

INTER-UNIT GROUP TRANSFER OF AN IMMATURE MALE OF THE COMMON CHIMPANZEE AND HIS SOCIAL INTERACTIONS IN THE NON-NATAL GROUP

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ABSTRACT In the Mahale Mountains National Park, Tanzania, a mother-son pair of the common chimpanzee transferred from K group to the neighboring M group. This inter-group transfer resulted from the decrease of the male members of K group. The male immigrant of 5-year-old had varied relations with the M group members of each age-sex class. He mated with estrous females, played with adolescents and juveniles, though had few interactions with non-estrous females. In particular, while he was away from his mother for 10 days, he unilaterally followed the adult males of M group, though his younger brother who had been born in this group was killed and eaten by them. The present case clarifies two characteristics of common chimpanzee society, the strong tie between mother and son and the attractiveness of adult males for immature males.

Key Words: Common chimpanzee; Male group transfer; Mahale Mountains National Park.

INTRODUCTION

The basic social unit of the common chimpanzee is a patrilineal unit (Itani, 1980, 1985). In both the Mahale Mountains and Gombe National Parks, Tanzania, where long-term observation has been done since the 1960s, no male chimpanzee, except a few immatures, has been observed to transfer from one unit-group (community) to another. On the contrary, female chimpanzees frequently left their natal groups and transferred to other groups (Nishida, 1979; Goodall, 1983; Hiraiwa-Hasegawa et al., 1984).

In October, 1982, a mother and 5-year-old son, who had belonged to the K group of the Mahale chimpanzee population, began to associate with the neighboring M group. This was the third case of inter-group transfer by an immature male in Mahale. In July 1983, the immigrant's mother gave birth to another son, which was subsequently killed and eaten by the M group males (Takahata, 1985). After this infanticide took place, however, the social relationship between the mother-son pair and the M group chimpanzees became stable: the mother and son frequently moved with the M group chimpanzees, regardless of the mother's sexual states.

In this paper, we describe how the male immigrant's relations with the M group chimpanzees changed after the infanticide, and discuss why he was not subsequently attacked.

MATERIALS AND METHODS

The research was carried out in the Kasoje area of the Mahale Mountains National Park, where the K group chimpanzees have been provisioned since 1966, and the M group chimpanzees since 1968 (Nishida, 1979). In December 1982, the last reproductively mature male of K group disappeared, thus, K group became almost extinct (Nishida et al., 1985). On the contrary, M group consisted of 105 chimpanzees, including 11 adult males and 39 adult females as of May 1982 (Hiraiwa-Hasegawa et al., 1984).

The research is divided into three periods as follows: Period I (6–15 July 1983): Succeeding the infanticide of 5 July 1983, the male immigrant, *Masudi*, left his mother, *Wantendele*, and followed the M group members. He was observed by the focal-animal sampling method (Altmann, 1974) for 203 minutes. Period II (4 August–2 September 1983): *Masudi* and *Wantendele* were seen with the M group members again. *Wantendele* had resumed sexual cycling. *Masudi* was observed for 345 minutes. Period III (16 June–31 August 1984): *Wantendele* gave birth to another son. She and *Masudi* consistently moved with the M group members. *Masudi* was observed for 1,031 minutes.

TRANSITIONAL STAGES OF FEMALE INTER-GROUP TRANSFER

Reviewing the female transfers from K to M group, Uehara (1981) recognized 5 stages—Stage 1: Females range within K group's home range associating only with the K group males; Stage 2: Females range within K group's range, but alternately associate with both the K and M group males in the overlapping area of the two groups' ranges; Stage 3: Females range throughout the home ranges of K and M groups, and alternately associate with the males of both groups; Stage 4: Females range only within M group's home range, and alternately associate with the K and M group males; Stage 5: Females range only within M group's home range associating only with M group males. Uehara concluded that the stages 1 and 5 could be regarded as stable ones, and the stages 2, 3, and 4 as unstable transitional ones of female transfer.

RESULTS

Personal History of the Male Immigrant, *Masudi*

Masudi was born in K group in 1977. His mother, *Wantendele*, had entered K group in 1972, and in 1974 bore a son, which was later killed by M group members in 1976 (Nishida et al., 1979). Since 1975, the K group males have disappeared one after another; some of them are believed to have been killed by the M group members. Meanwhile, most cycling females transferred from K to M group. In December 1982, the last reproductively mature male disappeared, thus K group became almost extinct (Nishida et al., 1985). From 1982 to 1984, survivors of K group were scarcely observed.

In 1979, *Wantendele* and *Masudi* remained within K group, this was perhaps because *Wantendele* had not resumed sexual cycling. She came to be in estrus in 1980, and mated with the K group males. In January 1981, when *Wantendele* was out of estrus, she and *Masudi* happened to encounter M group chimpanzees, and were severely attacked until human observers interrupted the attack (Nishida & Hiraiwa-Hasegawa, 1985).

In October 1981, however, *Wantendele* and *Masudi* spontaneously came in contact with the M group members, perhaps because of the decrease of male members of K group. *Wantendele* mated with the M group males, but the relationship between *Wantendele* and the M group members was still precarious, and hence she and *Masudi* were severely attacked again on 18 November 1981. From that day on, they were not seen within M group. In these episodes, the M group males mainly attacked *Wantendele*, not *Masudi* (Nishida & Hiraiwa-Hasegawa, 1985).

From 7 October 1982, *Wantendele* and *Masudi* began to associate with M group again. They were not attacked any more, but they were seen in M group only while *Wantendele* was in estrus staying within the overlapping area of the K and M groups' ranges; they were still in the unstable transitional stages, the stages 2 or 3 defined by Uehara (1981). *Wantendele* became pregnant, and disappeared from M group accompanying *Masudi* during 30 March to 4 July 1983.

On 5 July 1983, *Wantendele* and her male newborn were attacked by the M group males. *Ntologi* (1st-ranking male) took the newborn away from her, and ate it with others. *Wantendele*'s ranging pattern may have motivated the males to kill her infant (Nishida & Kawanaka, 1985; Takahata, 1985). *Wantendele* had received many wounds and was not seen until 4 August. Meanwhile *Masudi* appeared alone, and came in front of *Ntologi* who was eating his brother. He had no wound, and apparently he had not been severely attacked. When M group began to move southward, he mingled with them.

Social Interactions Observed between *Masudi* and the M Group

Chimpanzees during Period 1

Between 6 and 15 July 1983, *Masudi* became independent of his mother, and traveled with the M group members. He even went into the southern area of M group's range beyond the border of K group's. No severe attack on him occurred. On 15 July, he was hurt on his hand, but not seriously. Once *Kasangazi* (10th-ranking young adult male) aggressively hit and kicked *Masudi*, but the attack was not extended any further. On 16 July, when M group came into the overlapping area of K and M groups' ranges, *Masudi* disappeared from M group, this was perhaps because he met with *Wantendele* then.

During this period, *Masudi* tended to stay near adult males of M group. Proximity was unilaterally initiated by *Masudi*'s approaches most of the cases. *Masudi* approached adult males 24 times, and was approached by them only 4 times (Table 1). Similarly, *Masudi* unilaterally groomed adult males (Table 2).

Among 10 adult males of M group, *Masudi* most frequently approached *Musa*

Table 1. Approaches observed between *Masudi* and adult or adolescent chimpanzees in period I. Approach is defined as the behavior in which an individual comes up to within 3 m of another and halts, or some active interactions take place.

		<i>Masudi</i> approached and							Other chimpanzee approached and						
		GR	PL	BC	GT	CF	FO	Other	GD	PL	AG	SE	CF	FD	Other
Adult male	<i>Bakali</i>			1										1	
	<i>Kagimimi</i>	1						1							
	<i>Musa</i>	1				4	5	3					1		
	<i>Luhulungu</i>			1	1										
	<i>Kasulamemba</i>						3	1							
	<i>Kasangazi</i>	1						1	1		1				
Adolescent male	<i>Bembe</i>									2					
	<i>Mwale</i>		1												
Adult female	(semi-estrus)						1								
Adolescent female	(estrus)											1			
	(semi-estrus)		1												1
	(non-estrus)		1							1					2

GR: groomed; GD: be groomed; PL: played; BC: body-contact; GT: greeted; GE: be greeted; AG: threat or aggression; CF: co-feeding; SE: sexual interaction; FO: followed; FD: be followed; Other: other interactions.

Table 2. Grooming episodes.

Period I		Masudi groomed	Masudi was groomed
Adult male	<i>Kagimimi</i>	3 (406'')	
	<i>Musa</i>	1 (37'')	3 (160'')
	<i>Kasangazi</i>	2 (40'')	
Adolescent female (not in estrus)	<i>Pulin</i>		1 (8'')
Period II			
Adult female (in estrus)	Unidentified	1 (66'')	
	<i>Wantende</i>	1 (681'')	
Adult female (in semi-estrus)	<i>Wantende</i>	1 (1'')	
Adolescent male	<i>Shike</i>	2 (99'')	
Juvenile	<i>Shinako</i>	1 (20'')	1 (20'')
Period III			
Adult male	<i>Musa</i>	1 (9'')	
Adult female (in estrus)	<i>Gwekulo</i>	1 (69'')	
	Unidentified		1 (18'')
Adult female (in semi-estrus)	<i>Chausiku</i>	1 (140'')	
Adult female (not in estrus)	<i>Wantende</i>	11 (1539'')	18 (2923'')
Adolescent female (in estrus)	<i>Muminsa</i>	1 (468'')	2 (187'')
Infant	<i>Wantende's</i> newborn	1 (109'')	

(4th-ranking), as if he had depended on *Musa* for receiving psychological relief, and *Musa* on his part tolerated *Masudi's* presence. *Musa* was the sole adult male that groomed each other and co-fed with *Masudi* (Tables 1 & 2).

Case 1 (15 July 1983)

15:31:35 *Masudi* started grooming *Musa*.

15:32:12 *Musa* started grooming *Masudi*, who presented his body to *Musa*.

15:33:42 *Musa* stopped grooming, and moved away. *Masudi* followed him.

15:35:46 *Masudi* and *Pulin* (adolescent female immigrant) wrestled, but *Musa* continued to move, and *Masudi* and *Pulin* followed *Musa*.

15:38:24 *Musa* climbed into an *Acacia sieberiana* tree, and *Masudi* also climbed into the tree.

15:41:26 *Musa* descended from the tree, and *Masudi* also followed him down. He ate *A. sieberiana* fruit near *Musa*.

Table 3. Play-partners and play-bouts.

		Period I	Period II	Period III	Total
Adult female	<i>Wasalamba</i>		1		1
Adolescent male	<i>Shike</i>	1	2		3
	<i>Bembe</i>	2			2
	<i>Aji*</i>		2		2
	<i>Nsaba</i>			1	1
	<i>Miwale</i>	2		2	4
Adolescent female	<i>Plum</i>		1		1
	<i>Pulin</i>	2		1	3
	<i>Muminsa</i>	1			1
	<i>Labule</i>			1	1
Juvenile & Infant	<i>Kantamba</i>			1	1
	<i>Shinako*</i>		2	4	6
	<i>Sofia</i>		1		1
	<i>Penelope</i>	1		2	3
	<i>Wantende's</i> newborn			9	9

*orphan

It is noteworthy that *Musa* had not directly attacked *Wantendele* and her newborn on 5 July 1983. Nishida and Hiraiwa-Hasegawa (1985) also reported that *Musa* intervened in the attacks on *Wantendele* and *Masudi* in 1981.

Differing from adult males, adult females had few interactions with *Masudi* (Tables 1 & 2). *Masudi* most frequently played with adolescents and juveniles (Table 3). On 6 July 1983, *Masudi* was unusually active, and intermittently played with many partners. He may have been stimulated by having got many play partners after the three-month-separation from the M group members.

Case 2 (6 July 1983)

- 10:44:49 *Masudi* approached *Muminsa* (natal female adolescent) and wrestled with her for a short time.
 10:45:57 *Penelope* (three-year-old female infant) rushed up to *Masudi* and tackled him. *Masudi* rolled and pressed her down on the ground, with play-pants.
 10:54:31 *Bembe* (male adolescent) ran after *Masudi*. He hit *Masudi*'s back, and wrestled with him. They tried to bite each other, then they began round-chasing play. But *Bembe* soon left *Masudi*.
 10:55:07 *Kasangazi* approached *Masudi*, tackled and hit him. *Masudi* tried to flee, but *Kasangazi* bit, kicked, and dragged him by his hand. *Masudi* screamed.
 10:56:56 *Kasangazi* left *Masudi*, and *Masudi* self-groomed.
 10:59:01 *Masudi* climbed into a tree, and *Bembe* climbed into the tree, too.
 11:03:30 *Masudi* and *Bembe* began chasing play in the tree.

Social Interactions Observed during Period II

From 4 August 1983, *Wantendele* resumed sexual cycling, and she and *Masudi* returned to M group again. They began to use the southern area of M group's home range, mingling with the M group members even while *Wantendele* was not in estrus; their ranging and association patterns corresponded to the stage 5, defined by Uehara (1981) as "stable" stage.

During this period, *Masudi* stayed near *Wantendele*. He unilaterally approached and groomed her (Tables 2 & 4). Generally, *Wantendele* did not take much care of *Masudi*, partly because she tended to have sexual interests in the M group males.

In contrast to period I, only a few interactions took place between *Masudi* and adult males. When adult males approached *Wantendele*, who was in estrus, *Masudi* tended to avoid them. He once tried to disturb copulation between *Wantendele* and *Ntologi*, but in vain.

Case 3 (31 August 1983)

- 10:06:29 *Wantendele* and *Masudi* approached *Ntologi*.
 10:07:24 *Ntologi* mounted *Wantendele* with thrusting. *Masudi* touched *Wantendele*'s back, uttering "gwa", but they ignored him.
 10:08:04 After the copulation, *Ntologi* began grooming *Wantendele*. *Masudi* sat near them.

During this period, few interactions other than sexual occurred between *Masudi* and females (Tables 4 & 5). *Masudi* played mostly with adolescents and juveniles, in particular with *Shike* (13-year-old male), *Aji* (10-year-old male), and *Shinako* (5-year-old female). He also groomed with *Shike* and *Shinako* (Table 2).

Social Interactions Observed during Period III

Between 21 May and 15 June 1984, *Wantendele* gave birth to another son. On 15

Table 4. Approaches observed between *Masudi* and adult or adolescent chimpanzees in period II.

		<i>Masudi</i> approached and							Other chimpanzee approached and					
		GR	PL	BC	GT	CF	FO	Other	PL	AG	SE	CF	FO	Other
Adult male	<i>Ntologi</i>						1	1		1				2
	<i>Bakali</i>			1	1								1	
	<i>Musa</i>													1
	<i>Kalunde</i>						2	2						
Adolescent male	<i>Kasulamemba</i>			1										
	<i>Shike</i>	1	1			1			1					
	<i>Aji</i>		1						1				1	
	<i>Nsaba</i>													1
<i>Wantendele</i>	(estrus)					1	5	2						
	(semi-estrus)			1			2	2					1	
	(non-estrus)					1	3							
Adult female	(estrus)	1	1								3			
Adolescent female	(estrus)										5			4

See Table 1 for details.

Table 5. Mating partners and copulation observed in periods II and III.

	Period II		Period III		Total
	Masudi initiated	Female initiated	Masudi initiated	Female initiated	
<i>Wasalamba*</i>		1			1
<i>Wakapala**</i>		1			1
<i>Gwekulo**</i>				1	1
<i>Gwakakumo**</i>			3	2	5
<i>Chausiku**</i>			1	1	2
<i>Plum***</i>	1	2		6	9
<i>Pulin***</i>				3	3
<i>Tomato***</i>				2	2
<i>Opal***</i>		1			1
<i>Muminsa***</i>				1	1
<i>Pinky***</i>				1	1
<i>Viola***</i>				1	1
Total	1	5	4	18	28

*Old-aged female; **Mid-aged female; ***Young adult or adolescent female.

June, she closely followed *Kagimimi* (3rd-ranking male) and *Kalunde* (7th-ranking male), holding the newborn. The infant lived until February 1985 without being attacked by the M group members, though it disappeared between March and August 1985 (Takasaki, Hiraiwa-Hasegawa, & Hayaki, unpublished data). Meanwhile *Wantendele* and *Masudi* constantly mingled with the M group members, using even the southern area of the M group's range.

As in the period II, *Masudi* unilaterally approached and followed *Wantendele* (Table 6), though reciprocal grooming took place frequently between them (Table 2). When *Masudi* was threatened by adult males, he ran back to *Wantendele*, and touched her. The body contact with *Wantendele* seemed to calm *Masudi*, though she did not actively help him in such situation.

Masudi played with his new brother 9 times (Table 3). The play usually started as follows: *Masudi* ran his fingers through the infant's mouth, and the infant watched and gripped him. However, *Masudi* did not seem so eager to play with his brother, as compared with the play with other adolescents and juveniles. *Masudi* sometimes ignored the infant's invitation to play. *Wantendele* seldom intervened in their play.

Social interactions between *Masudi* and adult males seldom occurred (Table 6). *Masudi* was observed to greet only *Bakali* (2nd-ranking male). *Masudi* usually stood face to face with *Bakali* showing the pout face, and uttered pant-grunts. *Bakali* responded to the greeting twice by touching *Masudi*'s head with his hand.

As in the period II, few interactions except sexual were observed between *Masudi* and adult females (Table 6). *Masudi* sometimes inspected the sexual skins of adult females by sniffing, or by poking with his fingers, though no inspection was followed by copulation. During the periods II and III, *Masudi* mated with 12 females 28 times (Table 5). Out of these 28 cases of copulation, 23 cases were initiated by females, and 5 by *Masudi*. He performed branch- or vine-shaking and stamping to elicit female response.

Masudi tended to mate with young females rather than with older ones (Table 5). As Hayaki (1985a) pointed out of the copulatory behavior of immature males in

Table 6. Approaches observed between *Masudi* and adult or adolescent chimpanzees in Period III.

		<i>Masudi</i> approached and									Other chimpanzee approached and								
		GR	GD	PL	BC	GT	SE	CF	FO	Other	GR	PL	BC	GE	AG	SE	CF	FO	Other
Adult male	<i>Ntologi</i>									1					1			1	
	<i>Bakali</i>					3				1			1	2				1	
	<i>Kagimimi</i>																		1
	<i>Musa</i>	1			1				1	1									
	<i>Lubulungu</i>									1									
	<i>Lukaja</i>									1									
	<i>Kasulamemba</i>								1										1
Adolescent male	<i>Kimaro</i>								1										
	<i>Mtwale</i>			2															
Adult female	<i>Wantendele</i> (non-estrus)	3	3		3		1	5	24	11							1		1
	(estrus)						5			2	1				1	6			3
Adolescent female	(semi-estrus)				1														1
	(estrus)						2				1	1				11			4
	(semi-estrus)															2			
	(non-estrus)					1			1	1									1

See Table 1 for details.

general, *Masudi* tended to mate, especially with adult females, in places far away from adult males. Once, when *Masudi* mated with an adult female, she vocalized, then *Ntologi*, hearing the vocalization, charged them.

Besides these cases of copulation, *Masudi* mounted *Wantendele* with thrusting twice. She was not in estrus, and showed no reaction to the mounting. This should not be regarded as true copulation.

Throughout this study, *Masudi* played with one adult female, and with three adolescent females (Table 3). He usually played with these females while they were in estrus. These play episodes might be closely related to sexual behavior, since the play tended to end in a short time, while copulation often occurred either before or after the play.

Masudi's main play-partners were male adolescents and a female juvenile. *Shinako* (Table 3). Mix-type play (Hayaki, 1985b) of wrestling and chasing often took place. *Masudi* played with *Shinako* particularly for long duration. It may have been partly because *Shinako*, having lost her mother and always following her elder brother (*Kimaro*), mingled with adolescent males and had frequent chances to play with *Masudi*.

DISCUSSION

The present case of inter-group transfer of a mother-son pair should be regarded as an exceptional case following the decrease of male members of a group, since female chimpanzees tended to transfer only in the nulliparous stage, and females who have offspring seldom transfer (Nishida, 1979; Goodall, 1983, 1986).

The present case clarifies two characteristics of common chimpanzee society; (1) the strong tie between mother and immature son, and (2) the attractiveness of adult males for immature males. All the male inter-group transfers observed in Mahale were probably caused by their mothers' transfers. Between 1966 and 1984, 4 females with immature sons transferred from K group to M group. Among these 4 sons, one, *Katabi*, remained within K group (Hiraiwa-Hasegawa & Hasegawa, 1988), but the rest transferred with their mothers, though the first one, *Masisa*, eventually parted from his mother and returned to K group, and the second, *Lulemyo*, disappeared from M group after 5 years of transfer, and only *Masudi* remained within M group. The tie between mother and immature son is apparently so strong that the son follows his mother at the risk of being attacked or even killed by the members of a non-natal group.

In the present case, *Masudi* had varied relations with the M group members of each age-sex class. He mated with estrous females, played with adolescents and juveniles, though no relation with non-estrous females. In particular, while *Masudi* traveled independently from his mother for about 10 days, he unilaterally approached and followed adult males. Since the formation of a unit-group of the chimpanzee is patrilineal (Itani, 1980, 1985), immature males should be closely kin-related with adult males. Male orphans depended on adult males for providing care; for example, *Aji* closely followed an old male, *Rashidi*, and was groomed with high frequency by

him until he died in 1983. It is interesting that *Masudi* stayed near adult males, not adult females when he moved with M group members during the period I. It might be a general tendency for the immature males who part from their mothers to be attracted to adult males and to depend on them, regardless of actual kin-relations.

However, why did the M group males not attack *Masudi*, who was sired by one of the K group males? Even at the attacks on *Wantendele* and *Masudi*, observed in 1981, the main target was *Wantendele*, not *Masudi* (Nishida & Hiraiwa-Hasegawa, 1985). It would have been easy for them to kill *Masudi*, if they had wanted, since even adult males can be killed (Goodall et al., 1979).

There are two differences between the male immigrants and the infanticide victims. First, all the male immigrants were 4 to 9 years old, much older than the victims of infanticide, who were one month to three years old (Bygott, 1972; Goodall, 1977; Nishida et al., 1979; Kawanaka, 1981; Norikoshi, 1982; Nishida & Kawanaka, 1985). A boundary may exist in the young males' age, below which the infanticide is induced. Second, the mothers of the male immigrants were usually in sexual cycling, differing from the mothers of infanticide victims who were not cycling. If one of the motives of infanticide was to make mothers resume estrus by killing their infants, as Sugiyama (1965) and Hrdy (1979) suggested for *Presbytis entellus*, it would not be necessary for the males of a new group to kill the male immigrants.

It is interesting to note that there existed individual differences among the adult males in the attitude toward unfamiliar male immigrants, as Nishida and Hiraiwa-Hasegawa pointed out (1985). Two adult males of M group, *Bakali* and *Musa*, with whom *Masudi* later came to be closely associated, did not attack *Wantendele* and her newborn on 5 July 1983. They also intervened in the attacks on *Wantendele* and *Masudi* in 1981. On the contrary, *Ntologi*, *Kagimimi*, *Lubulungu*, and *Lukaja* often participated in attacking *Wantendele* and her sons. In this respect, *Masudi* chose less-aggressive males as his association partners while he was away from his mother.

ACKNOWLEDGEMENTS We thank the following persons: the Directors of Tanzania National Scientific Research Council, Serengeti Wildlife Research Institute, and Wildlife Division, for the permission to conduct this study and to publish this paper; the Coordinator and staff of Mahale Mountains Wildlife Research Centre, for the cooperation; Profs. T. Nishida, K. Kawanaka, S. Uehara, Drs. M. Hiraiwa-Hasegawa, T. Hasegawa, H. Hayaki, and H. Takasaki, for the kind permission to use their unpublished data; Prof. J. Itani, Dr. D. Sprague, and the members of the Laboratory of Human Evolution Studies, Kyoto University, for the valuable advice and comments. The research was supported by the Overseas Scientific Research Fund of the Ministry of Education, Science, and Culture, Japan (No. 404130 of 1979, No. 56041019 of 1981, to T. Nishida), and Grant-in-aid for Scientific Research (No. 60790116 of 1985, 1986), and partly by the Japan International Cooperation Agency.

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—Received September 14, 1988

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