, including ≥6 adult females with infants and/or juveniles that had not been in the fig, were nearby.

At least 2 males pant-hooted from about 200 m to the west at 1015 h. The resting males looked in that direction, but did not otherwise respond. Subsequent events revealed that OR and GRA were there, along with adolescent males BRA, RO, and WAL, that we also had seen earlier in the day. They had presumably been farther to the west and might have been approaching when the calls were made.

At 1020 h, beta male HO charged at BF, MW, PI, and GTZ, interrupting a grooming bout between BF and MW; they avoided him. BT, which was resting behind HO, did not respond. All the males resumed resting within one min.

The Attack

At 1021 h, an unidentified chimpanzee screamed about 75 m to the west of BT, HO, and the other resting males. All immediately ran towards the sound, screaming, with HO in front and BT last, and observers lost sight of them for about 30 sec. When we caught up with them, of the males that we had seen earlier that morning had surrounded and were attacking GRA; several of them held him by the arms and legs and were biting and hitting him. OR was nearby, but stayed $\geq$10 m from the attackers.

The attack lasted about 5 min. GRA screamed and gave wah-barks throughout, twice tried unsuccessfully to escape, and repeatedly pushed at attackers, but apparently did not bite any of them: none were visibly wounded. The attackers and bystanders also repeatedly screamed and gave wah-barks. BF, MW, and PI were the main attackers: all 3 were prominently involved in immobilizing GRA and bit him repeatedly. MW was the 7th ranking male and a former alpha, while BF was 9th ranking and PI ranked below GRA. BF probably bit GRA more than any other did and probably inflicted the most damage. MW and PI also inflicted major wounds. At one point, PI pulled strongly on GRA's leg and bit his foot several times while other males pulled GRA's forelimbs in other directions, pinned him to the ground, and bit his shoulders, head, and thorax. Adults BT, MI, MO and BS also bit and hit GRA and helped to immobilize him. MO and MI participated throughout the attack, though both briefly broke away from the attacking group several times before joining in again. Alpha male BT made contact with GRA at the start. For much of the next 2 min, though, he mostly stayed on the edge of the circle of attackers, in contact with some of them but not necessarily with GRA, or he displayed away from the attackers, then returned. However, when BF re-escalated the attack after the second lull, BT joined in vigorously; he hit, bit, and held GRA repeatedly thereafter. BS, a young but high-ranking male (8th rank), also stayed in the circle of attackers throughout the attack. For some of the time he did not try to make contact with GRA, but he also intermittently held, hit, and bit him.

HO participated in the start of the attack, but moved away from the others within the first minute. He continued to display nearby and chased females or adolescent males or both several times, but did not rejoin the attack. PA and DO were near the scene but apparently did not participate in the attack (unless they had done so, but already moved away from GRA, in the first few seconds before observers arrived). Low-ranking ST stayed on the edge of the attacking group for *ca.* 1.5 min and made physical contact with several of the attackers (stretching his arm out to them, embracing them, or placing an arm on their backs or shoulders from behind), but apparently did not make contact with GRA. DZ, the lowest-ranking adult male,

stayed in the attacking group throughout, made repeated physical contact with attackers, and at least once touched GRA with his arm, but apparently did not bite him. Notably, high-ranking adult male HA apparently did not participate in the attack.

Adolescent MOR was also in the attacking group and contacted GRA several times, but he might not have bitten him. After *ca.* 2 min, he climbed 2 m up a small tree above GRA and his assailants. He descended and stood at the edge of the group of attackers *ca.* 1 min later. There he screamed and stretched his arm out towards several of them appeasingly. Whether he was trying to protect GRA or just himself was unclear, but he did not direct aggression at any of the attackers. Instead, MO charged at him; he fled, and MO chased him away from the scene. MO immediately returned and rejoined the attack; MOR did not, but stayed nearby.

Young adolescent ROL, which had apparently been with GRA, stayed next to the attackers for *ca.* 1 min before he fled from them. During that time he briefly climbed into a small tree over GRA and the others, stretched out an arm towards them while screaming, and even hit alpha male BT lightly, but he neither participated in the attack nor seriously tried to defend GRA.

GRA pushed at his attackers for about the first 30 sec, but then simply sat or crouched, and he was supine for *ca.* 20 sec in the middle of the attack. He was effectively immobilized most of the time. The 7 main participants—BS, BT, MI, MO, and, most notably, BF, MW, and PI—all helped to immobilize him by holding and pulling on his forelimbs and hind limbs, holding his shoulders, using their combined mass to pin him to the ground, and simultaneously attacking from several directions. Their actions resembled behavior during gang attacks on extra-community males (Goodall, 1986; pers. observ.) and allowed them to bite GRA with impunity.

However, GRA was not completely immobilized throughout the attack. *ca.* 1 min after observers arrived, all attackers briefly broke contact with him. He tried to flee, but BF, MW, and PI grabbed him, with others quickly joining them. *ca.* 1 min later the males again temporarily ceased their attack. Several surrounded GRA while he sat and screamed. BF (also screaming) stood over him and put his arm on GRA's shoulder while reaching towards some of the other males (directly towards MI) in what looked like a request for reassurance or even a protective gesture. Any protection was short-lived, though: BF himself resumed the attack after only a few sec by biting GRA in the shoulder, and others quickly joined in again, with PI the first male after BF to bite GRA. *ca.* 15 sec later, all males again briefly ceased hitting and biting GRA. He sat and screamed, while MW semi-embraced him from behind and other males displayed or embraced each other or both or reached towards each other for reassurance. MO approached MW from behind, sat down, and embraced him. Meanwhile, BF, which had moved away from

GRA, displayed back towards him, circled around him, then reared over GRA from the side, seized him by the shoulders, hit him, and again bit into his shoulder. BS immediately also rejoined the attack, and hit and bit GRA more intensely than he had done before that point. MW and BT quickly followed BS. BT, which had broken off his assaults to display next to the attackers and to embrace ML and MO, escalated the intensity of his physical aggression at that point. The last lull came *ca.* 30 sec later. GRA stood and tried to move away, but BF grabbed him from behind, pulled him backwards, and again bit him, and other males immediately also resumed attacking him. Finally, *ca.* 30 sec later, the attackers again loosened their grips and GRA again tried to flee. They did not restrain him, though all ran alongside or after him, and he ran *ca.* 15 m and climbed 6 m up a small tree.

HA, ML, and PI immediately followed GRA up the tree. HA was closest to GRA and stayed next to him until GRA descended. OR also stayed nearby, on the ground. For *ca.* 10 min, most of the other males, now including DO and PA, stayed nearby, and several displayed on the ground or in other small trees nearby. Several adult females with infants or juveniles or both, which had been in the area but had not tried to approach the males while the attack was ongoing, climbed trees close to GRA and watched him. Many chimpanzees, including GRA, continued to give wah-barks. At 1026 h, ML and PI climbed to $\leq$2 m of GRA. HA then stood above them and gave a branch-swaying display, at which they descended. He seemed to make contact with GRA during his display and certainly did afterwards, but did not bite or hit him. HA then sat in the center of the tree, immediately below GRA. At 1028 h, GRA climbed about 2 m higher and into a second tree; HA followed and again sat under him. GRA at first sat there, then lay supine, with his back, shoulders, and hips supported by the trunk and main branches and his forelimbs and hind limbs draped over other branches. He started to lick the wounds on his hands. When GRA sat up again, and as he did, HA put his right hand on the branch on which GRA's left thigh rested and might have touched GRA; GRA screamed, extended his left arm down towards HA, and touched HA on the shoulder as if seeking reassurance. Throughout this time, GRA appeared fearful of HA, but HA did not threaten him and seemed to protect him.

At 1110 h, GRA slowly climbed down to the ground. By then, all other adult males except HA and OR had moved out of sight, mostly to the west, though they were $\leq$100–200 m away. Several females were still watching GRA. GRA started to walk east slowly, with HA and OR following closely behind. He turned to the south after going *ca.* 200 m. He continued to walk SSE, with occasional pauses, until 1230 h, by which time he was about 2 km from the attack site. HA and OR stayed with him all the way, and HA remained close to GRA while GRA rested, groomed his wounds, and ate

fallen *Monodora myristica* fruit, until 1550 h. A heavy thunderstorm broke than, and A. Magoba, who had stayed with GRA, lost him in the storm. Observers did not see him again, nor has he been seen as of February, 2004. On November 9th, 2002. Ten days after the attack, we found a chimpanzee skeleton, freshly stripped of most soft tissue by safari ants, in the area where we last saw GRA.

Most of the attackers were together on October 30, when several males that had not been present for the attack joined them. Field assistants saw HA by himself that morning; he rejoined most of the other males on the 31st. Observers next saw OR on Nov. 6th, when he joined a large party that included 13 other adult males in the central part of the study area.

During the attack, GRA received at least the following wounds:

1. 10-cm long, deep, dorsolateral gash on the R thigh.
2. 10–12-cm long gash along the lateral side of the L shin.
3. A deep canine puncture in the frontal region, at the midline of the brow ridge.
4. Multiple punctures and slashes in both ears (also, blood was apparently coming from inside his L ear).
5. Multiple punctures and slashes on the digits and dorsal surfaces of both hands and feet and on both heels, both palms, and both soles. Most of the wounds seem to have occurred either while GRA was sitting and some males held his outstretched arms or while he lay prone, or reclining laterally, under the weight of several males and others grabbed and bit his feet.
6. A 6–8-cm ventrolateral canine puncture/slash to the ribcage on the left side of his chest.
7. A 5-cm canine puncture/slash in his left armpit.
8. Multiple bite wounds, including deep punctures, in both shoulders. These were inflicted from various directions, apparently mostly or entirely while GRA was sitting, but seemed to be mainly lateral and dorsal.

He might also have received other wounds on his arms and legs. Also, attackers repeatedly pummeled him with their hands and might thereby have inflicted internal damage. Several wounds, especially those on his shin and thigh, bled profusely.

Social Background to the Attack

All males at Ngogo regularly associate with each other. However, the community has also shown spatial and social sub-structuring among males,

including a western subgroup of several adults and adolescents, which have been relatively close associates (Mitani and Amsler, 2003). GRA had been a western male, and he and OR were somewhat peripheral even within this subgroup, though they were not the most peripheral males (ibid.; Watts, unpubl. data). For example, during 2002, I saw GRA on 44% (58/132) of all observation days. This was below the mean for all adults (50% of days), but I saw 7 others, including OR, RU (the oldest male at Ngogo), DZ (the lowest-ranking adult), BRU, which was younger than GRA, and LO, a high-ranking former alpha male, on fewer days. GRA and OR had consistently been closest associates to each other since at least 1999, and neither associated particularly often with any other males, though BF and PI were among their closest other associates (Mitani and Amsler, 2003).

Perhaps more importantly, GRA rarely groomed with other adult males when he associated with them, and he rarely formed coalitions. Adult males gave and received grooming from a mean of 15.6 adult male grooming partners in 2002 (s.d. = 4.5 for grooming given and 4.8 for grooming received). GRA groomed only 10 other males, received grooming from only 8 of them, and had a total of only 10 grooming partners. Only 2 males groomed fewer partners, and only 3 received grooming from fewer groomers. The number of grooming partners varies positively with male rank at Ngogo (Watts, 2000, unpubl. data), and GRA outranked all males with fewer grooming partners. Still, he spent proportionately less time grooming with other adult males than all but 3 other adults did, and contrasts with several of his peers were striking. BS, about 4 years older and already much higher-ranking, groomed 21 males and received grooming from 20 of them. GA, also about 4 years older and present on fewest observation days of all males in 2002 before the attack (n = 37), nevertheless groomed 17 other adults and was groomed by 14 of them, and spent a considerably higher percentage of time grooming with adult males than GRA did. OR, about the same age as BS and GA, groomed 14 males and received grooming from 12 of them despite being observed on fewer days (n = 46) than GRA. I saw GRA and OR give 5 joint charging displays at other males, 3 initiated by GRA and 2 by OR, in 2002. GRA initiated 2 charging displays that BF joined, and once joined BF, while GRA and GA each joined the other once and ML once joined GRA when GRA charged other males. Most low-ranking males at Ngogo rarely, if ever, join coalitions, but some that rise substantially in rank, e.g., BS, ML, are more active in coalitions and have more coalition partners than GRA did.

GRA received more aggression from alpha male BT than from any other male, and received aggression from beta male HO at the second highest rate. This was not unusual: all males received aggression at the highest dyadic rate from either BT or HO. None of the other males involved in the attack

gave aggression to GRA at unusually high rates, nor did he seem to be challenging any of them at the time of the attack. GRA regularly gave pant-grunts (formal signals of subordinate status) to BT, HO, MW, BS, and ML. GRA responded submissively to aggression from these males, and was not aggressive to them. He responded submissively to aggression from BF and MO, but I had seen him pant-grunt to BF only once in the previous 5 mo, though they were often together, and I had not seen him pant-grunt to MO. Pant-grunts are uncommon in many dyads of mid-to-low-ranking males at Ngogo, and both aggression and submission were unidirectional between GRA and BF and between GRA and MO. Still, BF and MO might have perceived GRA as a potential challenger.

BF, a principal attacker, was GRA's top grooming partner, though this might have been a sampling artifact: I probably missed much grooming between GRA and OR, his second-ranked partner, when they were off by themselves. MO and ML, also were heavily involved in the attack, were his third and fourth-ranked grooming partners.

GRA displayed at females relatively often (Watts, unpubl. data). However, his mating success—proportion of copulations achieved—was not unusually high. Mating success is positively related to rank at Ngogo, especially during periovulatory periods (Watts, 2003, in prep.), but GRA actually obtained relatively few periovulatory copulations with 3 parous females that were cycling during 2002 compared to the proportion expected for his rank.

DISCUSSION

The intensity of the attack on GRA and the number of attackers involved far surpassed any previously observed intracommunity aggression at Ngogo and resembled gang attacks on extra-community males. Observers at Ngogo have seen other intracommunity fights in which $\geq$2 males attacked and wounded single males, and GRA had been involved in $\geq$2 such incidents. On August 11, 2002, GRA and OR were attacked by 10 other males, though the attackers focused their attention on OR as GRA fled. GRA and OR had been feeding with all the attackers in a *Ficus mucuso*, but had gone west alone *ca.* 5 h earlier; the other males charged at them when they were re-united. HO was the main attacker, and BF, BS, BT, HA, MI, MO, and PA also participated, though OR also solicited support from BF and the HO/OR fight ended as HO chased BF. OR received several wounds on his hands and feet. On June 21, 2001, GRA had given a series of charging displays while traveling with 17 adult and 13 adolescent males that were with an estrous female. His displays were directed to adolescent males and females and were not close to any high-ranking males. However, when he walked

into a cluster of 7 adult males, including BF, BT, MW, MO, and PA, sitting below the estrous female, BF attacked him and the other males joined BF in chasing GRA on the ground and through the canopy. The ensuing mêlée lasted several minutes, and GRA received several bite wounds. However, in neither these nor any other incidents did males cooperatively immobilize their target as they did GRA in the fatal attack, nor did so many males try to inflict damaging wounds.

Nevertheless, the attack was less severe than 2 inter-community killings of adult males at Ngogo in 2002 (Watts, Mitani, and Muller, in prep.). In those cases, males kept their targets immobile until they were incapable of running away and continued the attack until they died. Circumstantial evidence from a third inter-community killing in Kibale, at Kanyawara, also indicated that the attackers immobilized their victim (notably, most of his wounds were ventral) and that he died during or shortly after the attack (Muller, 2002; Watts, Mitani, and Muller, in prep.). However, no absolute dichotomy exists in which intercommunity fatalities are immediate, but intracommunity targets survive the attack only to succumb to their wounds later. For example, several victims of intercommunity killings at Gombe did not die immediately, while the intracommunity attack on Luit at the Arnhem Zoo was not immediately fatal (de Waal, 1986), but that at Budongo was (Fawcett and Muhumuza, 2000). Ntologi, the victim at Mahale, did not die immediately, but was apparently unable to leave the attack site (Nishida, 1996).

Tensions related to a challenge for alpha rank can be ruled out as an explanation for the attack. The two highest-ranking males at Ngogo participated, but GRA had not been challenging either. Nor had he previously been alpha, so the attack could not have been retribution for a long history of past aggression received from GRA, as might have been the case at Mahale (Nishida, 1996). However, some participants might have perceived GRA as a threat to their status, and the history of previous coalitionary attacks on him could indicate that the attack involved forestalling challenges. That he was relatively non-gregarious, had few grooming partners, and did not groom extensively even with most of them, and had not developed effective alliances with any mid-to-high-ranking males could have made him an attractive target. The contrast between GRA and DZ, the lowest-ranking adult, is suggestive in this regard. DZ had the fewest grooming partners of all adult males, spent proportionately the smallest amount of time grooming, did not participate in coalitions at all, and received aggression at relatively high rates from many males. Yet observers have never seen other males mount coalitionary attacks on DZ, which is unusually small and has never challenged another male during the history of observations at Ngogo. DZ regularly pant-grunted to most adult males, was especially deferential to mid-to-high-ranking males, and was subordinate to several older adolescents in 2002.

Aspects of GRA's behavior and social relationships resembled those of Jilba, the ill-mannered male subjected to severe, but non-fatal attacks at Mahale that Nishinda *et al.* (1995) interpreted as punishment. However, fatal punishment would not be expected because chimpanzee males depend on fellow community members for support in potentially lethal aggression between communities. Also, punishment technically involves costly behavior by dominants that imposes greater costs on subordinates and eventually induces cooperation from subordinates (Clutton-Brock and Parker, 1995). Dead subordinates cannot cooperate. Instead, the extremely large number of males at Ngogo might have led to extreme targeted aggression or perhaps extreme scapegoating (de Waal, 1982) without a need to induce cooperation from GRA. The presence of so many males might have raised the stakes with regard to intracommunity mating competition. Ngogo has about twice as many adult females as adult males, but a female with a full sexual swelling can have all sexually mature males in the community traveling with her and trying to copulate with her, and Ngogo females within 4 days of detumescence and presumably periovulatory (Goodall, 1986) have copulated with $\geq$20 adult and 5 adolescent males in a single day (Watts, unpubl. data). When only one female is sexually receptive, the operational sex ratio (number of males ready to mate/number of females ready to mate) at Ngogo can thus be much higher than that at Budongo when male Zesta was fatally attacked there (Fawcett and Muhumuza, 2000). Zesta had been the main copulatory partner of the only female in estrus at the time, and Fawcett and Muhumuza (2000) speculated that this contributed to the severity of the attack. Nothing similar could have immediately precipitated the attack on GRA, but unusually intense mating competition might have been an underlying factor. Further, although success in inter-community aggression generally depends on the number of males (Boesch and Boesch-Achermann, 2001; Wrangham, 1999), the extremely large number of males at Ngogo means that loss of a single male has little effect on their ability to compete with neighbors.

GRA's fate could indicate the difficulties that maturing male chimpanzees face as they try to integrate themselves into the social networks of adult males and how extreme the consequences of failure to do so can be. However, ruling out some explanations that appeal to social strategies, e.g., competition for alpha status, does not mean that another seemingly consistent with the data is necessarily correct. Even if the attack was an outcome of mating and status competition, escalation to the point of inflicting fatal wounds might have been a mistake that happened when the other males passed some psychological threshold, involved in gang attacks, past which they temporarily could not restrain the intensity of aggression. Aggression can be even more intense in intercommunity lethal attacks, which argues

against the mistake hypothesis, as does the fact that the attackers paused several times. The number of known cases of fatal coalitionary aggression in chimpanzees is still small, which makes distinguishing among optional explanations – not all mutually exclusive – difficult, but careful comparative analysis (Wilson and Wrangham, 2003; Wilson *et al.*, 2004; Wrangham, 1999) does not support the claim that lethal aggression in chimpanzees is unnatural behavior interpreted according to prevailing cultural biases (Marks, 2002). Only continued long-term research can provide satisfactory explanations and can effectively address this criticism.

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