

Infanticide in Chimpanzees: Review of Cases and a New Within-group Observation from the Kanyawara Study Group in Kibale National Park

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ABSTRACT. A prolonged attack on a mother and 2-year-old infant that resulted in the death of the infant was observed in the Kanyawara study group in Kibale National Park. The mother was a border-area resident who was first observed associating with unit-group males six years previously. The attackers were an adult male and an adult female with a 6-week-old infant clinging ventrally to her. The attack was unusual in several respects: it is the first time a male and a female chimpanzee have been observed cooperating closely in an infanticidal attack; the adult female initially attempted to intervene in the victim's behalf, but later joined in the attack after receiving aggression from the male; and the episode was longer in duration than other reported cases. In the year following the incident, the mother did not increase her association with community males, but was seen with the male who killed her infant. The relevance of these observations to sexual selection-based explanations for infanticide in chimpanzees is discussed.

Key Words: Chimpanzee; Infanticide; Cooperation; Sexual selection; Kanyawara.

INTRODUCTION

Twenty cases of infanticide, of which 11 were observed directly, have been reported from three chimpanzee study areas (Budongo: SUZUKI, 1971; BAKUNEETA et al., 1993; Gombe: BYGOTT, 1972; GOODALL, 1977, 1986; Mahale: NISHIDA et al., 1979; KAWANAKA, 1981; NORIKOSHI, 1982; NISHIDA & KAWANAKA, 1985; TAKAHATA, 1985; HAMAI et al., 1992). Infanticide thus appears to be relatively common among wild chimpanzees.

No simple explanations have emerged for chimpanzee infanticide, however, because the behavior varies widely (HIRAIWA-HASEGAWA & HASEGAWA, 1994). For example, both males and females have been observed as killers (eight times for males, three for females); the victims and killer(s) have sometimes been in different communities, but have more often been members of the same community (different three, same eight); the killer(s) usually cooperated with others (ten cases), but in one case acted alone; some victims were eaten whereas others were abandoned; and finally, after the event, mothers of the victims sometimes continued and even increased their association with the killers (HAMAI et al., 1992), whereas others were never seen again (GOODALL, 1986) (see Tables 5 & 6).

This variability in chimpanzee infanticidal behavior differs dramatically from the general uniformity of infanticidal behavior observed in other primate species. In langurs (*Presbytis entellus*), for example, male immigrants consistently target unrelated infants of resident females thereby shortening the time before these females resume estrus and enabling males to derive direct reproductive benefit from infanticide (HRDY, 1977; NEWTON, 1988; SOMMER, 1994; but see BARTLETT et al., 1993), even in multimale groups (BORRIES, 1997). In mountain gorillas (*Gorilla gorilla beringei*), where infanticide by adult males accounts for over one third of infant deaths, males again appear to reap direct reproductive benefits from infanticide by influencing patterns of female immigration (WATTS, 1989, 1990). By contrast, although the majority of chimpanzee

infanticides have also been committed by males, in at least one case the probable father of the victim was among the attackers (TAKAHATA, 1985). The sexual selection hypothesis that males benefit reproductively from killing infants sired by rivals is thus not easily supported for chimpanzees.

Here we describe a chimpanzee infanticide observed in detail at a fourth study site, the Kanyawara community in Kibale National Park, Uganda. The victims of the attack were a mother/offspring pair that had been observed associating with Kanyawara males in the northern part of their range for six years. The incident shows the complex nature of violent interactions in which the aggressors do not enjoy a significant advantage in strength or numbers. Of particular interest in both respects was the behavior of a high-ranking adult female who at first attempted to intervene in the victim's behalf, and then cooperated vigorously in the attack, even while her own 6-week-old infant was clinging ventrally to her. Close cooperation between a male and a female has not previously been observed in infanticide by chimpanzees or, apparently, by any other primate. In general, it is not expected because the functional significance of infanticide is likely to differ between males and females.

Accordingly, we present a detailed account of this unusual incident. Although its explanation will depend on further observations, we also briefly consider the relationship of this case to the sexual selection hypothesis, and to the proposal that chimpanzee infanticide may be a form of sexual coercion (HAMAI et al., 1992).

METHODS

Observations were made in the Kanyawara study area in the Kibale National Park in western Uganda. The Kanyawara chimpanzees were first habituated from 1983–1985 by G. ISABIRYE-BASUTA (ISABIRYE-BASUTA, 1989), and have been under continuous observation since 1987 (see CHAPMAN & WRANGHAM, 1993, for details regarding the study site and animals). As of December 1996, the Kanyawara community included ten adult males, eight central adult females, an additional nine peripheral mothers intermittently observed in the northern and southern parts of the community range, and two adolescent males. With the exception of some northern and southern mothers, the community was fully habituated and could be observed at close range (<5 m). The Kanyawara chimpanzees have never been provisioned.

Data on community membership and dyadic associations were collected by a team of field assistants who searched daily for chimpanzees. The chimpanzees were often found in night nests known from the previous day's observation. If the location of night nests was not known, observers searched fruiting trees or areas of frequent use. Individual chimpanzee membership in parties was scored every 15 min, together with location and feeding activity.

The infanticidal attack was observed on December 14, 1996, by ACA and two field assistants (CHRISTOPHER MURUULI and PETER TUHAIRWE) from a distance of <7 m. The entire episode was recorded on cassette tape by ACA, including observations by the field assistants, whose voices were also picked up by the microphone.

RESULTS

INFANTICIDE OBSERVATIONS

Chimpanzees Present at the Infanticide

The chimpanzees who were present immediately prior to and during the infanticide are shown in Table 1. None of the females were sexually tumescent on December 14, 1996.

Table 1. Chimpanzees present prior to and during the infanticide.

Individual	Age (yr)*	Sex	Description
<i>MU</i>	22–27	F	“Northern” female (see Table 3), victim of attack. Frequently associated with <i>EK/ED/ES</i> .
<i>MB</i>	2	M	Son of <i>MU</i> , victim of infanticide.
<i>SY</i>	30–35	M	Former alpha male ($\leq 1988-1994$), now low-ranking. Right hand crippled from a snare (received January 1990).
<i>LP</i>	40–45	F	High-ranking (possibly alpha).
<i>LK</i>	13–14	M	Son of <i>LP</i> .
<i>LR</i>	7	F	Daughter of <i>LP</i> .
<i>LS</i>	6 week	M	Son of <i>LP</i> .
<i>KK</i>	11	M	Son of <i>KL</i> (not present).
<i>EK</i>	20–25	F	“Northern” female. Frequently associated with <i>MU/MB</i> .
<i>ED</i>	8	M	Son of <i>EK</i> .
<i>ES</i>	2	M	Son of <i>EK</i> .

*Ages over 12 yr are estimates.

Behavioral Context Prior to the Infanticide

On 28 days between November 25, 1996, and December 30, 1997, chimpanzees fed in a large, fruiting *Mimusops bagshawei* in the northern part of their range, often in large parties (Compartment K15, Trail 8E/7S). This *M. bagshawei* was the most productive tree known to have ripe fruit in the community range during this period. All ten adult males visited, together with six central females and three northern mothers.

MU and *MB* were first seen at the *M. bagshawei* on November 26, when they visited (as they always did to this tree) in the company of *EK/ED/ES*. They fed in a mixed party that included *SY* and *LP*. Both families came again on December 10, where they met *KK*, two central mothers (*OU* and *TG*) with their offspring, and *AL*, a 15-yr-old female. They next visited on December 13, when they ate *M. bagshawei* fruits and then slept together 200 m northwest of the fruiting tree.

At 07:50 on December 14, 1996, ACA, C. MURUULI, and P. TUHAIRWE observed *LP/LS*, *LK*, and *LR* arrive without vocalizing and feed in the *M. bagshawei*. No other chimpanzees were in the tree. Calls were heard further north on eight occasions between 07:50 and 08:51. At 08:51, apparently in response to hearing calls from the ground to the north, *LP* and her family descended from the tree and traveled 30 m on the ground. There they encountered *MU/MB* and *EK/ES*. *ED* was probably nearby.

Aggressive Interactions Leading up to and Including the Infanticide

Note: *LS* was clinging ventrally to *LP* throughout the entire interaction, as was *MB* on *MU*, except for when he was seized.

- 08:57 *MU* (with *MB* ventral) climbs 5 m up a small tree covered with a tangle of vines.
 <09:01 *LK* charges *MU* in the tree/vines, *MU* screams.
 09:01 *SY* arrives with *KK*, and climbs a second small tree nearby (the branches of the two trees were intermingled). *MU* continues to scream.
 09:04 *MU* continues to scream as *SY* climbs higher. *SY* feeds on leaves, then stands on a branch with hair erect, a few meters lower than *MU* and *LK*.
 09:05 *MU*, screaming, presents to *LK*, who touches her vagina and smells his fingers.
 09:06 *LK* inserts his finger in *MU*'s vagina and smells it. *MU* turns and grooms *LK*. *SY* stands and branch shakes in their direction, hair erect.
 09:08 *SY* stands and branch shakes.
 09:09 *MU* pant grunts, stops grooming with *LK*, and moves toward *SY*. *SY* moves towards *MU*, *MU* pant grunts, *SY* touches her, and they sit beside each other.

- 09:14 *SY* moves slightly, *MU* grunts several times, defecates, looks about, then slowly begins to descend the trunk. All individuals subsequently come to the ground.
- 09:23 *SY* charges *EK*, who screams and runs. *EK* then approaches *SY* pant grunting, passes him, and then walks off with *SY* following.
- 09:32 *SY*, standing bipedally, grabs a thin, 2-m-tall sapling, bends it back and forth in display so its crown hits the ground repeatedly, as he slowly walks around it (thus displaying in all directions). *MU* and *LP* sit nearby on ground, beyond reach of the sapling.
- 09:33 *SY* sits beside *MU*.
- 09:35 *SY* branch displays with another sapling, then jumps on *MU*, hitting *MU* several times. *MU* flees and *SY* chases her. They sit 5 m apart.

Note: *MU* screamed almost continuously from 09:35 to 10:30. Her screaming was interrupted only with occasional moments of silence or submissive grunting.

- 09:36:30 *SY* branch displays over *MU*'s head. *LP*, hooting, approaches *SY*. *SY* leaves *MU*, runs toward observers displaying, with *LP* chasing him for several meters. *SY* returns to within 2 m of *MU*, with *LP* sitting 5 m away.
- 09:36:40 *SY* displays with sapling again.
- 09:37:30 *LP* walks to *SY* and *MU*, who are 2 m apart, and sits between them.
- 09:40:00 *SY* grabs sapling and, bending it, hits *LP* on the head several times. *LP* and *MU* are still sitting together.
- 09:40:10 *SY* moves around to *MU*'s side, bends another sapling to hit *MU* on the head several times, while *MU* cowers beneath the branches.
- 09:40:20 *SY* climbs the sapling and defecates. *MU* squeaks and touches *SY* with her hand. *SY* urinates.
- 09:40:50 *MU* moves toward *SY*, who is standing on the sapling half a meter off the ground. *MU* touches *SY*, apparently poking him in the stomach. He just looks at her.
- 09:41:10 *SY* begins to hit *MU* on the head with the sapling's crown again. Initiated by a pant hoot from *LK*, a chorus of vocalizations erupts while *MU* is screaming.
- 09:41:30 *SY* attacks *MU*, grabbing and hitting her, while *LP* has her hand on *MU*'s back. *SY* runs to the small tree *LK* is sitting in and shakes it. *LP* and *MU* subsequently climb onto the trunk of a small tree.
- 09:43:00 *SY* climbs onto the small trunk that *LP* and *MU* are already on. *LP* is 5 m above the ground and *MU* is 3 m above the ground. *SY* stops between them.
- 09:43:35 *SY* briefly attacks *MU* in the tree.
- 09:46:10 *SY* jumps down past *MU*, then climbs back up toward her. *MU* screams intensely. *SY* climbs close to *MU*, *MU* squeaks, and *SY* touches her.
- 09:47:40 *SY* touches *MU*'s forehead with his lips, apparently kissing her.
- 09:48:30 *MB* nurses on *MU*, and *SY* climbs down the trunk, stopping below *MU*.
- 09:48:55 *SY* climbs beside *MU* and, bending a small branch, begins hitting her on the head with it. *MU* jumps to the ground, *SY* follows, and they both sit.
- 09:49:50 *SY* begins waving branches again, then attacks *MU* viciously for 20 sec, biting her several times. After he stops, *MU* reaches out to touch *SY*, and they touch hands.

Note: From this point on the attacks become more sustained, with occasional brief pauses.

- 09:51:50 *SY* sits 1 m from *MU*, and twice pulls down a sapling and bites at it while *MU* is pant grunting. *MU* approaches *SY*, then turns and screams as *SY* stands bipedally and attacks her, trying to grab *MB*. *MU* attacks *SY*, trying to bite him, and *SY* runs off. *LK* attacks *KK*, and a chorus of vocalizations erupts that lasts 25 sec.
- 09:53:15 *LP* runs to *MU* after *SY* runs off. *SY* returns to rejoin the attack, and *LP* begins hitting *MU* as well.
- 09:54:05 *SY* and *LP* get on top of *MU*, pounding on her with their hands. *MU* hunches over screaming, while *MB*, also screaming, is pressed to the ground. *LK* and *KK* fight with each other.
- 09:55:15 *MU*, with *SY* and *LP* still beating her, turns to attack *SY* briefly, then returns to her hunched position on the ground.
- 09:55:30 *SY* jumps on top of *MU* again, biting her on the back. *LP* also hits *MU*, and at times is on top of her.

- 09:56:35 *SY* moves off *MU*. *MU* moves to wedge herself between the ground and the trunk of a fallen, 1-m-diameter tree trunk.
- 09:56:50 *LP* climbs on top of *MU*, puts one hand on her head, then begins hitting her.
- 09:57:30 *SY* walks to *MU* and *LP*, crouches down next to *MU* and reaches under her for her infant, *MB*.
- 09:58:15 *SY* sits on the log above *MU*, *LP* sits on the ground beside *MU*. Then *SY* comes down from the log and sits beside *MU*.
- 09:58:30 *LP* grabs *MU* and pulls her over. *MU* has blood on her left hand, and a cut beneath her left eye. *LP* sits on the log where *SY* had been, and *SY* sits beside *MU*.
- 09:59:30 *SY* attacks *MU*, and *LP* joins him. *LP* pounds on *MU*'s back.
- 10:00:15 *SY* seizes *MB* and runs 10 m up the hill. *MU* follows and attacks *SY*, but fails to recover the infant.
- 10:00:45 *SY* sits on *MB*, holding him with his foot. *LP* interposes herself between *SY* and *MU*, then stands bipedally (exposing her own infant) and pushes *MU* away from *SY/MB* with both arms.
- 10:01:00 *SY* runs several meters with *MB* and sits.
- 10:01:20 *SY* bites the infant in the stomach and appears to be chewing. *LP* continues to push *MU* away from *SY*. *LP* has a cut on her head.
- 10:01:45 *SY* runs several meters with *MB*. We find a 5-cm-wide puddle of blood on and beside a leaf where *SY* was sitting with the infant.
- 10:02:15 *MU* recovers *MB* from *SY*.
- 10:02:45 *LP* attacks *MU*, hitting her on the back. *SY* comes around to the front of *MU* and reaches for *MB*. *MB* screams. Both *SY* and *LP* get on top of *MU* briefly, and then *SY* comes down to reach for the infant again, as *MU* hunches close to the ground.
- 10:03:30 *SY* moves off, while *LP* stays close to *MU*.
- 10:04:20 *MU*, hunched to the ground and holding *MB* ventrally, wraps one arm around the base of a small tree. *LP* grabs the flesh on the back of *MU*'s neck and pulls *MU* backward and upward. *MU* maintains her hold on the tree. *LP* begins to hit *MU*.
- 10:04:40 *LP* grabs with both hands the trunk that *MU* is hunched at the base of. Using the tree as support, *LP* jumps up and down with both feet on *MU*.
- 10:05:05 *LP* hits *MU* with her hands as *SY* watches from 1 m away.
- 10:05:20 *LP* hits *MU* again, then sticks her finger in *MU*'s vagina and smells it.
- 10:05:55 *LP* pulls on *MU*'s neck again, simultaneously reaching around, and alternatively under, *MU* toward the infant.
- 10:07:10 *LP* waves a branch at *MU*, then lunges for the infant. *MU* keeps her hold on *MB*. *SY*, with an open-faced grin, screams, and touches *LP*. The infant's eyes are open, but he is inert and his face appears puffy.
- 10:08:00 *SY* initiates a vocalization chorus with a pant hoot.
- 10:08:25 *SY*, sitting 1 m from *MU/MB*, eats leaves.
- 10:08:40 *SY* pant hoots. *LP* jumps on *MU*, then stamps on her with both feet while holding a trunk for support. *SY* approaches and reaches for the infant. *MU* turns and bites at *SY*. *SY* gets on top of her.
- 10:09:15 *MU* walks away. *LP* and *SY* follow her.
- 10:09:30 *SY* and *LP* attack *MU*. They both get on top of her, hitting.
- 10:10:10 *SY* pant hoots, initiating a chorus, while touching *LP*. *SY* and *LP* are sitting half a meter from *MU*. The other chimpanzees present are all watching arboreally.
- 10:10:35 *SY* attacks *MU*, getting on her back and hitting her. *LP* joins in hitting *MU*.
- 10:11:15 *SY* and *LP* both reach for the infant, while still hitting *MU*. The infant screams.
- 10:11:45 *SY* walks around *MU*, and then reaches under her arm. *SY* touches the wound on *MU*'s face. *MU* screams intensely and *SY* reaches under her arm again. Then *SY* jumps on *MU* again, attacking, as *LP* and *LS* watch.
- 10:12:30 *LP* joins the attack, pounding on *MU*, and also reaching for *MB*.
- 10:13:00 *SY* reaches gently under *MU*'s arm. *MU* stands and *SY* and *LP* attack her, biting. *MB* screams. *SY* appears to be chewing, and *LP* interposes herself between *SY* and *MU*. *LP* hits *MU*.
- 10:14:20 *MU* walks, *LP* and *SY* follow her. *SY* and *LP* attack *MU*, hitting and biting near her rump, possibly at the infant. *SY* and *LP* sit on *MU*, pounding on her. We see more blood on the ground.
- 10:15:50 The attack ends. *MU* walks away holding *MB* ventrally beneath her. *LP* and *SY* follow her.
- 10:18:00 *LK* and *KK* are on either side of *MU*. *SY* lies down and gazes upward.
- 10:20:20 *MU* walks away, and *LK* and *KK* follow her.
- 10:40 *MU* disappears north, with no one following.
- 11:40 We notice a bloody spot on the side of *SY*'s neck.

Summary of Behavioral Events

Table 2 shows a summary of seven types of behaviors observed during the episode, and their approximate durations. The entire episode lasted for 71 min, beginning with the first bipedal display by *SY* at 09:04. Overall, the event was dominated by a large number of relatively brief (<5 s) branch waving displays and attacks, with two longer attacks (about 5 min each) occurring shortly before and after the time when the infant was seized (10:00:15). The longer attacks were conducted jointly by *SY* and *LP*, who many times hit *MU* simultaneously, but who also often coordinated their actions more complexly. For example, at 10:00:45, *LP* pushed *MU* away from *SY* after *SY* had seized *MB*; and several times *SY* grabbed for the infant in front as *LP* attacked *MU* from behind (e.g. 10:02:45, 10:08:40).

Three submissive behaviors by *MU* could be categorized as attempts at reconciliation subsequent to the initiation of physical attacks by *SY* at 09:35. *LP* also appeared to intervene on *MU*'s behalf after these initial attacks (09:36:30 and 09:37:30). After the apparent interventions by *LP*, *SY* hit *LP* with branches (09:40:00), and by 09:53:15 *LP* joined *SY* in the attack on *MU*. The long series of displays and attacks was interrupted several times by reassurance interactions, both between attacker and victim (*SY* and *MU*) and between the two attackers (*SY* and *LP*). The episode also included two sexual inspections.

MU's ASSOCIATION WITH THE KANYAWARA COMMUNITY PRIOR TO AND FOLLOWING THE INFANTICIDE

From 1990–1996, party composition data for Kanyawara chimpanzees were collected during a total of 6823.9 observation hours, or 974.8 ± 312.5 hr/yr. Some females were seen less often than others because they ranged farther away from the field station where the density of fruiting trees is lower than in the central range area. Consequently, adult females in the community are classified as “northern,” “central,” or “southern” according to where they are most commonly observed. The frequency at which individual females in the three classes were seen varied widely during the six years prior to the infanticide, from a mean of 16.3 hr/individual/yr for five northern females, to 215.6 hr/individual/yr for eight central females (Table 3).

MU was a northern female. She was first identified in February 1990, carrying an infant male (*MR*) estimated to be 1 yr old. *MU* and *MR* were seen together in eight months between February 1990 and February 1993. *MU* then disappeared until March 1996, when she was seen with *MB* for the first time (RWW obs.). *MB* was estimated to be 2 yr old. *MU* was never seen copulating or with a full sexual swelling. During the 36 months from March 1993 to February 1996, when *MU* was not seen, it is presumed that *MR* died and *MB* was conceived (probably in 1994). Whether *MU* mated with the males of the Kanyawara community and/or those of other communities is unknown. *MU* and *MB* were seen together in five months in 1996 (March–April and October–December: Table 4).

After the infanticide, *MU* was not seen for 26 days. On January 9, 1997, ACA and C. MURUULI observed her feeding in a *M. bagshawei* tree approximately 1 km north of the site of the attack, accompanied by an adult male (*SL*) and a mother (*EK*, with offspring *ED* and *ES*). *MB* was absent. He was therefore assumed to have died from the wounds sustained on December 14. *MU* was seen only once again in 1997 (March 18) in the company of six adult males, including *SY*, two adolescent males, and eight adult females and offspring. *LP* was not present. Each of the other four northern mothers (*EK*, *JO*, *PE*, and *PU*) was seen at least four times in 1997 (January, March, May, June, September, October, and December).

Table 2. Summary of seven types of behaviors observed before and during the infanticidal attack.

Behavior	Participants	Description	Duration	Time
Charges	<i>LK</i> → <i>MU</i>	<i>LK</i> climbs fast toward <i>MU</i> , <i>MU</i> screams	≤ 5 s	9:00
Bipedal display	<i>SY</i> → <i>MU/LK</i>	<i>SY</i> stands on branch, hair erect, looking toward <i>MU</i> and <i>LK</i>	≤ 5 s	9:04
Branching	<i>SY</i> → <i>MU/LK</i>	<i>SY</i> stands on branch, hair erect, shakes limb while looking toward <i>MU</i> and <i>LK</i>	≤ 5 s	9:06
		<i>SY</i> stands on branch, hair erect, shakes limb while looking toward <i>MU</i> and <i>LK</i>	≤ 5 s	9:08
	<i>SY</i> → <i>MU/LP</i>	Standing, <i>SY</i> slaps bent sapling on ground	≤ 10 s	9:32
		Standing, <i>SY</i> slaps bent sapling on ground	≤ 10 s	9:35
	<i>SY</i> → <i>MU</i>	Standing, <i>SY</i> waves bent sapling over <i>MU</i> 's head	≤ 5 s	9:36:30
		Standing, <i>SY</i> waves bent sapling over <i>MU</i> 's head	≤ 5 s	9:36:40
		Standing, <i>SY</i> waves bent sapling over <i>MU</i> 's head, and hits her on head with it	≤ 5 s	9:40:10
		Standing, <i>SY</i> waves bent sapling over <i>MU</i> 's head, and hits her on head with it	≤ 5 s	9:41:10
		<i>SY</i> hits <i>MU</i> on head with a branch he is bending back and forth	≤ 5 s	9:48:55
		<i>SY</i> waves branches at <i>MU</i>	≤ 5 s	9:49:50
		<i>SY</i> pulls down sapling, biting at it	≤ 5 s	9:51:45
	<i>SY</i> → <i>LP</i>	Standing, <i>SY</i> waves bent sapling over <i>LP</i> 's head, and hits her on head with it	≤ 5 s	9:40:00
	<i>SY</i> → <i>LK</i>	<i>SY</i> shakes small tree <i>LK</i> is in	≤ 5 s	9:41:30
	<i>LP</i> → <i>MU</i>	<i>LP</i> waves branch at <i>MU</i> , then lunges for infant	≤ 5 s	10:07:10
Sexual inspections	<i>LK</i> → <i>MU</i>	<i>MU</i> presents, <i>LK</i> touches her vagina, smells his finger	≤ 5 s	9:05
	<i>LP</i> → <i>MU</i>	<i>LP</i> sticks finger in <i>MU</i> 's vagina and smells it during attack	≤ 5 s	10:05:20
Submissions	<i>MU</i> → <i>SY</i>	<i>MU</i> approaches <i>SY</i> while pant grunting	≤ 5 s	9:09
		<i>MU</i> squeaks and touches <i>SY</i>	≤ 5 s	9:40:20
		<i>MU</i> pokes <i>SY</i> gently in stomach	≤ 5 s	9:40:50
		<i>MU</i> approaches <i>SY</i> pant grunting	≤ 5 s	9:52:00
Reassurances	<i>SY</i> ↔ <i>MU</i>	<i>SY</i> touches <i>MU</i> after submissive approach	≤ 5 s	9:09
		<i>SY</i> approaches and touches <i>MU</i> , as she squeaks	≤ 5 s	9:46:10
		<i>SY</i> puts his lips to <i>MU</i> 's forehead, apparently kissing her	≤ 5 s	9:47:40
		<i>MU</i> reaches to <i>SY</i> after he attacks her, and they touch hands	≤ 5 s	9:49:50
	<i>SY</i> ↔ <i>LP</i>	<i>SY</i> , screaming with an open-faced grin, touches <i>LP</i>	≤ 5 s	10:07:10
		<i>SY</i> initiates a vocalization chorus with a pant hoot, while touching <i>LP</i>	≤ 20 s	10:10:10
Interventions	<i>LP</i> → <i>SY</i>	<i>LP</i> approaches <i>SY</i> hooting, <i>SY</i> flees, <i>LP</i> chases a few meters	≤ 5 s	9:36:30
		<i>LP</i> sits between <i>SY</i> and <i>MU</i>		9:37:30
	(?)	<i>SY</i> abandons attack on <i>MU</i> , <i>LP</i> runs to <i>MU</i> (then <i>SY</i> rejoins attack, with <i>LP</i>)	≤ 5 s	9:53:15
	<i>LP</i> → <i>MU</i>	<i>LP</i> , standing bipedally, pushes <i>MU</i> away from <i>SY</i> , who has captured <i>MB</i>	≤ 15 s	10:00:45
Attacks	<i>SY</i> → <i>MU</i>	Hitting, chasing	≤ 10 s	9:35
		Shaking, hitting	≤ 30 s	9:41:30
		Hitting	≤ 5 s	9:43:35
		Hitting, shaking, biting	≤ 20 s	9:49:50
		Hitting, shaking, biting, grabbing at infant, <i>MB</i>	4.50 min	9:52:05
		Hitting, shaking, biting, grabbing at <i>MB</i>	≤ 20 s	9:57:55
		Hitting, shaking, biting, grabbing at <i>MB</i>	45 s	9:59:30
		Hitting, grabbing at <i>MB</i>	45 s	10:02:45
		Grabbing at <i>MB</i>	35 s	10:08:40
		Hitting	40 s	10:09:40
	<i>LP</i> → <i>MU</i> *	Hitting, stamping, biting, grabbing at <i>MB</i> , with occasional brief pauses	5.25 min	10:10:35
		Hitting, shaking, biting, grabbing at <i>MB</i>	5.25 min	9:53:15
		Hitting, shaking, biting, grabbing at <i>MB</i>	45 s	9:59:30
		Hitting, while <i>SY</i> grabs at <i>MB</i>	45 s	10:02:45
		Hitting, stamping on, pulling on neck, grabbing at <i>MB</i>	95 s	10:04:20
		Lunges for <i>MB</i>		10:07:10
		Hitting, stamping on	35 s	10:08:40
		Hitting	40 s	10:09:40
		Hitting, stamping, biting, grabbing at <i>MB</i> , with occasional brief pauses	5.25 min	10:10:35
	<i>SY</i> → <i>MB</i>	<i>SY</i> seizes <i>MB</i> , runs with him, sits on him	80 s	10:00:15
		<i>SY</i> bites <i>MB</i> in stomach		10:01:20
	<i>MU</i> → <i>SY</i>	Bites at <i>SY</i> in defense	< 5 s	9:55:15
		Chasing, hitting, grabbing, trying to bite <i>SY</i> , who has her infant, <i>MB</i>	≤ 30 s	10:00:15
		<i>MU</i> recovers <i>MB</i> from <i>SY</i>		10:02:15
		Bites at <i>SY</i> in defense		10:08:40

*Joint attacks by *SY* and *LP*.

Table 3. Amount of time principle Kanyawara adults and adolescents from different geographical areas were seen by observers, January 1990–December 1996.

Subgroup ¹⁾	N ²⁾	Mon/yr (mean±SD) ³⁾	Hr/yr (mean±SD) ³⁾
Northern females	5	2.4±0.4	16.3±3.8
Central females	8	10.1±1.1	215.6±80.5
Southern females	4	3.3±1.4	22.6±12.4
Males	13	10.5±0.9	328.2±70.0

1) Northern females: *EK, JO, MU, PE, PU* (excluding *MA*, last seen in 1993); Central females: *AL, AR, FG, KL, LP, MG, OU, TG*; Southern females: *BL, GO, NG, UM*; Males: *AJ, BB, BF, LB, LK, LM, MS, TU, SL, ST, SY, YB* (excluding *NJ*, who disappeared in 1993, and *RZ*, who died in 1992). 2) *N*: Number of individuals. 3) Figures exclude months before the individual was first identified.

Table 4. Association patterns of *MU* with Kanyawara community, 1990–1996 vs 1997.

Associate	Of the total number of days <i>MU</i> was observed, the % of days she was seen with	
	1990–1996 (of 35 days in 13 months)	1997 (of 2 days in 2 months)
Northern females	20.0 (4) ¹⁾	25.0
Central females	13.9 (8)	18.7
Southern females	0.7 (4)	12.5
Adult males	31.7 (10)	50.0
<i>SY</i> (No. 2) ²⁾	40.0	50.0
<i>LP</i> (No. 5) ³⁾	14.3	0.0
Mean party size (±SD)	10.6±6.5	15.5

1) Number in parentheses is number of individuals in that group in 1996; 2) *SY* was *MU*'s second most frequent male associate in 1990–1996; 3) *LP* was *MU*'s fifth most frequent central female associate in 1990–1996.

From 1990 to 1996, *MU* was seen on a mean of 5.8 days per year, compared to 2 days in 1997. In the 35 days when *MU* was seen from 1990 to 1996, the average Kanyawara male was with her on 31.7% of days, with *SY* the second-most frequent male associate, at 40.0% of days. Thus, *SY* was apparently a relatively frequent associate of *MU* before the infanticide, and there was no evidence of a rise in *MU*'s association with Kanyawara males following the infanticide (Table 4).

Although *MU* was seen infrequently in the year following the infanticide, we note the possibility that *SY* consorted with *MU* in February and March 1997. Circumstantial evidence for this possibility is that although *SY* was seen at a high rate in 1997 (50.6% of the 328 days when chimpanzees were observed), he had two extended absences. One was from February 6 to March 17. On March 18, he and *MU* joined a large party in the northern part of the Kanyawara range. *SY* was the only Kanyawara male who was not seen during the February 6-to-March 17 period (the nine other males were seen on a mean of 41.3% of days, range 9.5–66.7). Coincident absences of a male and a female have previously been found to be evidence of sexual consortships (GOODALL, 1986).

REVIEW OF PREVIOUS CHIMPANZEE INFANTICIDES

Of the 20 infanticides previously reported in wild chimpanzees, the mothers of the victims were non-residents in 6 cases (Table 5), and central or peripheral residents in 12 cases (Table 6). In two cases the identity of the mother was not known (Table 6). Victims included both male and female infants.

Table 5. Summary of between-group chimpanzee infanticides, 1967–1996.

Date (m/yr)	Capture observed	Captor's sex	First seen owner's sex ¹⁾	Kill observed	Killer's sex	Individuals involved in kill	Infant's age (yr)	Infant's sex	Cannibals	Source
Mahale (K-group) 4/74	No	AM?	AM	No	AM?	3 AMs found eating a carcass	3	M	AMs	NISHIDA et al., 1979
Mahale (M-group) 1/76 ²⁾	No	?	?	No	?	?	1.5	M	AMs	NISHIDA et al., 1979
Gombe 9/71	Yes	AM	—	Yes	AMs	5 AMs attack mother; 2 AMs kill infant while eating	1.5–2.5	?	AMs	BYGOTT, 1972
10/75	No	AM?	AM	No	AM?	?	1.5–2.5	M	AMs	GOODALL, 1977
11/75	Yes	AM	—	Yes ³⁾	AMs	5 AMs attack mother; many handle infant; mother attempts submission	1.5–2.0	F	None	GOODALL, 1977
3/79	Yes	AM	—	Yes	AM	7 AM/2 IM attack mother	1.5–2.5	?	AMs	GOODALL, 1986

1) First owner is first animal observed with infant, when actual capture not observed. AM: Adult male; AF: adult female; IM: immature male. 2) This infanticide was inferred based on the following observations: one day subsequent to an invasion by M-group males into K-group territory, a severely wounded K-group female was observed joining a K-group subgroup without her infant. This infant had been seen five days previously in a healthy condition, and both the mother and infant at that time were socializing normally with resident males. 3) Infant dies from wounds later that day.

Table 6. Summary of within-group chimpanzee infanticides, 1967–1996.

Date (m/yr)	Capture observed	Captor* or first seen owner ¹⁾	Kill observed	Killer's sex	Mother's status ²⁾	Individuals involved in kill	Infant's age	Infant's sex	Cannibals	Source
Budongo										
11/67	No	AM	Yes	AM	?	2 AMs handle infant before death	Newborn	?	AM	SUZUKI, 1971
1992 ³⁾	No	?	No	?	?	?	<3 yr	?	?	BAKUNEETA et al., 1993
Mahale (M-group)										
1/77	No	AM	No	?	R (5)	?	2.5 mon	M	AMs	NORIKOSHI, 1982
6/79	No	AM	No	?	B (0)	?	1.5 mon	M	AMs, AFs	KAWANAKA, 1981
7/83	Yes	AM*	Yes	AM	B (1)	AMs	Newborn	M	AMs, AF, IF	TAKAHATA, 1985
12/83	No	AM	No	AM?	B (4)	?	3.0 mon	M	AMs, AFs	NISHIDA & KAWANAKA, 1985
7/85	Yes	AM*	Yes	AM	R (3)	Solo attack	10 mon	M	None	MASUI, in HAMAI et al., 1992
10/89	Yes	AM*	Yes	AM	R (5)	Solo attack, then 4 AMs handle infant before death; AM blocks mother from rescuing infant	6 mon	M	AMs, AFs, IMs, IFs	HAMAI et al., 1992
7/90	No	AM	Yes	AMs	R (4)	AM/AF attack mother to prevent recovery of infant	5 mon	M	AMs, AFs, IMs	HAMAI et al., 1992
Gombe										
8/75	Yes	AF*	Yes	AF	R (12)	Mother/daughter attack mother	3 wk	F	AF, IFs, IM	GOODALL, 1977
1/76	No	?	No	?	R (13)	?)	Newborn	M	None	GOODALL, 1977
10/76	Yes	IF*	Yes	IF	R (13)	Mother/daughter attack mother	3 wk	M	AF, IFs, IM	GOODALL, 1977
11/76	Yes	IF*	Yes	IF	R (13)	Mother/daughter attack mother	3 wk	F	AF, IM	GOODALL, 1977
?	No	AF	No	?	?	AFs in adjacent community observed eating an infant	?	?	AFs	Unpubl. obs. in PUSEY et al., 1997
Kibale (Kanyawara)										
12/96	Yes	AM*	Yes ⁵⁾	AM	B (6)	AM and AF with clinging infant attack mother	2 yr	M	AM ⁶⁾	This study

1) First owner is first animal observed with infant, when actual capture not observed. AM: Adult male; AF: adult female; IM: immature male; IF: immature female. 2) R: Resident of unit-group; B: border female, ranging in territorial border area and presumably interacting with males of two communities. Numbers in parentheses are years since mother seen regularly interacting with unit-group members. Infant status in Budongo case unknown. 3) This infanticide is inferred from the discovery of large clumps of chimpanzee hair in a chimpanzee dung. 4) Mother discovered holding her dead infant in company of males from her own group, after observers attracted to group by screams. 5) Mother rescued severely wounded infant (eyes open but completely limp and inert) and escaped. When the mother was next observed three and a half weeks later the infant was not with her. 6) Although the infant was not consumed, SY was observed chewing after he had possession of the infant. Since all reports of cannibalism have noted the slowness of chimpanzee infant consumption as compared with other animal prey (HAMAI et al., 1992), we consider it possible that SY was beginning to eat the infant, and may have continued had the mother not recovered it. It's worth noting that SY also consumed leaves during the interaction, a behavior that typically accompanies meat eating in chimpanzees. The alternative explanation is that SY was only clearing his mouth of blood and flesh obtained inadvertently while biting the infant.

Infanticidal attacks were most often conducted by more than one attacker. In all the three between-group cases in which the capture was observed, gangs of adult males conducted the attacks on the mother. In the six within-group cases in which the capture was observed, three adult males conducted the attack on the mother in one case (7/83), an adult and subadult female (mother and daughter) attacked the mother in three cases (8/75, 10/76, and 11/76), and a single adult male captured the infant in two cases (7/85 and 10/89).

The durations of the between-group assaults ranged from 2 min (9/71 and 3/79) to 50 min (11/75: two 10-min attacks separated by a 30-min pause in aggression). The durations of the within-group assaults ranged from a few minutes (8/75 and 10/76) to 20 min (10/89).

Most of the victims were at least partially eaten. Cannibalism was observed in five of the six between-group incidents, in all cases by adult males. Of the 14 within-group incidents, cannibalism was observed in 11 cases and inferred in 1 case (based on the presence of clumps of chimpanzee hair in the dung). Within-group cannibals included adult and immature males and females.

Females participated in infanticidal attacks less than males. In addition to the three intragroup cases from Gombe committed by a mother and her daughter, an adult female directed aggression toward the mother in only one case (7/90), helping an adult male to block the mother from recovering her infant from another male.

We note that at both Mahale and Gombe females have been observed to participate in severe attacks on mother/offspring pairs that did not result in infant deaths. In all cases the females joined attacks led by gangs of males, and the mother rather than the infant appeared to be the primary target of aggression (NISHIDA & HIRAIWA-HASEGAWA, 1985; GOODALL, 1986). In one case (NISHIDA & HIRAIWA-HASEGAWA, 1985) the observers intervened on behalf of the victims, preventing what they perceived to be an inevitable infant death. Finally, two Gombe females were reported to have attempted to steal an infant from a mother (in PUSEY et al., 1997).

DISCUSSION

Since the reproductive success of females and males is limited in different ways (TRIVERS, 1972), the functional significance of infanticide is likely to differ between them. Thus, females that commit infanticide appear to gain long-term benefits in some species by reducing resource competition or the risk of their own offspring being the victims of infanticidal attacks by other females (e.g. rodents: TUOMI et al., 1997). Infanticidal males, on the other hand, commonly gain immediate reproductive benefit by inducing the females that they control to resume estrus cycling, or by inducing females to associate with them (e.g. lions: PUSEY & PACKER, 1994).

Both male and female chimpanzees have been observed to kill unrelated infants. Consistent with sexual selection theory, explanations for infanticide by chimpanzees have in general differed according to sex. There are two ways that males could benefit by killing infants. First, by killing neighboring infants they could eliminate future rivals and/or increase the chances of gaining reproductive access to neighboring females (NISHIDA & KAWANAKA, 1985; TAKAHATA, 1985). Second, by killing infants within their group, males could induce resident females to mate more restrictively with them (HAMAI et al., 1992). Female chimpanzees, on the other hand, could profit by eliminating competition for resources in their core areas, and/or by gaining nutritional benefit from cannibalism (GOODALL, 1986).

The conditions necessary to support sexual selection-based explanations for infanticide (HRDY, 1974) have not always been met or confirmed for male chimpanzees: males have not

always been unrelated to their victims (NISHIDA & KAWANAKA, 1985; TAKAHATA, 1985), data on subsequent interbirth intervals of the victims' mothers have not been systematically collected, and males have not always had subsequent mating access to the victims' mothers (i.e. for between-group cases: GOODALL, 1986; although one Mahale female did transfer into the group of the male that killed her infant: NISHIDA et al., 1985). In spite of these empirical limitations, however, HAMAI et al. (1992) propose that within-group infanticide may function to coerce normally promiscuous females to mate more restrictively with infanticidal males. Thus while promiscuous mating may represent a female strategy to confuse paternity in order to discourage infanticide by unrelated males (HRDY, 1981), it might not guarantee protection in chimpanzees. To support this suggestion, HAMAI et al. (1992) note that the mothers of within-group infanticide victims at Mahale all mated promiscuously, whereas females that were sexually monopolized by the alpha male never had their infants killed.

Our data are insufficient to test HAMAI et al.'s (1992) hypothesis for within-group infanticide. *MU*'s March 18 appearance with *SY* after their long absence from the community suggests that they may have engaged in a sexual consortship. If true, this would support the hypothesis that within-group infanticide by males induces restrictive mating. However, genetic data will be necessary to determine whether *SY* is in fact the father of *MU*'s future offspring. In addition, since *SY* was a relatively frequent associate of *MU*'s before the attack, it is possible that he was the father of *MB*, making his attack on *MB* genetically costly rather than potentially beneficial. Nonetheless, *MU*'s long absences from the community could have had the behavioral effect of reducing paternity certainty. Thus her absences may have increased the potential for aggression from *SY* upon reunion, as has been suggested for the within-group Mahale infanticides in which the probable father was among the attackers (NISHIDA & KAWANAKA, 1985; TAKAHATA, 1985). Again, genetic data will be necessary to determine whether *SY* was related to his victim, *MB* (FAHEY, in prep.).

We note here that if the primary benefit of infanticide to a male is to increase his chances of siring future offspring with a specific female, then there should be no sex bias in the choice of victims. Of the ten cases in which males were either the observed captor or the first observed owner of the victim, both female and male infants were targeted (Tables 5 & 6). Although there appears to be a preference for male victims (Table 6), HAMAI et al. (1992) have shown that at Mahale, where most of the within-group cases committed by males have been documented, this is a consequence of sampling bias. Thus there is no evidence to support the idea that males benefit from infanticide by eliminating future competitors (TAKAHATA, 1985), in which case they would be expected to preferentially target male infants.

Infanticidal chimpanzee females, in all cases the same mother/daughter pair from Gombe, have possibly benefited by reducing resource competition and gaining nutrition (GOODALL, 1986; HIRAIWA-HASEGAWA, 1992). However, we suggest that, in general, there is not likely to be strong selection for infanticidal behavior in female chimpanzees because the risk of injury is too high. Adult chimpanzees commonly inflict serious, even lethal wounds on each other, making attacks dangerous. Moreover, in contrast to males, as well as to their counterparts in some female-bonded species, in which individual females are afforded protection by the presence of numerous relatives (e.g. many cercopithecines: PUSEY & PACKER, 1987), female chimpanzees do not usually live among kin or form strong non-kin-based alliances, making them more vulnerable in physical confrontations. Consequently, the potential resource benefits to female chimpanzees are probably rarely sufficient to outweigh the risks, especially if they have vulnerable offspring with them. This would explain why females are much less likely than males to

participate in infanticidal attacks or lethal raiding (GOODALL, 1986; Tables 5 & 6). In this regard, it is noteworthy that the infanticidal females at Gombe were an adult female and her adolescent daughter, the latter being able to participate actively in the attack, as opposed to being a vulnerable burden.

The Kanyawara infanticide is the first observed case in which a male and a female chimpanzee cooperated closely in attacking a mother/offspring pair. Given that, as we have argued, females have less than males to gain from escalated aggression, *LP*'s participation in this episode can be explained in two ways. First, the presence of an adult male could have reduced the risk to her, and thereby increased the potential benefit of participation. Second, *LP* could have faced a greater risk of injury from *SY* by not participating in the attack than she did from *MU* by joining the attack.

We reject the first explanation, since the risk to *LP*, who was carrying her 6-week-old infant, must have been significant. Neither of the attackers were in optimal condition for attack: *SY* had a crippled hand, and *LP* had an infant ventrally clinging to her. The fact that both *SY* and *LP* sustained injuries during the infanticide suggests that the attack was indeed dangerous. Had *MU* managed to bite *LS*, as opposed to *LP*, the cost to *LP* could have been great. Moreover, the behavior of all three participants suggests that the attack was not carried out with a significant power advantage. The episode was much longer in duration than other reported cases, consisting of many brief attacks which failed to overwhelm the victims. *MU*, in addition, continued to attempt reconciliation well into the episode, perhaps suggesting that she herself did not perceive the kind of imbalance of power that is typically associated with lethal attacks in chimpanzees (MANSON & WRANGHAM, 1991). Finally, since *MU/MB* were border-area residents from whom *LP* did not suffer significant competition, it is hard to see how *LP* could have greatly benefited from the infanticide in any case.

The alternative explanation is that *LP* chose the least risky behavior available to her by joining *SY* in the attack, a possibility that emphasizes the constraining effect that male reproductive strategies might have on the behavior of female chimpanzees (WRANGHAM, 1979). With presumably little to gain by attacking *MU*, and much to lose by being in proximity to an aggressively aroused male, *LP* initially appeared to try to buffer *SY*'s aggression. First *LP* chased *SY* after *SY* behaved aggressively toward *MU*, and then *LP* interposed herself between *SY* and *MU*, a behavior similar to "peacemaking" behaviors that have been observed in captivity (DEWAAL, 1982). After *SY* directed aggression toward *LP*, however, *LP* joined the attack on *MU*. Our interpretation of this is that *LP* and her young infant risked serious attack from *SY* by not forming a coalition with him: captive male chimpanzees are known to attack group members that support their rivals (DE WAAL, 1982).

Since it is clear that *SY* and *LP* did not stand to gain equivalent benefits from the infanticidal attack, the incident reaffirms the complexly political nature of chimpanzee behavioral interactions. We suggest that chimpanzees are not only capable of lethal aggression, but may also coerce unwilling individuals to participate.

Acknowledgements. Long-term data were collected by JOHN BARWOGESA, JOSEPH BASIGARA, KIIZA CLEMENT, KATEEBA DEO, CHRISTOPHER KATONGOLE, FRANCIS MUGURUSI, DONOR MUHANGYI, CHRISTOPHER MURUULI, and PETER TUHAIRWE. Funding support for the Kibale Chimpanzee Project was provided by the Leakey Foundation, the National Geographic Society (No. 5626-96), and the National Science Foundation (NSF SBR-9120960). We thank Makerere University for permission to conduct research at the Makerere University Biological Field Station at Kanyawara, and the Uganda Wildlife Authority for permission to work in the Kibale National Forest.

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— Received: May 29, 1998; Accepted: October 21, 1998

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