# New Records of Within-group Infanticide and Cannibalism in Wild Chimpanzees

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ABSTRACT. Two cases of within-group infanticide and cannibalism were observed among the M Group chimpanzees of the Mahale Mountains, Tanzania. In both cases, victimized infants were male, 5-6 months of age, and in good health when killed. Four to five years have passed since the mothers of the victims immigrated into M Group as nulliparous immigrants. In one case the 2nd-ranking male was observed to detach the infant from the mother's belly. Both infants were finally killed by the alpha male after several adult males scrambled for the bodies. There was no evidence that the mothers had mated with males other than those of M Group. Nor was there evidence that the mothers had restrictive mating relationships with some of the M Group adult males. What little evidence is available shows that the mothers had mated mostly with adolescent and other immature males during their conception cycles. However, at least in one case, the mother began to mate more with adult males rather than with immature males after the infanticide. It is proposed that the function of withingroup male infanticide can be explained by the male-male competition hypothesis developed for hanuman langurs and other nonhuman primates.

Key Words: Chimpanzee; Infanticide; Cannibalism; Mahale Mountains.

## INTRODUCTION

It has been reported from three African study sites that wild chimpanzees kill and eat infants of their own species (for review, see GOODALL, 1986; HIRAIWA-HASEGAWA, 1987). Cases reported from Mahale, Tanzania, are of special interest because adult males kill and eat those infants which not only belong to the same unit-group (community) but are likely to be their own offspring (KAWANAKA, 1981; NORIKOSHI, 1982; NISHIDA & KAWANAKA, 1985; TAKAHATA, 1985; MASUI, 1986). It has been difficult to explain this form of infanticide in terms of modern evolutionary theory. This paper reports two recent observations of infant-killing and cannibalism, reviews the previous episodes, and suggests that the function of within-group male infanticide can be explained by the male-male competition hypothesis developed for hanuman langurs and other nonhuman primates (HRDY, 1979).

# **METHODS**

Chimpanzees have been studied in the Mahale Mountains National Park for 25 years, and demographic data are available (HIRAIWA-HASEGAWA et al., 1984; NISHIDA et al., 1990). The study group, M Group, consisting of about 90 chimpanzees, has been monitored for 15 years. M Group has accepted female immigrants from other unit-groups including another study group, K Group. K Group lost adult males and became extinct around 1982

when most of the adult females transferred to M Group (NISHIDA et al., 1985; HASEGAWA, 1989; NISHIDA et al., 1990).

#### RESULTS

INFANTICIDE AND CANNIBALISM IN 1989

### Observations

On October 3, 1989, the 6th case of within-group infanticide among Mahale chimpanzees was observed. T. Asou, M. Nakamura and two cameramen of a video team of ANC Productions Inc. from Tokyo, and R. Nyundo of the Mahale Mountains Wildlife Research Centre succeeded in shooting most of the important scenes of the infanticide and cannibalism. M. H. and L. T. observed the later process of cannibalism. The following account was based on their memos and video tapes:

At 07:30, chimpanzees attempted to hunt colobus monkeys but were unsuccessful. At 07:50, chimpanzees including the 2nd-ranking male *Kalunde* and 5th-ranking male *Lukaja*, were sitting on the ground, looking at a warthog. *Lukaja* and others ran after the warthog and *Kalunde* remained alone. Then, a primiparous female, *Mirinda*, approached *Kalunde* slowly while lowering her body as if crawling on the ground, and pant-grunting. Her 6-month-old male infant was under her belly. She approached *Kalunde* from behind and assumed the presentation posture, looking back at him through her shoulder. *Kalunde* grasped and pulled her waist with his hands and covered her buttocks with pelvic thrusts. *Mirinda* screamed and tried to push him away with her left hand. *Kalunde* pulled her infant from her belly and the infant screamed, clinging more tightly to *Mirinda*. During another such tug of war, when *Mirinda* pushed *Kalunde* with her right hand, *Kalunde* detached the infant with his left hand, and ran away tripedally with the infant on his belly. *Mirinda* ran screaming after him.

After 10 min, when the infant was rediscovered, it was held by a past-prime male, Musa. Three other males, Bakali (past prime), Aji and Nsaba (both young adult), were competing for possession of the infant. Around 08:20 after a scuffle in the bush, Lukaja appeared with the infant. He was carrying it on his belly and supporting it with his left hand, while grinning maximally and screaming. Immediately after him, Kalunde, Shike (the 3rd-ranking male), and Mirinda followed. All of them grinned and screamed. The infant's right hand was already bitten and the wrist bone exposed. Kalunde prevented Mirinda from recovering the baby by standing bipedally with both arms abducted between her and Lukaja, while slapping her on the back. Kalunde, Shike, Lukaja with the baby, and Mirinda ran away in this order.

Earlier, Lukaja had hidden himself in a rock cave. Now Shike and several adult females searched for the infant there by removing vegetation covering the hole. All the chimpanzees present appeared greatly excited with hair erect; some stood bipedally and stamped the ground.

Meanwhile, *Lukaja* handed the infant to the alpha male *Ntologi*, who dragged, tossed, and slapped it against the ground. *Ntologi* climbed a tree with the infant in his mouth. He waved it in the air, and finally killed it by biting it on the face. This cannibalism was similar in appearance to chimpanzees feeding on the carcass of other species. Conspicuous competition for meat and meat-sharing was observed as usual. Three adult males and an adult female obtained meat from *Ntologi*. Two adult females, two juvenile females, a juvenile male, and an infant recovered scraps from the ground or were given scraps. At 13:00, *Ntologi* was still holding the skin of the carcass.

#### Status of Mirinda Before and After Infanticide

Mirinda was first observed in M Group in October 1984. She gave birth to this infant in April 1989. Mirinda was observed in 1988 while in estrus. She mated mostly with imma-

ture males and was never observed to mate with the alpha male *Ntologi* (K. Takasaki & H. Takasaki, unpubl. data). During her conception estrus around September 1988 she was observed to mate on six occasions, four times of which with older adolescent males, once with an infant and only once with an adult male (T. Hasegawa, K. Takasaki, & H. Takasaki, unpubl.), although she usually moved in a large party which included adult males.

After the infanticide, however, she was observed to mate with *Ntologi* as well as *Kalunde*. On 18 of 34 mating occasions observed on an ad libitum basis in November and December 1989, *Mirinda* mated with adult males, although observers (T. N. & M. H.) were then following mother-infant pairs and therefore sampling was heavily biased to immature males as mating partners. She was observed in M Group until July 27, 1990, after which date she has been missing for unknown reason (K. KAWANAKA, unpubl.).

## Infanticide and Cannibalism in 1990

#### Observations

On July 24, 1990 at 11:05, M. B. KASAGULA, our research assistant, observed five adult males including *Ntologi* excitedly displaying. *Ntologi* had in his hand the 5-month-old infant of *Betty*, a primiparous immigrant. The infant was still alive. *Ntologi* began to bite on the fingers of its right hand. He struck the infant against a tree trunk, and also dragged it on the ground as he displayed. As a result the infant was finally killed. After a while, *Musa* began to feed on the fingers of the left hand, and *Bakali* and *Lukaja* fed on the toes. *Musa* pulled at the legs, while *Ntologi* pulled the upper part of the body, and consequently the body was split apart. *Musa* and *Lukaja* fed on the lower part, and *Ntologi* on the upper part. *Bakali* occasionally obtained meat from *Ntologi*. Moreover, three adult females also occasionally obtained meat directly from *Ntologi*.

In total, ten adult females and eight adult males came to eat. *Ntologi*, *Lukaja*, and *Musa* consumed a greater portion of meat. Finally, three adult females and three adult males gathered around *Ntologi* to form a meat-eating cluster.

From the beginning, Betty incessantly followed Ntologi. He attacked Betty twice and the alpha female also attacked her three times, preventing her from recovering the body. Betty began to bleed from the face after the second attack by Ntologi, and watched her infant being eaten. At least two adult females, an adolescent male, and two juvenile males recovered meat scraps from the ground. Three hours later, chimpanzees were still eating the carcass.

## Status of *Betty* Before and After Infanticide

Betty was first observed in M Group in February 1986. Her first infant, which was the target of the lethal attack, was born in February 1990. From February 1987 to December 1988, Betty mostly moved with the core members of M Group although she was usually in the periphery of the party, and mated mostly with immature and low-ranking adult males (K. Takasaki & H. Takasaki, unpubl.). Unfortunately, during her conception estrus period around June 1989, M Group ranged mostly in the hilly part of the group range and was rarely observed (T. Tsukahara, pers. comm.). Therefore, her mating partner was unknown. She gave birth to a male infant between May 19–22, 1991 (M. Hamai, unpubl.).

## COMPARISONS ACROSS SEVEN CASES OF WITHIN-GROUP INFANTICIDE

Table 1 lists the characteristics of seven victimized infants and their mothers.

Table 1. Within-group infanticide and cannibalism in Mahale: attributes of mothers and victimized infants.

	Source	Nоrікоshi, 1982	KAWANAKA, 1981	Таканата, 1985	NISHIDA & KAWANAKA, 1985	MASUI, 1986	This study	This study	
	Birth order	2nd	lst	1st	2nd	lst	lst	1st	
	Sex	Σ	Σ	Σ	Σ	Σ	Σ	M	
Infants	Age in month	2.5	1.5	71	3	10	9	5	
	Parity at transfer	z	Σ	Σ	Д	z	Z	Z	
	Age* at incident	14	24	22	25	13	15	17	
	Tenure after transfer (yr)	5	0	-	4	3	\$	4	
	Age* at transfer	6	24	21	21	10	10	13	
		×	[K]**		×	i	ن	i	
Mothers	Name <sup>†</sup>	ND	ИА	QM	CH	TM	MN	BT	
	Date	Jan. 13, 1977	June 14, 1979	July 5, 1983	Dec. 15, 1983	July 16, 1985	Oct. 3, 1989	July 25, 1990	

\*Estimated; \*\*[K] indicates that the mother was first identified in K Group but it is unknown whether she was born in the group or immigrated. †Abbreviations: ND: Ndilo; WA: Wakasunga; WD: Wantendele; CH: Chausiku; TM: Tomato; MN: Mirinda; BT: Betty.

#### Attributes of Victimized Infants

All the victims were small male infants below 1 year of age (median 3 months), and mostly their mothers' first born. All of them were healthy before being killed. There was no evidence of the deliberate killing of unhealthy or deformed infants.

It is intriguing that only male infants were killed. The binomial probability of seven male but no female infants being killed is only  $(1/2)^7 \cong 0.008$ , given that the sex ratio at birth is parity, i.e. 1:1, which may not seem an unrealistic assumption from the data obtained during the ten years between 1980 and 1989 (Table 2).

However, this probability is based on the assumption that mothers are equally vulnerable to infanticidal attack regardless of their status. During the same period at least, the sex ratio at birth differed between immigrant (within five years after immigration) and resident (>5 yr) females. Only infants of immigrant females were killed. Immigrant females tended to give birth to sons significantly more often than to daughters (17 male, 6 female, 3 unsexed, binomial test, p=0.017, data after 1982). If this birth sex ratio (approximately 3:1) is applied, the probability of seven male but no female infants being killed by chance is  $(3/4)^7 \approx 0.13$ .

Table 2. Causes of death of infants under 1 year old: all the infants born in M Group in 1980 – 1989.

		Suspected		Mother's			Survive first	
	Cannibalism	aggression	Disease	death	Predation	Unknown	12 months	Total
Male	5	2	2	2	2	6	13	32
Female	0	1	4	2	1	3	24	35
Sex unknown	0	0	2	0	0	2	2	6
Total	5	3	8	4	3	11	39	73

#### Attributes of Mothers

All the mothers of victims were born outside of M Group, and the median number of years that passed from the time of immigration to the incident was four. Four mothers were young (13-17 years old) and primiparous, and three were middle-aged (22-25 years old) females that transferred from K Group or had initially immigrated to K Group from another group and transferred to M Group when K Group was in the process of disintegration (NISHIDA et al., 1985).

## Patterns of Aggression

Table 3 summarizes the patterns of infanticidal aggression. Infanticide occurred mostly in the morning during an intensive feeding period. All seven cases of infanticide were observed in the northern half of M Group's range. Six of them were located within the overlapping area of the original K Group's range (Fig. 1). Six locations were close (within 1 km) to the Kansyana research camp, which is in the vicinity of the most well observed area. This strongly suggests that some similar incidents ended without being observed, because within-group infanticide is unlikely to occur only in the proximity of the camp. Indeed, there were other cases of infant loss suspected to have been caused by infanticide (Table 4).

Twice the identities of the captor and killer of the infant were confirmed. In 1983, *Ntologi* both caught and killed, and in 1989 *Kalunde* caught and *Ntologi* killed the infant.

Table 3. Within-group infanticide and cannibalism in Mahale: patterns of aggression.

ved         of kill/         to         at kill         adult         No. of         eaten         Parts           ?         ?         No         >12         6         M>4         Arm,         Whole           ?         ?         No         >12         6         M>4         Arm,         Whole           ?         ?         No         >17         7         M4, F1         Face         Whole           NT         Strangle         Face         40         9         M5, F7         Wrist,         Brain,           hip,         nnus         14         1         M5, F1         Head,         Whole           ?KZ         ?         No         14         1         M5, F1         Head,         Whole           r         NT         Bite face         No         1         M5, F1         Head,         Whole           r         NT         Bite face         No         30         9         M4, F3,         Hand,         Whole           r         brandish         Face         13         M4, F3,         Finger         3           r         brandish         Face         13         M4, F2,         Finger			Place			First		Method	Injuries	Party size No. of	No. of		Parts				
1   2   2   2   2   2   2   2   2   2		Name of	(see	Method of		observed		of kill/	5	at kill		No. of	eaten	Parts	Change	Unusual Time of	Time of
1 ? ? (KI) ? ? No >12 6 M>4 Arm, Whole head body 2 ? (JG) ? ? No >17 7 M4, F1 Face Whole 3 Communal NT — NT Strangle Face, 40 9 M5, F7, Wrist, Brain, attack by 4 NSolo ? KZ ? NO 14 1 M5, F1 Head, Whole attack 5 Solo NT — NT Bite face No 50 9 Not — Oatmatick 6 Solo DE — NT Throw, No 35 9 M4, F5, Hand, Whole capture 7 ? NT NT M7 Bite, Face 13 8 M4, F2, Finger ?  Production of the complex of the	Date	mother	Fig. 1)	capture	Captor		Killer	apnse	mother		males	cannibals	first	consumed	of owner		consumption
2 ; ; (JG) ; ; No >17 7 M4, F1 Face Whole attack 3 Communal NT — NT Strangle Face, 40 9 M5, F7, Wrist, Brain, by 4 4 ?Solo ?XZ KZ ?X No 14 1 M5, F1 Head, Whole attack 5 Solo NT — NT Bite face No 50 9 Not — — eaten* 6 Solo DE — NT Throw, No 35 9 M4, F3, Hand, Whole capture 7 ? ; NT NT Bite, Face 13 8 M4, F2, Finger ?  1  Page body 6 Bite, Face 13 8 M4, F2, Finger ?	Jan. 13, 1977	ND	1	i	٠,	(KI)	٠,	3	S <sub>o</sub>	>12	9		Arm,	Whole	Yes	Slow	27 hr
3 Communal NT — NT Strangle Face, 40 9 MS, F7, Wrist, Brain, attack by 4 4 Solo 1KZ KZ 1KZ 1 No 14 1 MS, F1 Head, Whole attack 5 Solo NT — NT Bite face No 35 9 M4, F5, Hand, Whole capture 6 Solo DE — NT Throw, No 35 9 M4, F5, Hand, Whole bite, annash 7 1 1 NT NT Bite, Face 13 8 M4, F2, Finger 1	June 14, 1979	WA	2	ن	6	(30)	٠.	٠	ž	>17	7		head Face	body Whole	Yes body	eating None	3.5 hr
attack by 4  1 Solo	July 5, 1983	WD	En.	Communal	NT			Strangle	Face	. <del>6</del>	. 6		Wrist.	finger Brain.	) 2		>1.5 hr +
by 4  1 Solo				attack					hip,				face	legs,			
4 ?Solo ?KZ KZ				by 4					anns					belly +			
strack         ANT         Bite face         No         50         Not         —         —         —           eatrack         Solo         DE         —         NT         Throw, No         35         9         M4, F5, Hand, Whole face         Whole brandish           capture         brandish, brandish         brandish         IM4         face         body body bite, Face         13         8         M4, F2, Finger         ?           7         ?         ?         NT         NT         Bite, Brandish         IM3         IM3	Dec. 15, 1983	CH	4		ίKZ		?KZ	į	% S	14	_		Head,	Whole	Yes	?None	>3 hr
5         Solo         NT         Bite face         No         50         9         Not         —													legs	body			
attack         eaten*           6 Solo         DE — NT Throw, No 35 9 M4, F5, Hand, Whole capture           brandish, bite, smash         IM4 face body bite, smash           7 ? ? NT NT Bite, Face 13 8 M4, F2, Finger ? brandish         IM3	July 16, 1985	TM	S		NT		NT	Bite face	No No	50	6		ŀ	ı	1	1	ı
6 Solo <i>DE</i> — <i>NT</i> Throw, No 35 9 M4, F5, Hand, Whole capture brandish, bite, smash 7 ? NT NT Bite, Face 13 8 M4, F2, Finger ? brandish IM3				attack								eaten*					
capture         brandish,         IM4         face         body           bite,         smash         smash         NT         Bite,         Face         13         8         M4, F2,         Finger?         Prandish         IM3	Oct. 3, 1989	MN	9	Solo	DE		NT	Throw,	N <sub>o</sub>	35	6		Hand,	Whole	Yes	None	3.5 hr
Diffe, smash 7 ? NT NT Bite, Face 13 8 M4, F2, Finger ? brandish IM3				capture				brandish,					face	body			
7 ? ? NT NT Bitter. Face 13 8 M4, F2, Finger ? brandish IM3								bite, smash									
IM3	July 25, 1990	BT	7	٠,	ż			:	Face	13		M4, F2,	Finger	į	No No	ن	>5 hr
								_				IM3					

\*The mother retrieved her baby from the alpha male. After that she could resist cooperative attack by other adult males. However, the baby died because of injuries to the head, leg, and fingers of both hands (Masur, 1986). 15ee the abbreviations on Table 1.

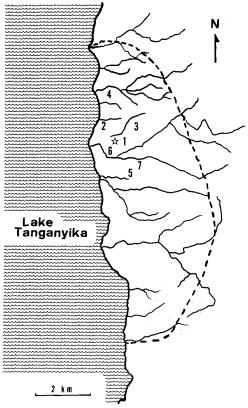


Fig. 1. M Group range and places where infanticide and/or cannibalism were observed. 1. January 1977 (Norikoshi, 1982); 2. June 1979 (Kawanaka, 1981); 3. July 1983 (Takahata, 1985); 4. December 1983 (Nishida & Kawanaka, 1985); 5. July 1985 (Masui, 1986); 6. October 1989 (this study); 7. July 1990 (this study); ☆ Kansyana Research Camp.

Except for one case, party size at the killing site was large (15-50) and there were many adult males present (>6) when infanticide occurred. On six of the seven occasions, captors or first-observed possesors of the infants were alpha or beta males. Group attack was observed in at least three cases.

In all infanticide cases (N=4), the mother persistently attempted to recover her infant from adult males so long as it was still alive. However, males (and once, even a female) effectively blocked the attempts one after another. An infant was recovered by its mother only in a single case. On one occasion, the mother of a victim was heavily injured while protecting her infant from infanticidal males. On another occasion, the mother suffered injury in her attempt to recover her infant. On five occasions, mothers were not injured at all when their infants were taken.

Infants were killed while being eaten in all known cases. The fatal injury was a bite to the face in two cases, and suffocation by a hand in the other case (in one case, the exact injury which caused death is not known).

The part first eaten was either the face, head, or the distal part of one of the four limbs. In four cases in which consumption was observed to the end, the whole body was con-

<b>Table 4.</b> Cases of sudden* loss of in	Table 4	oss of infants.
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Name of mother†	Mother's age**	Sex of infant	Year of death	Age of infant (month)	Days from last seen alive to loss of infant	Circumstantial evidence	Source
WA	27	M	1981	0	1	Infant with injured leg	Hiraiwa-Hasegawa et al., 1984
GM	21	F	1987	10	3	Extreme excitement heard	S. Uehara & T. Nishida, unpubl.
FA	38	M	1988	8	5	Corpse of infant not carried	T. HASEGAWA, K. TAKASAKI, & H. TAKASAKI, unpubl.
JN	15	M	1989	9	6	Corpse of infant not carried	T. TSUKAHARA, M. HAMAI, & L. A. TURNER, unpubl.

<sup>\*</sup>Only cases are tabulated in which the period from the last observation of a mother with her healthy infant to the first observation of the mother without it is less than one week. \*\*Estimated. †Abbreviations. WA: Wakasunga; GM: Gwamwami; FA: Fanta; JN: Juno.

sumed. The killing, dismembering, and eating of the infants differed little from the eating of other species such as infant monkeys (see UEHARA et al., 1992).

What appeared common in cannibalism but uncommon in predation on other species is that consumption of meat took a long time (>3 hr) and that the carcass-holder changed frequently, considering the prey size and the number of consumers. In one case, throwing and waving the dead body was observed, but even this behavior has occasionally been seen in predatory episodes.

In all cases of cannibalism, many chimpanzees (up to 14) ate meat by sharing or by recovering scraps. There were always more than four adult male cannibals. The mother has never been seen to eat from the carcass of her own offspring. Meat-sharing occurred at the same rate as in feeding on other mammals of similar sizes.

## Behavior of Mothers After Infanticide

## Ranging Patterns

As in previously reported cases (for review, see NISHIDA & KAWANAKA, 1985), all the mothers remained within M Group's territory after infanticide. None of the lethal attacks on the infant encouraged the mother to move out of the group. In contrast, when these females gave birth again after infanticide (N=5), all of those who were monitored systematically (WA, WD, CH, TM) began to move with adult males for at least a few months. This means that these females shifted their core areas to the more central part of the group's territory.

#### Mating Patterns

In two instances, females were observed to mate with the cannibal males during the time they conceived their later-victimized infants. However, "restrictive mating" (HASEGAWA & HIRAIWA-HASEGAWA, 1983) was never observed between the seven victims' mothers and any adult males during the conception cycles, although focal sampling was not always done for these females at the time of probable conception. Their observed mating partners were mainly adolescent and other immature males.

After infanticide, all the mothers resumed first post-partum estrus within three months (median = 42 days). Immigrant females tended to change their mating partners from younger to older and from lower- to higher-ranking males, and their mating patterns from opportunistic to restrictive as years passed (TAKASAKI, 1985).

TAKASAKI (1985) noted that two ex-K Group females, Chausiku and Wakasunga, who had never been observed to mate restrictively with the alpha male from 1980-1982 (HASEGAWA & HIRAIWA-HASEGAWA, 1983), did so during his study period from late 1983 to early 1984. Wakasunga's infants were killed by M Group males in 1979 and probably in 1981. Chausiku's infant was killed in 1983.

#### DISCUSSION

#### SITUATIONS MOTIVATING INFANTICIDE

The new observation in 1989 suggests that the attempt to hunt another mammal directly triggered the killing of an infant chimpanzee. Notably, most infanticide occurred during the morning intensive feeding period which also corresponds to the period of most frequent hunting (NISHIDA et al., 1979). Unfortunately, the behavior of infanticidal males was not monitored in detail in other cases of infanticide. This suggestion, therefore, remains speculative.

Interestingly, once an adult male caught or attempted to catch an infant, other males and females became excited and tried to hold the infant themselves or to seek portions of the victim. It appears as if once an infant fell into the hands of an adult male, it suddenly changed to a lump of meat rather than a conspecific, even though it was still alive.

## FUNCTION OF WITHIN-GROUP MALE INFANTICIDE

There are several hypotheses explaining within-group male infanticide (Table 5). First, Kawanaka (1981) proposed an "elimination of the product of incest" hypothesis, a kind of group selection hypothesis which was criticized elsewhere (NISHIDA & KAWANAKA, 1985).

Next came four versions of the male-male competition hypotheses. NISHIDA and HIRAIWA-HASEGAWA (1985) suggested that males of one clique destroy infants of females who closely associated with males of the rival clique (2a in Table 5). This is unlikely because, if this is the case, most infants would be lost to infanticidal males, given that malemale alliances prevail most of the time.

SPIJKERMAN et al. (1990) proposed that infanticide functions as a kind of display which serves to consolidate male social status, or "to increase control over the attention of others" (2b in Table 5). This explanation would fit one of the Mahale cases, i.e. the infant-killing by a young adult male in 1983, but is not adequate for infant-killing by prime adult males, and by the alpha male in particular.

NISHIDA and KAWANAKA (1985) and TAKAHATA (1985) suggested that within-group male infanticide occurred as a consequence (or extension) of between-group, male-male competition. The infanticidal males may have judged that the infants were fathered by males of neighboring unit-groups (2c), K Group in particular, since all the mothers of the first four victims were immigrants from K Group whose core areas were in the overlapping area of M and K Groups. Three recent cases of infanticide, however, occurred after K Group be-

Table 5. Hypotheses explaining within-group infanticide by adult male chimpanzees.

	Proximate cue	Ultimate cause	Basis of hypothesis	Source
1.	Female transferees from neighboring group	Eliminate the product of incestuous mating	Only ex-K Group females were attacked	Kawanaka, 1981
2a.	Mother interacting closely with rival male coalition	Destroy rival's offspring	Immigrant female was protected by 2nd-ranking but attacked by 5th- ranking male	Nishida & Hiraiwa- Hasegawa, 1985
2b.	Infant with many elder brothers	Increase control over the attention of others; Reduce the size of rival kin group	Late adolescent kill smallest of 5 brothers	Spijkerman et al., 1990
2c.	Mothers ranging in the periphery of unit-group; Misunderstanding paternity	Destroy offsprings of unrelated males (e.g. of neighboring groups)	Mother associates frequently with adult males after infanticide	Nishida & Kawanaka, 1985; Takahata, 1985
2d.	Mother who mated opportunistically and rarely with adult males	Earlier resumption of estrus of mother; Coerce females to mate more restrictedly	Small infants were killed; high-ranking males often commit infanticide in cooperation	This study
3.	Male infant	Destroy future competi- tors for resources	Only male infants were killed	Nishida & Kawanaka, 1985; Hiraiwa- Hasegawa, 1992
4.	?	Nutrition (cannibalism)	Killing and feeding methods do not differ from predation on other species (see text)	Hiraiwa-Hasegawa, 1992

came extinct. The mothers of victims in recent observations (MASUI, 1986; this study) were all nulliparous adolescents at immigration, and interacted only with M Group males. In other words, "the killing of bastards" hypothesis appears less likely to be appropriate than before.

The common feature through the seven cases of within-group infanticide is that mothers of victimized infants mated more with older adolescent and other immature males rather than with fully adult males before they gave birth to victims. In at least two cases, mothers mated with infanticidal adult males during the conception cycles (KAWANAKA, 1981; NISHIDA & KAWANAKA, 1985). However, they were not nulliparous adolescent females but parous females secondarily immigrated from K Group. Copulation with an adult male, or even with an alpha male, does not guarantee safety from aggression by the male. However, there was no observation that the victims' mothers mated restrictively (were treated possessively or engaged in consortships) with adult males during their conception cycles (HIRAIWA-HASEGAWA, 1987). Promiscuous mating is sometimes said to be effective against male infanticide (e.g. ANDELMAN, 1987). On the contrary, female chimpanzees whose infants were killed had engaged in promiscuous mating (HASEGAWA, 1989), but none of the infants born to females who had been sexually monopolized by the alpha male were killed (NISHIDA, unpubl.).

We suggest, therefore, that one function of infanticide might be to "correct" a female's promiscuous habit and coerce her into more restrictive mating relationships with adult males, and especially with high-ranking males. High-ranking males, the alpha male in particular, have copulatory priority, and are more likely to mate with females who have resumed estrus after the loss of an infant. The victims' young ages suggest that the major

function of infanticide is to have mothers resume estrus. When two females of K Group, Wakasunga and Wantendele, immigrated into M Group, their weaned sons (6-7 years old) were not killed (KAWANAKA, 1981; TAKAHATA, 1985), although their paternity must have been apparent to M Group chimpanzees as well as to human observers. This would be understandable given that the killing of weaned offspring has no function in the resumption of estrus. It cannot be attributed to the larger size of the offspring that they were not killed, since chimpanzees are capable of killing even adult males (GOODALL, 1986).

One might argue that high-ranking adult males should engage in restrictive mating with young immigrant females rather than kill their infants. However, since young females are far less likely to become pregnant than mature resident females, it would be risky to have a lengthy possessive or consort relationship with them.

An alternative, but not always conflicting hypothesis (HIRAIWA-HASEGAWA, 1992) is that cannibalism would be the major function of infanticide in chimpanzees [4 in Table 6 (HIRAIWA-HASEGAWA, 1992)]. Her hypothesis is based on the fact that infanticide followed by cannibalism has been recorded only for chimpanzees among the infanticidal episodes observed so far among nonhuman primates. Several facts support her hypothesis. First, in the case of the 1989 observation, male chimpanzees appeared to be in a "hunting mood" before capturing the infant. Second, the methods of eating infant chimpanzees did not differ much from those of eating infant monkeys or piglets, except that the feeding bout is usually longer despite the prey size. Although this view is worth noting and consumption of meat is nutritionally valuable, it does not explain why some infants (i.e. only small infants of immigrant mothers with shorter tenure) but not others are killed and eaten.

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