



Severe Aggression Among Female *Pan troglodytes schweinfurthii* at Gombe National Park, Tanzania

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Abstract Aggression is generally more severe between males than between females because males gain greater payoffs from escalated aggression. Males that successfully defeat rivals may greatly increase their access to fertile females. Because female reproductive success depends on long-term access to resources, competition between females is often sustained but low key because no single interaction leads to a high payoff. Nonetheless, escalated aggression can sometimes immediately improve a female's reproductive success. Resisting new immigrants can reduce feeding competition, and infanticide of other females' young can increase a female's access to resources. East African chimpanzees live in fission-fusion communities in which females occupy overlapping core areas. Growing evidence indicates that reproductive success correlates with core area quality, and that females compete for long-term access to core areas. Here we document 5 new cases of severe female aggression in the context of such competition: 2 attacks by resident females on an immigrant female, a probable intracommunity infanticide, and 2 attacks on a female and her successive newborn infants by females whose core areas overlapped hers. The cases provide further evidence that females are occasionally as aggressive as males. Factors influencing the likelihood and severity of such attacks include rank and size differences and the presence of dependable allies. Counterstrategies to the threat of female aggression include withdrawing from others around the time of

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parturition and seeking male protection. We also discuss an unusual case of a female taking the newborn infant of another, possibly to protect it from a potentially infanticidal female.

Keywords aggression · Chimpanzee · female competition · Gombe · infanticide · *Pan troglodytes*

Introduction

In mammals, intrasexual competition is usually more intense among males than among females, as demonstrated by higher rates of wounding (Jurmain 1997; Le Boeuf and Laws 1994; Smuts 1987; Wilson and Boelkins 1970) and death from aggression (Daly and Wilson 1988) in males. Besides sexual dimorphism in weaponry (Harvey *et al.* 1978), researchers commonly attribute the difference to differences in the payoffs of escalated aggression in the 2 sexes because of differences in the nature of the resources for which they compete (Clutton-Brock *et al.* 1982; Smuts 1987). By engaging in escalated aggression in a few interactions over short periods, males can sometimes greatly increase their access to fertile females, on which their reproductive success depends. In contrast, because female reproductive success depends primarily on the ability to invest in offspring (Trivers 1972), competition over the required resources is often more sustained, but low key, because no single interaction is likely to significantly change the female's access to such resources (Smuts 1987). In addition, female primates that carry their young risk injury to them and to themselves during escalated fights (Goodall 1986; Nishida 1989; Smuts 1987).

Nevertheless, there are circumstances in which intense aggression by females can have a large payoff. Among cooperatively breeding species such as meerkats and marmosets, in which the reproductive success of the α -female depends on the help she receives from group members in rearing her young, α -females sometimes kill the infants of subordinate females, thereby reducing competition for the help they require (Bezerra *et al.* 2007; Clutton-Brock *et al.* 1998; Digby 2000). By killing infants of other females, female ground squirrels appear to gain access to burrows essential for breeding (Sherman 1981) and lactating black-tailed prairie dogs may gain better access to feeding territories near their burrows (Hoogland 1995). In species in which the number of females in the group is highly constrained, females sometimes aggressively target other females and drive them from the group (red howlers: Crockett 1984 and ring-tailed lemurs: Vick and Pereira 1989), or aggressively prevent new females from entering (red howlers: Sekulic 1982). Even in species that normally exhibit very stable female hierarchies based on nepotism or age, intense female aggression occasionally occurs when there is a chance of permanently changing or establishing the rank order. Female baboons fought intensely, using behavior similar to that of males, during a dramatic change in the hierarchy (Smuts and Nicolson, *unpub. data* in Smuts 1987). Female chimpanzees in a newly formed captive group likewise exhibited aggressive behavior more typical of males during the first months after the group formed (Baker and Smuts 1994).

Though aggression is generally more frequent and intense among males than among females in natural chimpanzee populations (Goodall 1986; Muller 2002),

evidence is gradually accumulating that females sometimes exhibit severe aggression toward other females. Each new observation helps to develop a clearer understanding of the payoffs and costs incurred in escalated fights. Chimpanzees live in permanent, fission-fusion communities of ≤ 150 individuals (median=46.3; Wrangham *et al.* 2006) in which individuals associate in temporary parties of varying size and composition (Goodall 1986; Mitani *et al.* 2002; Nishida 1968). Adult males range widely and jointly patrol and aggressively defend the community range. Whereas adult females in West African populations associate with others at high rates and range throughout the community range (Lehmann and Boesch 2005; Sakura 1994), females in East African populations spend considerable time alone and concentrate their ranging in smaller overlapping core areas within the community range (Emery Thompson *et al.* 2007; Hasegawa 1990; Murray *et al.* 2007a; Williams *et al.* 2002; Wrangham and Smuts 1980). At several sites, the core areas are clustered into ≥ 2 neighborhoods within the community range (Emery Thompson *et al.* 2007; Williams *et al.* 2002). Male chimpanzees generally remain in their natal communities, but females usually leave them at adolescence and join a new community before breeding. However, at all sites ≥ 1 female remained in her natal community (Boesch and Boesch-Achermann 2000; Kahlenberg *et al.* 2008; Nishida *et al.* 2003). In the Kasekela community at Gombe, a larger proportion of females, almost half of all females born in the community, have settled in their natal communities (Pusey *et al.* 1997), though most had visited other communities during adolescence (Goodall 1986; Pusey 1979). Females that stayed when their mothers were still alive settled in virtually the same core area as their mothers (Williams *et al.* 2002).

Kahlenberg *et al.* (2008), Murray (2007), Nishida (1989), Pusey *et al.* (1997), and Wittig and Boesch (2003) ranked female chimpanzees into a dominance hierarchy on the basis of submissive pant-grunts and the direction of agonistic interactions. Rank significantly correlates with age, but there is considerable variation in the rank of females of the same age. Rank correlates significantly with several measures of foraging efficiency (Kahlenberg 2006; Murray *et al.* 2006; Pusey *et al.* 2005; Wittig and Boesch 2003) and reproductive success (Pusey *et al.* 1997). Most parous females show strong site fidelity over many years (Emery Thompson *et al.* 2007; Williams *et al.* 2002). At Gombe, high-ranking females show significantly higher site fidelity and occupy smaller, higher-quality core areas (Murray *et al.* 2006, 2007a). High-ranking females also occupy higher-quality core areas at Kanyawara, Kibale (Kahlenberg *et al.* 2008). Possible advantages to remaining faithful to a core area include intimate knowledge of resources and familiarity with neighbors (Williams *et al.* 2002). New female immigrants receive aggression from resident females (Goodall 1986; Kahlenberg *et al.* 2008; Nishida 1989; Pusey 1980) and settle away from high-ranking females (Murray *et al.* 2007a; Williams 2000). Together the observations suggest that there is a high payoff to female chimpanzees that acquire and retain a high-quality core area and that female chimpanzees compete for such areas.

The most extreme aggression between female chimpanzees is infanticide. Goodall (1977, 1986) described how over a 2-yr period an adult female (Passion) and her adolescent daughter (Pom) brutally attacked 2 females from the same community and snatched and ate their infants on 3 occasions, and were the probable killers of a fourth infant. Passion and Pom also made 3 unsuccessful attempts at infanticide in

the following 2 yr (Goodall 1986, 1990), and Goodall (1977, 1986) suspected that 5 additional newborns that disappeared might have fallen victim to them. On the basis of infant disappearances during other periods, and a general tendency of mothers of newborns to associate with adult male protectors, Goodall (1977) suggested that infanticide might be a more general phenomenon and not restricted to the 2 females.

Though Goodall (1977) thought it was premature to speculate about the functional significance of infanticide by female chimpanzees, others suggested that the females were removing feeding competitors while they were still vulnerable (Hrdy 1981, p. 109; Pusey 1983). A more recent observation at Kanyawara in which a male apparently coerced a female to aid him attack another female and take her infant (Arcadi and Wrangham 1999) does not so easily fit the explanation, because the victim lived in a different neighborhood from her attacker. However, Muller (2007) and Townsend *et al.* (2007) interpreted 3 recent cases of observed and inferred infanticide by females at Budongo as resulting from competition over space. Here, the aggressors were resident females and the victims were females that were part of a recent influx of 13 adult females into the community. At Taï, females were found eating an infant, but the origin and identity of the infant and the circumstances of the killing are unknown (Boesch and Boesch-Achermann 2000).

Given the potential risk of infanticide both by females and, in some cases, by males of the community (Hamai *et al.* 1992; Murray *et al.* 2007b; Sakamaki and Itoh 2001), we might expect females to show counterstrategies to decrease the risk. In several fission-fusion species, females avoid the rest of the group around the time of parturition. Female lions (Packer *et al.* 2001) and hyenas (East *et al.* 1989) keep their newborn cubs in solitary dens or burrows for several weeks before bringing them to join the crèches or communal dens with other females. Goodall (1986, p. 86) noted that female chimpanzees often disappear around the time of parturition—dubbed maternity leave by Hiraiwa-Hasegawa (Nishida *et al.* 1990)—but quantitative data are not available.

We describe several new incidents of severe aggression at Gombe in which the perpetrators were known or suspected to be female chimpanzees. We estimate the frequency of infanticide by females and discuss the influencing factors. We discuss counterstrategies to female aggression, including seeking male protection, and provide evidence that females withdraw from the group around the time of birth when offspring are most vulnerable to infanticide. We also discuss an incident in which a female took her daughter's newborn infant, possibly as a protective measure against a potentially infanticidal female.

Methods

Study Site, Population, and Observation Methods

Gombe National Park is on the eastern shore of Lake Tanganyika in Tanzania. The 35-km² park is crossed by deep valleys that fall from the rift escarpment to the lake. Evergreen forest in the valley bottoms gives way to woodlands on the slopes and grassland on the ridges (Goodall 1986). From north to south the park contains 3 chimpanzee communities: Mitumba, Kasekela, and Kalande. The Kasekela

community was fully habituated by 1966 and individuals were sometimes provisioned with bananas at an artificial feeding area until 2000. Pairs of Tanzanian field researchers have conducted daily all-day focal follows in the Kasekela community since 1975 during which they record party composition and location every 15 min. They also note the behavior of the focal individual and major events in the party (Goodall 1986). During the years of the incidents reported here (1993–2006), the population of the Kasekela community grew from 44 individuals to 62 individuals. Efforts to habituate the Mitumba community began in 1988, but the core members were not fully identified until 1995. Researchers have conducted daily, focal follows in Mitumba since 1994 via the methods described in the preceding text. In 1994, the Mitumba community contained 22 known individuals, as well as additional unidentified individuals. In 2005, the community comprised 22 individuals.

Videographer William Wallauer (W.W.) began filming at Gombe in 1993. He followed and filmed adult female Gremlin for 19 d from late pregnancy to 5 d after she gave birth in 1993. He was joined by researcher Charlotte Uhlenbroek, who took notes on a tape recorder during an attack on Gremlin. W.W. filmed the same female after 2 more births in 1998 and 2004. Researchers Carson Murray (C.M.) and Emily Wroblewski (E.W.) followed chimpanzees during several field seasons between 2001–6 and 2005–7, respectively.

We describe 7 recent events that illustrate aggressive competition among females: 2 attacks by adult females on an adolescent female attempting to immigrate, the aftermath of an infanticide apparently committed by adult females, 3 cases of aggression toward new infants, and 1 case in which a mother took an infant from her daughter, possibly to protect it from aggression by another female. Because the events are rare and unusual, with few reports of similar events available in the literature, we provide detailed narrative descriptions based on the notes of observers and, when available, videotape.

Maternity Leave

To determine whether females isolate themselves from others when about to give birth, we compared the length of a female's absence from observation records around the time of parturition (maternity interval) with the length of her absences at other times (intersighting interval). We have compiled a record of sightings during daily follows and arrivals at the artificial feeding area for all individuals in the Kasekela community from 1974 to 1993. For 51 births to 22 females during the 20-yr period (1–5 births per female), we measured the number of days that the female was unobserved around the birth and compared it to the mean number of days between sightings of the same female in the year surrounding the birth (182 d before and 182 d after the birth).

Results

Attacks on an Immigrating Female by Mitumba Females

In 2004 and 2005, Mitumba females made a series of brutal attacks on Schweini, an adolescent female from the Kasekela community. Schweini was born in 1991. At the

time of the attacks, her mother, adult sister, and her sister's daughter all lived in the southern part of the Kasekela range. Schweini experienced her first maximally tumescent sexual swelling during which she mated with an adult male in her natal community in January 2004. Schweini first tried to immigrate into the Mitumba community in February 2004. She was severely attacked and returned to the Kasekela community the next day. In October 2005, a female that was probably Schweini joined the Mitumba community for 3 d and was attacked again. We relate the observations in detail below.

February 21, 2004

Researchers Gabo Paulo and Simon Yohani followed adult female Flossi and her juvenile and infant sons within the range of the Mitumba community. At *ca.* 1000 h they heard distant pant-hoots and waa-barks, and Flossi walked quickly toward the calls. They arrived at 1008 h to find a large party consisting of most of the community members: 3 adult males, 6 adult females and their offspring, 2 natal adolescent females, and a juvenile female orphan (Table I). On the ground, several chimpanzees attacked a young female unknown to the observers (later identified as Schweini). She was screaming and covered in grass. She did not have a sexual swelling. Over the next 9 h, until 1946 h, females of the group attacked Schweini ≥ 13 times; in ≥ 8 of them, ≥ 2 females attacked her simultaneously. In 4 cases, there was a single attacker. In between the attacks some of the females approached and inspected Schweini's wounds and genital area, and even groomed her. When possible, the observers identified the attackers. The number of physical attacks, threats (chases or aggressive approaches), and affiliative behaviors recorded for each of the Mitumba females present are in Table I. In 5 group attacks and 3 group threats by females, the identities of the females were unspecified (females in Table I). In cases where the female's identity was specified, all the aggression was by younger females ($R^2=0.46$, $p=0.065$, $N=8$, simple linear regression of age and combined number of attacks and threats). Among females known or suspected to be immigrants the number of attacks and threats correlate negatively with the minimum number of years since immigration ($R^2=0.76$, $p<0.05$, $N=6$, simple linear regression). The 2 natal females were as aggressive as the young immigrant females (Table I).

None of the males attacked Schweini; instead they frequently protected her. One or more of the 3 adult males intervened and stopped 10 of the attacks by displaying at and sometimes attacking the Mitumba females and then staying near Schweini. Some of their attacks on the resident females were severe but did not cause discernible injuries. In one case, one of the males tried to hit a resident female with a stick. At least one other attack on Schweini appeared to stop because the attacker noticed the presence of the adult males. On ≥ 5 occasions, the females appeared to be preparing for a new attack on Schweini but were prevented by ≥ 1 of the males moving nearer her, displaying at, or attacking the aggressive females. From 1600 h on, Rudi was the closest of the males to Schweini; he interrupted attacks on her, and she tried to follow him. He eventually escorted her away from the rest of the group and the observers lost them.

Schweini received serious wounds during the attacks. By mid-day she had a deep wound on the top of her head that bled heavily. Later in the afternoon she had bleeding wounds on her neck, hands, genital area, legs, toes, and the soles of her

Table 1 Behavior of adults and adolescents present during attack on Schweini in Mitumba, February 21, 2004

Individual ^a	Age (yr)	Minimum yr since immigration	No. of offspring	Age of youngest offspring (yr)	Aggression ^b	Intervention	Inspect wounds	Inspect genitals	Groom
<i>Vincent</i>	28					6	1		
<i>Rudi</i>	18					9			3
<i>Edgar</i>	15					4			
Eva	39	16	1	7.3					
Aphro (K)	31	16	1	5.9					
Loretta	24	11	1	3.1					
Konyagi	20	9	1	2.8	A4 T2		1	1	1
Flossi (K)	19	8	2	2.3	A1 T3			1	1
Darbie (K)	20	5	0		A3 T4		1		4
Vánilla	16	Natal	0		A4 T2				1
Bima	16	Natal	0		A2				
Females					A5 T3				

^a Italics = males; regular font = females; (K) = immigrant from Kasekela.

^b A = attack; T = threat; numbers = number of events.

feet. Though she sometimes tried to join the adult males, she was unable to keep up with them because of her wounds.

The next day, C. M. found Schweini back in the northern part of the Kasekela community range with a deep wound on her head exposing her skull and numerous other wounds. We regularly observed Schweini in the Kasekela community for the rest of 2004 and 2005, until October 2005. She resumed cycling in November 2004, and cycled regularly and mated through 2005.

In October 2005, a female unknown to the observers again joined the Mitumba chimpanzees. Her small size, apparent lack of fear of the observers, and the fact that Schweini was absent from Kasekela suggest that she was probably Schweini.

October 21, 2005

Ramba Hilali and Selemani Hamisi followed 19 members of the Mitumba community from their nests (Table II). They traveled and fed in the central part of their range. Nulliparous female Mgani had a sexual swelling and mated with a juvenile male. Nulliparous female Darbie had a partial swelling. At 1024 h observers noticed a female stranger with a full swelling in the party. She stayed with them for the rest of the day. From 1024 to 1430 h, there was almost continuous commotion in the party, as the female and others screamed, waa-ed, pant-hooted, and pant-grunted. Because of the rapid action, the observers wrote only a qualitative account rather than attempting to detail each event. All the males including the juveniles mated with the stranger repeatedly and ignored the other swollen females. The stranger female was very vocal, giving sharp copulation calls as she mated and sometimes beginning her copulation calls while still approaching the male to mate. Between mating with the males, she was repeatedly pursued and attacked by the younger females, especially swollen females Mgani and Darbie; the adolescent natal female Bima; and sometimes, adult female Konyagi (Table II). The adult males repeatedly intervened to stop the attacks. By 1400 h the observers noted that because she had been continuously engaged in copulating, being attacked, screaming or calling, and not feeding at all, she was hoarse and exhausted. They also noted that the 2 adult males seemed tired from intervening. At 1430 h most of the females left the party, leaving the 2 adult males and Konyagi, Mgani, and Bima with the female. Some rejoined the party at 1630 h and nested with them. Unlike the 2004 episode, the observers noted no wound.

The female remained in the community for the next 2 d, staying close to adult male Edgar in smaller parties and mating with him repeatedly. Observers recorded 2 additional incidents of aggression with females. While Mgani was grooming the female, she put her mouth close as though to pick off a tick, and then bit her. The female screamed and Edgar chased Mgani. Another time, when Bima, with hair erect, looked ready to attack, the female screamed and Edgar chased Bima.

We observed Schweini sporadically in her natal Kasekela community in late 2005 and throughout 2006, where she gave birth in September 2007.

Probable Infanticide by Mitumba Females

In 1994, researchers witnessed a female eating the infant of another female in Mitumba. The mother of the infant was Rafiki, a parous female first recognized in

Table II Behavior of adults and adolescents present during attack on immigrant female (probably Schweini) in Mitumba, October 21, 2005

Individual ^a	Age (yr)	Minimum yr since immigration	No. of offspring	Age of youngest offspring (yr)	Aggression ^b	Intervention	Mate
<i>Rudi</i>	19.3					++	++
<i>Edgar</i>	16.3					++	++
Eva	40.3	17.3	1	1.4			
Aphro (K)	32.3	17.3	1	7.6			
Loretta	25.3	12.7	1	4.8			
Konyagi	21.3	11.3	1	4.5	A+		
Flossi (K)	20.7	9.8	3	0.5	A++		
Darbie (K)	21.6	6.9	0		A++		
Lucy (I)	18.3	4.8	1	3.8	A++		
Mgani (I)	14.3	1.4	0		A++		
Bima	17.3	Natal	0		A++		

^a (K) = from Kasekela; (I) = known immigrant. Italics=males; regular font=females; (K)=immigrant from Kasekela; (I)=immigrant from another community.

^b A = attack. Behavioral events were not quantified in the report: + = small number of events, ++ = large number.

the community in 1988. She had a juvenile son estimated to be born in 1986, and had lost an infant daughter to infanticide by the Kasekela males in 1993 (Wilson *et al.* 2004). Observers first saw her next infant on February 10, 1994, age <2 mo.

On February 17, 1994, Gabo Paulo, searching for chimpanzees, heard distant waa-barks and screams at 1624 h and traveled to the area, which was in the heart of the Mitumba community range. At 1655 h, he heard noises from an infant and located a party of chimpanzees climbing into a large tree, making a great deal of noise including food-grunts, growls, pant-hoots, waa-barks, and screams. He counted a total of 16 chimpanzees: 1 adult male, 7 adult females, 2 adolescent females, and 6 infants and juveniles. He recognized and named 9 individuals in his notes, including 3 adult females and their young, and an adolescent female. On the basis of their behavior and their central positions in the tree, he believed that the unnamed individuals were also members of the Mitumba community that were not yet habituated.

As Paulo arrived, he saw adult male Gorbachev attack adult female Moeza, pulling and pushing her by the shoulders repeatedly while she held onto a tree. Gorbachev then displayed and left. At the top of the tree, an unidentified adult female with a bald head fed on what Paulo initially assumed to be a colobus carcass. At 1742 h, Paulo realized that this was actually the carcass of an infant chimpanzee. He inferred that it was Rafiki's infant because it was missing and Rafiki was limping and dangling her left hand. Next to the female with the carcass sat an unidentified female with a ventral infant and a juvenile and another unidentified female. The other females and young were lower in the tree. At 1700 h, the female with the

Table III Presence and age of individuals during each incident involving Gremlin

Female	Offspring	February 17, 1993	July 15, 1998	January 18, 2004 ^a	April 29, 2006
Gremlin		22 (middle)	28 (middle)	33 (middle)	35 (high)
	<i>Galahad</i>	4.9	10.3		
	Gaia	Newborn	5.4	10.9	
	Golden, Glitter <i>Gimli</i>		Newborn	5.5 newborn	2.0
Gaia	<i>Godot</i>				13 (low) newborn
Gigi		39 (high)			
	<i>Mel</i> (orphan)	9.1			
Fifi		35 (high)	40 (high)	46 (high)	
	Fanni				
	Flossi	8.0			
	<i>Faustino</i>	3.8	9.2	14.7	
	<i>Ferdinand</i>	0.5	5.9	11.4	
	Flirt		In utero	5.5	
	Furaha			1.3	
Fanni		11.9 (low)	17 (middle)	23 (middle)	25 (middle)
	<i>Fax</i>	0.8			
	<i>Fudge</i>		1.6	7.1	9.1
	<i>Fundi</i>			3.6	5.7
	Familia				1.8

Regular font = females; italics = males. Age of each individual on each date is in yr. Dominance rank of adult females is in parentheses (low, middle, or high).

^aOther individuals were also present; see text.

carcass hit out with it at the 2 nearest females as they approached her, scattering them and then climbing higher. They followed and sat close to her again. The infant's intestine was hanging down, and the juvenile touched and sniffed it. At 1709 h, 1 of the females sitting lower in the tree with the others noticed Paulo. All the females were startled and stared at him, and some of them started to climb down. By 1740 h, several of the chimpanzees had left. Remaining in the tree were the female with the carcass, the female with the 2 offspring, Rafiki and her son, and Aphro and Moeza and their offspring. At 1742 h, the female with the 2 offspring exited the tree, followed by the female with the carcass. Rafiki tried to pass Aphro and Moeza to follow the female with the carcass as they all climbed down. The party traveled fast and the female with the carcass was nervous of the observer and sped up when she saw him. Paulo heard many pant-grunts in the party ahead but could not see them. He lost the party at 1836 h.

Rafiki continued to reside in the Mitumba community and she gave birth to twins in March 1995, but she and they died in April 1996 during a respiratory epidemic. The infants of 3 other Mitumba females that were born in 1995 disappeared in their first 2 mo of life.

Attacks on a Kasekela Female and Her Successive Newborn Infants by Kasekela Females

Between 1993 and 2004, adult female Gremlin gave birth to a daughter, twin daughters, and a son. All infants survived, but 3 females (Fifi, Gigi, and Fanni) severely attacked Gremlin after the birth of her daughter, and 2 females (Fifi, Fanni) attacked her *ca.* 2 d after the birth of the twins. Fifi was again aggressive after the birth of Gremlin's son, but the presence of adult males probably prevented an attack. In 2006, Gremlin took her daughter's newborn infant after the approach of one of her former attackers (Fanni), perhaps as a defensive measure. The ages and dominance ranks of the participants and their offspring in each incident are in Table III.

Gremlin was born in the Kasekela community in 1970 and remained there as an adult. She was middle-ranking during the first 3 incidents and high-ranking during the fourth. Of the attackers, we first identified Gigi in the Kasekela community in 1963 as an adolescent. She remained in the community as a large, high-ranking and sterile adult, and died in 1994. We first identified Fifi in 1963 as the 5-yr-old daughter of high-ranking female, Flo. Fifi remained in the community and gave birth to 9 infants, 7 of which were still living in 2007. She attained high rank in 1978 and maintained it until she disappeared and died in 2004. Fanni, Fifi's daughter, was born in 1981. She remained in the community and gradually rose in rank with age.

Attack on Gremlin and Gaia

W. W. followed Gremlin continuously February 1–19, 1993 in her normal core area. She nested alone with her son, Galahad, on the 12th and they remained alone the next day. On the morning of the 14th, Gremlin was obviously uncomfortable and spent long periods resting. When she traveled, she frequently stopped to stare back at the trail and then looked around in all directions before moving on. Eventually she

made a large nest and gave birth at 1835 h. There were pant-hoots in the distance after the birth but Gremlin did not respond. In the 2 d after the birth, Gremlin stayed alone with her infant and son in the vicinity of the birth site. There were ≥ 3 bouts of distant vocalizations over this period and each time Gremlin looked in their direction but remained silent.

In the afternoon of February 16, an adult male and low-ranking adult female joined Gremlin briefly. She greeted them nervously but there was no aggression. Later, a low-ranking adult female and her juvenile son joined Gremlin with no aggression, nested in the vicinity, and left the next morning. On the 17th, Gremlin traveled for the first time away from the birth area, feeding and making several nests in which she rested through mid-day and into late afternoon.

At 1717 h, while Gremlin was feeding (with her infant clinging to her belly and her juvenile son nearby), Fifi and her family (Table III) arrived beneath the tree. Gremlin gave loud submissive pant-grunts, then pant-hooted as she looked down at them. Fifi's family joined in the pant-hoots. Gremlin waa-ed. Fifi's daughters Flossi then Fanni climbed into the vines near Gremlin and she panted-grunted and pant-hooted. Then Fifi, with her infant clinging to her belly, displayed up into the vines toward Gremlin. Gremlin screamed and moved to the edge of the vine tangle as Fifi displayed bipedally and vigorously swayed the vines beside and above her for 1 min, nearly knocking Gremlin out of the tree. At 1719 h, Gremlin and Fifi gave waa-barks as Gigi and orphan juvenile male, Mel, arrived at the base of the tree. Gremlin submissively extended her hand to Fifi, pant-grunting. Gigi pant-hooted and Fifi and others joined her in a chorus. Fifi and Fanni rushed down to the ground. Fifi and Gigi greeted excitedly with erect hair and fear grins, each presenting to and being embraced by the other. Fanni peered into Gigi's face. Gremlin barked from the tree above. Gigi, Fifi, and Fanni sat on the ground and groomed, often looking up at Gremlin as she moved.

At 1722 h, Gigi led the others into the tree. Gremlin pant-grunted and barked. Fifi advanced and sat 2 m from Gremlin while Gigi sat 4 m below. Gremlin barked and turned her back to Fifi, cradling her infant and grooming her own arm. Fifi sat staring at the infant. Faustino approached Gremlin and put his face close to the infant. Gremlin grunted softly and pushed his head away. Fifi, then Faustino, pulled over a branch on which Gremlin had previously been sitting and sniffed the leaves. Gremlin watched, then she walked along a branch, passing ≤ 1 m of Fifi, constantly glancing up at her and giving small grunts. For the next 30 min, the 3 adult females were out of sight in the vines. Occasionally Gremlin pant-grunted and barked.

At 1757 h, Gremlin and the other 3 adult females reappeared at the top of the vine tangle. There were distant calls and the whole party responded with waa-barks. Gremlin pant-grunted and then started to scream, with the other females close around her. At 1800 h, all the females were screaming. For the next 16 min the 3 adult females made a series of concerted displays and attacks on Gremlin in the trees. Both Fifi and Fanni had their infants clinging to their bellies throughout the attacks and Fifi's juvenile offspring, juvenile Mel, and juvenile Galahad followed along, watching, but not participating. Fifi was the most active aggressor. Before the initial attack Fifi embraced Gigi, pulling her into the chase. Gigi and Fanni kept up with Fifi as she chased and displayed at Gremlin, and all 3 females surrounded Gremlin whenever she stopped, with Gigi generally closer to Gremlin and Fanni more to the

side. Fifi made violent displays, swaying branches beside Gremlin, and hitting her with their tips. Fifi kicked, slapped, and punched Gremlin several times, and at one point swung from her arms and kicked violently at Gremlin's infant ≥ 5 times. Fifi made several obvious grabs for the baby. Once Gremlin lunged back at Fifi, pulled hard at the hair on her head, and screamed in her face before jumping away. At other times, Gremlin crouched over her infant, fending off the blows and turning her back as Fifi and Gigi, in contact with her, milled around her trying to reach the infant. While they surrounded Gremlin, Fifi reached out a hand to touch Gigi, and another time put her hand in Gigi's open mouth as they both screamed. Fanni also embraced Gigi. At least twice, Gremlin reached to touch Fifi in appeasement. Several times, the females chased Gremlin up to the top of the vine-covered trees, forcing her to escape by making ≥ 5 great leaps, including one of ≥ 10 m, into trees below. During these attacks there were several choruses of pant-hoots from a distant party that came closer. At least once, Gremlin, and another time Gigi, responded with loud pant-hoots and the other females joined in.

At 1816 h, Fifi cornered Gremlin high in a tree and pant-hooted and stamped her feet. Gremlin also pant-hooted. From this time on there were no more attacks, but the females remained very excited. Fifi and later Gigi inspected Gremlin's vagina at length by poking a finger and sniffing, and Gigi groomed Gremlin. Gremlin once reached her hand into Fifi's mouth, and once into Gigi's mouth, while barking. Gigi put her hand in Fifi's mouth as both screamed. At 1825 h, the approaching party arrived at the bottom of the trees with loud hoots and pant-grunts. The party consisted of the rest of the females from the northern neighborhood (Williams *et al.* 2002, Fig. 3): high-ranking adult female Patti, her 5-yr-old infant and adolescent daughter, mid-ranking adult female Candy, her juvenile daughter California, and low-ranking adult female, Skosha. As the individuals climbed the tree, Fifi approached Patti, barking with a fear grin. Patti, screaming, presented to her and Fifi mounted her, touching her bottom with her hand. Others pant-hooted.

The group remained in the large tree for the next 15 min. Gremlin sat alone, high on a branch, ≥ 5 m from the others. The group gave several choruses of pant-hoots, at least one initiated by Gremlin. At 1851 h, most of the group climbed down and left, but Patti, Skosha, and California remained in a tree next to Gremlin's and Gremlin pant-grunted whenever Patti moved. At 1915 h, as darkness fell, Gremlin gave a soft pant-hoot. There was no reply. At 1933 h, Skosha and California climbed down. Patti remained resting on her branch, apparently waiting for Gremlin. At 1937 h, Gremlin started to move in the direction of the others. Galahad left his nest and followed. Immediately, Patti climbed down the same route that the others had taken. Patti reached the ground and started to walk away. Halfway down the tree, Gremlin stopped abruptly and rushed back up the tree and hurriedly moved through the trees in the opposite direction. Then she climbed down to a path and ran with Galahad for about half a km away from the others in the dark. At 1955 h, she was sitting in a tree and had not made a nest when the observers left.

W. W. observed Gremlin and her family alone the next day, and found them again the following day (19th) feeding in a tree with Fifi, her family, Fanni, and Fifi's adult son, Frodo. Gremlin stayed close to Frodo, and at least once moved to his other side when Fifi approached. Later that day they joined a large group including many adult males and females.

Attack on Gremlin and Twins

We last observed Gremlin before the birth on July 10, 1998. On July 15, Gremlin arrived at the artificial feeding area at 0940 h with her 2-d-old twins, juvenile daughter, and adolescent son, Galahad. W. W. filmed her behavior all day. Gremlin greeted α -male Frodo submissively. Two other adult males and an adolescent female were there at the beginning, and 3 other adult males arrived later. Gremlin was very submissive to all the males. They showed interest in the twins but no aggression. At 0948 h, Fanni and her 1.5-yr-old son, Fudge, arrived. Fudge ran up to Gremlin and kissed her mouth, then presented. Gremlin groomed him. Fanni sat 1 m away staring at the twins, bowing her head to get a view of them under Gremlin's arm. Fudge made several attempts to look at the twins and Gremlin fended him off with her hand. Gremlin sat close to Frodo and followed him whenever he moved away, pant-grunting and often grooming him. She initiated pant-hoots, which were joined by others. When Gremlin moved, Fanni sniffed the ground where Gremlin had been sitting and followed her to stare at the twins. Each time Fanni approached, Gremlin moved around Frodo, keeping him between her and Fanni.

At 1025 h, the males departed and later gave distant pant-hoots. Fudge approached Gremlin again, peered at the twins, then squeaked and ran to Fanni as Gremlin emitted a mild cough-threat and pushed him away. At 1040 h, Gremlin left the feeding area, walking slowly with one hand supporting the twins and often stopping to rest. Fanni followed, looking at the twins. Gremlin emitted a cough-threat. Gremlin pant-hooted on 2 occasions but Fanni remained silent. At 1100 h Gremlin climbed a tree with her offspring, while Fanni walked on out of sight.

At 1420 h, Gremlin descended and traveled slowly on. At 1438 h, Gremlin was lying on the ground when she saw chimpanzees approaching: Fifi's 2 juvenile and adolescent sons (Ferdinand and Faustino) in front with Fifi, Fanni, and Fudge in the distance (Table III). Gremlin quickly sat up, cradling her twins and panting. Ferdinand approached her and crouched with a fear grin, looking at the twins. Gremlin kissed him and pushed him away with her mouth. Faustino approached in an aggressive, bipedal swagger and Gremlin, screaming, hit at him. He presented to her. Gremlin stood bipedal, holding her twins and screaming and then pant-hooting as she watched Fifi and Fanni arrive. Fifi pant-hooted. Gremlin retreated from the young males, barking, and Fanni arrived and sat 5 m away, staring at the twins, with a glance back to Fifi. Fifi sat 5 m away with hair erect, staring intently at the twins. For 15 min, they all stayed on the ground. Fifi's sons tried to look at the twins, but Gremlin's offspring Galahad and Gaia stayed between them and Gremlin. When Gremlin moved, Fifi and her sons sniffed the spot where she had been sitting.

At 1459 h, Fanni stood and Gremlin pant-barked then stood, supporting the twins with one hand and reaching the other submissively to Fanni, then sat. Fanni backed up to her, making contact, squeaking with a fear grin. Gremlin squeaked and walked away as Fanni (with Fudge ventral) and Fifi followed her closely. Gremlin started to run bipedally and then tripped on a rock and screamed with the others chasing her. Fanni rolled the rock in a display and Fifi stood bipedally. Fanni reached back to Fifi with a fear grin. All sat. At 1501 h, Gremlin pant-grunted as Fanni extended her wrist toward Gremlin's mouth, then she kissed Fanni's hand, squeaking. Fanni withdrew her hand and rolled the rock in a display. Gremlin pant-grunted and

hunched over the twins. At 1504 h, Fanni and Fifi came around in front of Gremlin. Gremlin pant-grunted and then barked as Fifi grabbed a thick hanging vine attached to a tree on the ground behind Gremlin. Fifi displayed and repeatedly thrashed Gremlin on the shoulders with the vine. Fanni, with Fudge ventral, moved in front of Gremlin and with an aggressive, compressed-lips face, and pulled the vine down onto Gremlin's head several times. Fifi displayed bipedally next to Fanni, swinging her arms to and fro so that one touched the twins. Then Fanni reached and grabbed at the twins. Gremlin, screaming, lunged forward and grabbed Fanni's head and hit at her several times. Fanni, screaming, stood bipedally and pounded Gremlin on the head with each hand many times as Gremlin hunched over the twins and made a few punches at Fanni. Fifi watched from <1 m away with Ferdinand on her back, then followed them into the undergrowth where all 3 females grappled in contact, screaming loudly. Sequences of the attacks appear in the BBC film *Chimpanzee Diary* (BBC 1998).

At 1505 h, Gremlin broke away and ran, supporting the twins with one hand and screaming. Fanni followed, grabbing the hair on Gremlin's back. Fanni and Fifi chased Gremlin with aggressive grunts. After running 15 m, Gremlin rushed 10 m up a tree and sat on a branch with her back to the 2 females, who climbed after her. Fifi climbed over Fanni and past Gremlin so that she was surrounded. Gremlin waa-ed. For the next 25 min, Fifi stayed beside Gremlin in the tree, often looking at the twins, while Fanni sat behind her, blocking her way down. At 1506 h, 1512 h, and 1517 h, Fifi gave 3 vigorous displays beside and over Gremlin, despite the fact that she was heavily pregnant and sometimes seemed to lose her balance. She stood bipedally on the branch, holding other branches above her and swayed the branch on which Gremlin was sitting violently to and fro. At other times she thrashed Gremlin with branches. Gremlin waa-ed, screamed, and struggled to remain seated. Once Gremlin reached out her hand and held Fifi's bottom, whimpering. Fifi grinned briefly but then compressed her lips and displayed some more. Another time Gremlin put her fingers to Fifi's lips and Fifi leant forward and kissed Gremlin's palm. After her last display, Fifi moved around Gremlin and inspected and sniffed her vagina as Gremlin barked.

At 1508 h, there were distant pant-hoots, and both Gremlin and Fifi responded. Gremlin gave 2 more rounds of pant-hoots at 1520 h and 1544 h, but there was no reply. From 1518 h, Fifi stayed close to Gremlin for 30 more min, blocking her way down the tree, frequently looking at the twins while Gremlin turned away. Fanni sat on the ground below. At 1549 h, Gremlin turned and extended a hand to Fifi, pant-grunting, but Fifi just looked at her. At 1552 h, Fifi finally exited the tree and walked away with her family. Gremlin descended and walked in the opposite direction. She met Patti, her juvenile daughter, and infant son, and pant-grunted but there was no aggression. Later in the evening, Gremlin met Fifi and Fanni with no further incident. Fifi gave birth on July 20, 5 d after the attack.

Aggression Toward Gremlin and Gimli

We last observed Gremlin before Gimli's birth on January 8, 2004. C. M. next observed her with a new baby on January 17 and followed her until she nested. The next day W. W. followed and filmed her. She spent the morning alone with her 5-yr-old twins, traveling, feeding, and resting in several nests. There were sporadic choruses of

pant-hoots from a distant party. In the afternoon she climbed down and headed in the direction of the party. When the party called again from nearby, Gremlin pant-hooted for the first time, evoking a volley of calls.

As Gremlin joined the group her daughter Gaia rushed up, screaming with a fear grin. She hunched over her mother and then stepped aside as others approached to inspect the new baby. Gremlin's brother Gimble approached with hair erect and looked; then Sheldon, the α -male, arrived. Sheldon climbed after Gremlin, who rushed to him submissively. Fanni approached to inspect the baby and Gremlin climbed down away from her and sat near Gimble, with nervous looks and calls, then rushed to Sheldon and sat again, calling. Some group members sat nearby and stared. When the younger individuals approached very close, Gremlin threatened them away.

Later, Gremlin was in a tree with some females and the males had moved further on. Fifi arrived at the tree and approached quickly, climbing 5 m to where Gremlin sat on a low branch. Gremlin pant-grunted, but Fifi stood with hair erect and started to rock back and forth in a display with her infant on her belly. Gremlin screamed and leapt to the ground and ran, then walked rapidly away, screaming and looking over her shoulder. Fifi pursued but was not able to catch up to Gremlin before they disappeared from view in the direction that the adult males had gone. Other chimpanzees followed as Gremlin and Fifi disappeared.

When W. W. caught up to the group, chimpanzees were screaming and charging and displaying in all directions. Sheldon and Gimble were there and Gremlin had reached them before Fifi caught her. Between the male displays, Gremlin submissively approached and groomed Sheldon and several of the other males, and stayed close to them. At one point, Fanni was chased and attacked by a male. Fifi sat to the side staring at Gremlin, but showed no further aggression. Gremlin remained with the group for the rest of the day, maintaining close proximity to the adult males.

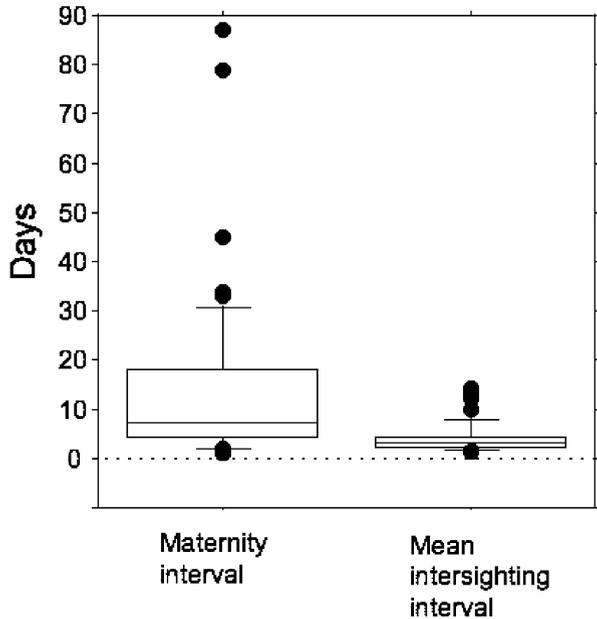
Gremlin Takes Gaia's Infant

We last observed pregnant Gaia without an infant on April 27, 2006. In the evening of April 29, E. W. and Matendo Msafiri started following Fanni with her 3 offspring (Table III). At 1730 h, Fanni and her family encountered Gremlin with her son Gimli and adult daughter Gaia, who had a newborn infant (Wroblewski 2008). As Fanni approached the other females, the observers heard pant-grunts from them, and Gremlin took Gaia's infant from her. Both Gremlin and Gaia seemed fearful of Fanni, though Fanni did not exhibit any aggression. Gremlin was protective of the baby, and Gaia did not attempt to get it back. Gremlin kept the baby from that day on, nursing both it and Gimli, until September 25, 2006 when the baby died (Wroblewski 2008).

Maternity Leave

Females were absent from observation significantly longer around the time of parturition than at other times (Fig. 1, median maternity interval=7.0 d, range=1–87 d; median intersighting interval=2.8 d, range=1.4–14.3 d; $n=51$ births to 22 females, $p<0.0001$, Wilcoxon signed rank test, $z=-5.1$).

Fig. 1 Comparison of the maternity interval and the mean intersighting intervals at other times. Maternity interval is the number of days that the female was not observed around the time of parturition. The mean intersighting interval is the mean of the intersighting intervals of each female during the year that she gave birth. The box-and-whisker plot contains the median and the range of the maternity interval for all births and the median and range of the mean intersighting intervals of the mother for all births. Horizontal lines indicate the 10th, 25th, 50th, 75th, and 90th percentiles. Boxes enclose the interquartile ranges.



Discussion

Our observations provide further evidence of severe aggression by female chimpanzees toward other females in 2 contexts: aggression toward immigrating females and aggression toward females of the same community when they have just given birth.

Aggression Toward Immigrant Females

Researchers have described aggression toward immigrant females by resident females at several sites: Gombe (Goodall 1986; Pusey 1980), Mahale (Nishida 1989), Tai (Boesch and Boesch-Achermann 2000), Kanyawara (Kahlenberg *et al.* 2008; Muller 2002). The cases involved chases, displays, and attacks, sometimes by several resident females together, but none resulted in injury. The aggression Mitumba females directed at Schweini is the most severe described so far. However, Goodall (1986, p. 501) reported that 3 young females (in 1966, 1977, and 1983, respectively) bore severe wounds similar to the ones inflicted on Schweini after absences during which they likely visited other communities.

Several factors may have contributed to Schweini's violent reception. 1) Unlike most immigrating females (Boesch and Boesch-Achermann 2000; Nishida *et al.* 1990; Pusey 1980), she did not have a sexual swelling at the time of her first immigration attempt. She was also at a very early stage of her reproductive career, having only just started full sexual swellings and was thus relatively unattractive to adult males (Muller *et al.* 2006; Wrangham 2002). Though the males repeatedly came to Schweini's rescue, they may have been more motivated to stay close to her had she been sexually receptive and older. 2) Schweini is a small female and was

greatly outnumbered by the resident females. 3) Female competition for space in Mitumba may be particularly severe because the community lies between the park boundary and the larger Kasekela community in a relatively small range. However, another female (Mgani) immigrated successfully into Mitumba in 2004 shortly after the first attack on Schweini. In contrast to Schweini, Mgani was fully swollen during her first visit and mated frequently with adult males. Though she received some aggression from the resident females in the first weeks, she was a large, assertive female and even successfully fought back against Flossi, one of the high-ranking resident females (D. Mjungu, *pers. comm.*).

Though all the resident Mitumba females were present during Schweini's visits, some were much more aggressive than others. On her second visit, she was swollen and mated frequently with all the males, and the most aggressive females were those with swellings. The observers interpreted the behavior as sexual jealousy (Goodall 1986; Nishida 1989). On the first occasion, however, when there was no mating, the same young females also attacked her. In general, there is a negative correlation between age, immigrant status, and aggression given such that the youngest and presumably least settled females were the most aggressive. The finding is in contrast to that of Kahlenberg *et al.* (2008) that at Kanyawara high-ranking resident females are more aggressive to immigrants than natal females are. Interestingly, one of the aggressive natal females, Bima, subsequently remained in Mitumba and gave birth in May 2007, and thus clearly benefited from preventing Schweini from joining the community.

Suspected and Attempted Intracommunity Infanticides

The incidents of a Mitumba female in possession of a dead infant of a community member following sounds of a fight and of females in Kasekela attempting to seize the infants of a female neighbor, together with recent observations of infanticide by females at Budongo (Townsend *et al.* 2007), provide further evidence that infanticidal behavior by female chimpanzees is a general phenomenon rather than an aberrant behavior unique to Passion and Pom.

Examination of 42 yr of demographic records allows us to estimate the frequency of infanticide by females at Gombe. All the infanticidal attacks by females involved newborns, the oldest of which was 60 d. Of 114 live births to regularly observed females in the Kasekela community between 1965 and 2007, 13 infants (11.4%) died within the first 2 mo. Four of them died of causes other than infanticide (Williams *et al.* 2008). Three were observed and one was strongly suspected to have been killed by Passion and Pom, and 2 more disappeared during the same period (1974–1976; Goodall 1977). Of the remaining 3, Sophie's baby disappeared from one day to the next in 1966, and was presumed to have been killed (Goodall 1977). The second, Sprout's baby, disappeared in 1984 in its first 3 weeks during an absence by Sprout of 14 d, and the third, Kipara's infant, disappeared in 2004 at age 2 mo, and his mother bore wounds when researchers first observed her without him. Kipara was an immigrant female who briefly visited the community in 1997 and immigrated permanently in 2000. She had previously lost a 4-mo-old infant in 2000. It is possible that her initial peripheral status made her vulnerable to infanticide by community males (Hamai *et al.* 1992; Murray *et al.* 2007b; Nishida and Kawanaka 1985) and females, but after 2000 she mated frequently with all the Kasekela males,

making infanticide by males less likely. Infanticide by females thus accounts for the mortality of $\geq 3.5\%$ (including only known killings) and $\leq 7.9\%$ (including all infants that vanished in the first 2 mo) of infants resulting from live births in the Kasekela community. In the Mitumba community, of 21 live births between 1994 and 2007, 1 infant died in 1994 (the case described here), probably the victim of infanticide by females, and 3 others vanished within the first 2 mo, all in 1995, giving a minimum of 4.8% and a maximum of 19% mortality due to possible infanticide by females.

The rate of possible infanticide by females is increased further if we include in our calculations apparent full-term pregnancies in which we never observed the infant. By examining female cycling patterns and other information indicating a recent birth, Goodall (1977, 1986) identified 12 apparently full-term pregnancies from 1965 to 1984. Three occurred in 1966–1968, after the year that Sophie lost her baby, and a further 5 occurred between 1973 and 1978 around the period that Passion and Pom attacked and killed infants. Consideration of just the period of 1965–84 gives a minimum mortality rate due to infanticide by females of 7.2% (including just observed killings and known live births) and a maximum of 31.3% (including as potential infanticides all killings, infant disappearances in the first 2 mo, and full-term pregnancies in which researchers observed no infant). Identification of pregnancies in which no infant was observed for 1985–2007 awaits future analysis.

The data suggest that successful infanticide by Gombe females is generally rare, but clumped in time, with a known bout occurring in the late mid- to late 1970s in Kasekela, and possible bouts in the late 1960s in Kasekela and the mid-1990s in Mitumba. A likely reason is that despite advantages that females may gain from infanticide, the risk and difficulty of attacking another female usually outweigh the benefits. Factors leading to success in female aggression—a strong power differential between attacker and victim in terms of rank, physical condition, and the presence of committed allies—may only occasionally occur together (Nishida 1989). During Passion's killing spree she was 1 of the 2 high-ranking females in the community. Her victims in the observed killings were mid- and very low-ranking, respectively, and both were partially paralyzed by polio (Goodall 1977). The mothers of all the other females whose infants disappeared also ranked below Passion. In addition, Passion was closely aided in these attacks by her daughter, Pom, but even so, 1 victim put up a determined defense during a 10-min fight (Goodall 1986, p. 351). An attack by Passion on another female with a newborn appeared to fail because Pom did not participate (Goodall 1986, p. 355). At Budongo, the power differential between victim and attackers was overwhelming. Six resident females together attacked a presumed recent female immigrant (Townsend *et al.* 2007). The identity of the killer(s) in the 1994 Mitumba incident is unknown. However, the female in possession of the infant's carcass was not carrying a dependent infant and her bald head and assertive behavior suggests that she was a mature, high-ranking female. We suspect the female next to her in the tree was a mother (Baharia) later identified and known to die in a respiratory epidemic in 1996, leaving 2 orphans. It is possible that the 2 females collaborated in attacks in 1994 and 1995 and that the death of ≥ 1 of them ended the collaboration.

Our detailed observations of attacks on Gremlin reveal the challenges of attacking a healthy female. At the time of the attacks, Fifi and Gigi were 2 of the 3 high-ranking females in the community in 1993, and Fifi 1 of the 2 in 1998 (Murray *et al.*

2006). Nevertheless, in the 2 incidents, the females were cautious and ambivalent in their initial interactions with Gremlin and did not mount a physical attack until it was clear that they had the support of an ally. Fifi drew Gigi into the attack in 1993, and Fanni did not attack until Fifi was beside her in 1998. Despite being outnumbered, Gremlin managed to preserve her infants in each case. One difference between these attacks and those of Passion and Pom was that Passion and Pom carried out the killing attacks on the ground (Goodall 1986), while Gremlin remained in the trees in 1993 and escaped to a tree in 1998, where the considerable risks from falling (Goodall 1983) may hinder all-out gang attacks. Another difference is that both Fifi and Fanni were carrying young infants on their bellies during the 1993 attack, and Fanni was carrying an infant while Fifi was heavily pregnant in 1998. Neither Passion nor Pom had young infants during their successful attacks, but in a later unsuccessful attack, Passion had a young infant, and Pom was heavily pregnant and did not participate (Goodall 1986, p. 355).

One possible gain for a female in attacking another female's infant is meat (Hrdy 1979). However, though Passion and Pom completely consumed their victims (Goodall 1977), the victim in Mitumba was only partially consumed, and 2 of the 3 Budongo victims were not eaten (Townsend *et al.* 2007). Another possibility is that it is an extreme manifestation of female competition for resources. At Bundogo resident females attacked females that had recently immigrated during an influx that led to a considerable increase in population density (Townsend *et al.* 2007). However, at Gombe, females attacked neighbors that were long-term residents, and, in the case of Fifi, Fanni, and Gremlin, frequent companions (Goodall 1986; Greengrass 2005). We propose that by attacking new infants when they are most vulnerable, females may eliminate their competitors and those of their offspring. Female reproductive rates are lower when density is higher (Williams *et al.* 2004). Because females remain faithful to their core areas, the offspring of females whose core areas overlap with theirs represent long-term feeding competitors. Even if daughters transfer to other communities, they do not do so before the age of 10 yr, and although sons eventually start to range widely, as adults they still concentrate their space use in their mother's core area during times of low food availability (Murray *et al.* 2008). During 1976–1978, in which they attacked or killed infants, Passion and Pom resided in the southern neighborhood (Williams *et al.* 2002, Fig. 3a). The majority of their known or assumed victims resided in the northern neighborhood, but the 2 neighborhoods showed high overlap at the time (Williams *et al.* 2002, Fig. 3b) and Passion and Pom moved completely into the northern neighborhood in early 1980 after an unseen attack on them, probably by members of the southern, Kalande community (Goodall 1986; Williams *et al.* 2002). In 1988–1992, shortly before the attack on Gremlin and Gaia in 1993, Gremlin resided in the same neighborhood as Gigi, Fifi, and Fanni, and Gremlin's core area overlapped more completely with the core areas of Fifi and Fanni than with those of any other female (Williams *et al.* 2002, Fig. 3a). Gremlin, Fifi, and Fanni continued to occupy highly overlapping core areas in 1998, at the time of the attack on the twins (Murray 2006, p. 95). Fifi died in 2004, but Fanni and Gremlin continued to have high range overlap (Murray 2006, p. 96), and in 2007, Fanni and her 3 offspring now shared her core area not only with Gremlin and her son but also with her former victims, adult female Gaia, and the twins age 9 yr, all of whom still associated with

their mother Gremlin at high rates. The other high-ranking female in the community at the time of the attacks was Patti, whose core area also overlapped Gremlin's (Murray 2006; Williams *et al.* 2002). She did not attack Gremlin. However, she arrived at the scene after the attacks had stopped in 1993, and after the aggressors had left in 1998. Gremlin was submissive to her on both occasions and escaped from her in 1993.

Counterstrategies

Given the threat of aggression from other females, we might expect females to use counterstrategies to reduce it. Our analysis of maternity leave confirms Goodall's (1986) impression that females are absent from daily observation at Gombe significantly longer around the time of parturition than at other times. The hypothesis that they are away from other chimpanzees is supported by W. W.'s continuous observations of Gremlin before and after giving birth, which show that she was indeed alone with her son for >5 d, and her lack of vocalizations then and her cautious and watchful behavior on the day she gave birth suggest that she was avoiding other chimpanzees. An additional reason for an absence around the time of birth is that females are unable to keep up with other chimpanzees in late pregnancy or directly after the birth of the new infant, but this is unlikely to account for the absences of several weeks by some females (Fig. 1).

Another counterstrategy against the risk of female aggression is for females to seek the protection of males. Goodall (1977, 1986) described several instances in which adult males chased or attacked Passion after her victims had screamed in her presence or threatened her, or arrived at the scene after sounds of an attack. Goodall (1977) also showed that once females had rejoined the group with a new infant, they tended to follow and spend more time with adult males and less time alone with adult females than they did before the birth. Though researchers have not studied the pant-hooting behavior of females at any site, our observations of Gremlin's behavior suggest that she was closely attuned to the location of males. In the days before, during, and after she gave birth in 1993, she was alone and did not respond to calls, presumably because she was trying to stay away from other chimpanzees. Likewise, she did not respond to calls in 2004 until she was heading toward and about to join the calling party. As soon as she called, there were responses. In the 1993 and 1998 incidents, Gremlin was very vocal once it became clear that females were threatening her. She loudly responded to distant pant-hoots, and sometimes initiated pant-hoots on her own. Such pant-hoots would likely have attracted males to the scene had any been nearby. Nishida (1989) observed similar very vocal behavior by a newly immigrant female at Mahale. When she joined a group after the birth of her twins, Gremlin initially stayed close to α -male Frodo and kept him between her and Fanni. However, she did not follow the males when they left, quite possibly because she was able to travel only very slowly with the twins. Following the birth of Gimli, Gremlin joined a large party including adult males, and she was able to escape from Fifi's aggression and join the males, staying close to them for the rest of that day and the next.

Adult males intervene on behalf of newly immigrant females to stop aggression from resident females at Gombe (Pusey 1980), Mahale (Nishida 1989) and

Kanyawara (Kahlenberg *et al.* 2008) as the Mitumba males did on behalf of Schweini. At both Gombe (Pusey 1980, 1990) and Mahale (Nishida 1989) nulliparous immigrants tended to associate with adult males instead of with females in the first months or year after they immigrated, even when not in estrus, probably in part to gain protection from female aggression.

The extraordinary case of Gremlin taking her daughter's newborn infant may also be interpreted as protection of the infant from potential aggression (Wroblewski 2008). Because Gaia was in possession of her infant when Fanni arrived with her 3 offspring, and therefore presumably since the birth within the last 24–48 h, the fact that Gremlin took the infant immediately after Fanni's arrival suggests a causal connection. Gremlin may have perceived the risk to the baby from her old adversary and taken it from Gaia to protect it from Fanni. However, though Gremlin and Gaia were fearful of Fanni, Fanni showed no sign of aggression toward the new infant. Compared to the previous instances, the balance of power had shifted against Fanni (Table III). In the absence of Fifi, and with Gaia now an adult female, she was outnumbered.

In summary, our observations show that female chimpanzees can exhibit severe aggression, similar to that of males, when there is the potential for a high payoff: in this case, the long-term removal of feeding competitors. As a possible response to such threat, females withdraw from other chimpanzees around parturition and seek the protection of males when they rejoin the group or when immigrating to a new community. Female aggression and competition may be more intense at Gombe than elsewhere (Muller 2002; Nishida *et al.* 2003). However, infanticide by females and aggression to immigrants also occurs at other sites. Severe female aggression is rare even at Gombe, and the chance to observe it depends on the ability to follow females directly after parturition, and in the absence of males when rates of female aggression are higher (Kahlenberg 2006). Clear conclusions about the magnitude of differences between sites await further study of rates of female aggression using similar methods.

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