PRIMATES, 11: 47–87, 1970

Social Behavior and Relationship among Wild Chimpanzees of the Mahali Mountains

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ABSTRACT. Patterns of social behavior of the chimpanzees of the Mahali Mts. are listed briefly in this paper, where behavior absent in the other subhuman primates is especially focussed upon. Some are more analogous to those of mankind than to those of the other subhuman primates. This characteristic social behavior is more or less related to the peculiar social organization of wild chimpanzees. Differences of social behavior between two local populations (i.e., of the Mahali Mts. and the Gombe Stream Reserve) have not been recognized; namely, "dialect" differentiation does not seem to exist.

INTRODUCTION

The study of the social organization of wild chimpanzees is thought to provide many clues which may be of aid in the speculation of the social life of proto-hominids. The writer has previously reported on the social organization of chimpanzees from the standpoint of their social groupings (NISHIDA, 1968); in this paper he wishes to probe into the problem based on observations of their social behavior.

Many of the patterns of the social behavior of chimpanzees have already been made clear, especially by GOODALL (1965), but there are many unsolved problems concerning the significance of each behavioral group in relation to social organization. Descriptions and classification of the social behavior of chimpanzees, elucidation of some specially noteworthy behavioral patterns, their relation to the social organization, and inquiries into the significance of those characteristic behavioral patterns in the social evolution of the primates are the objects of the present paper.

Almost all observed instances of behavior were obtained at the feeding place (see Fig. 2). Chimpanzees have some characteristic interactions between individuals with regard to food which are not seen in other subhuman primates, so the observed instances of interactions among individuals are divided, for convenience' sake, into (1) behavioral groups which are not considered to have a direct bearing on food ("general interaction") and (2) interactions with regard to food. Hereafter the individual who initiates any behavior will be called "the subject" of the interaction, and the one who responds to it "the object." The present paper will not mention sexual behavior, which has been described briefly elsewhere (NISHIDA, 1968).

The observational period extended from October, 1965, to March, 1967, from July to November, 1967, from August to November, 1968, and from August to November, 1969, totaling 28 months. The study area was in Kasoge, West Tanzania.

The object of observation was confined to the chimpanzees belonging to the "Kajabara group" which has been 'provisionized' since March, 1966 (*vide* NISHIDA, 1967). Most of the records on behavior were obtained between July and November, 1966, between July and September, 1967, between August and September, 1968 and between August and October, 1969, totaling 13 months, when the Kajabara group

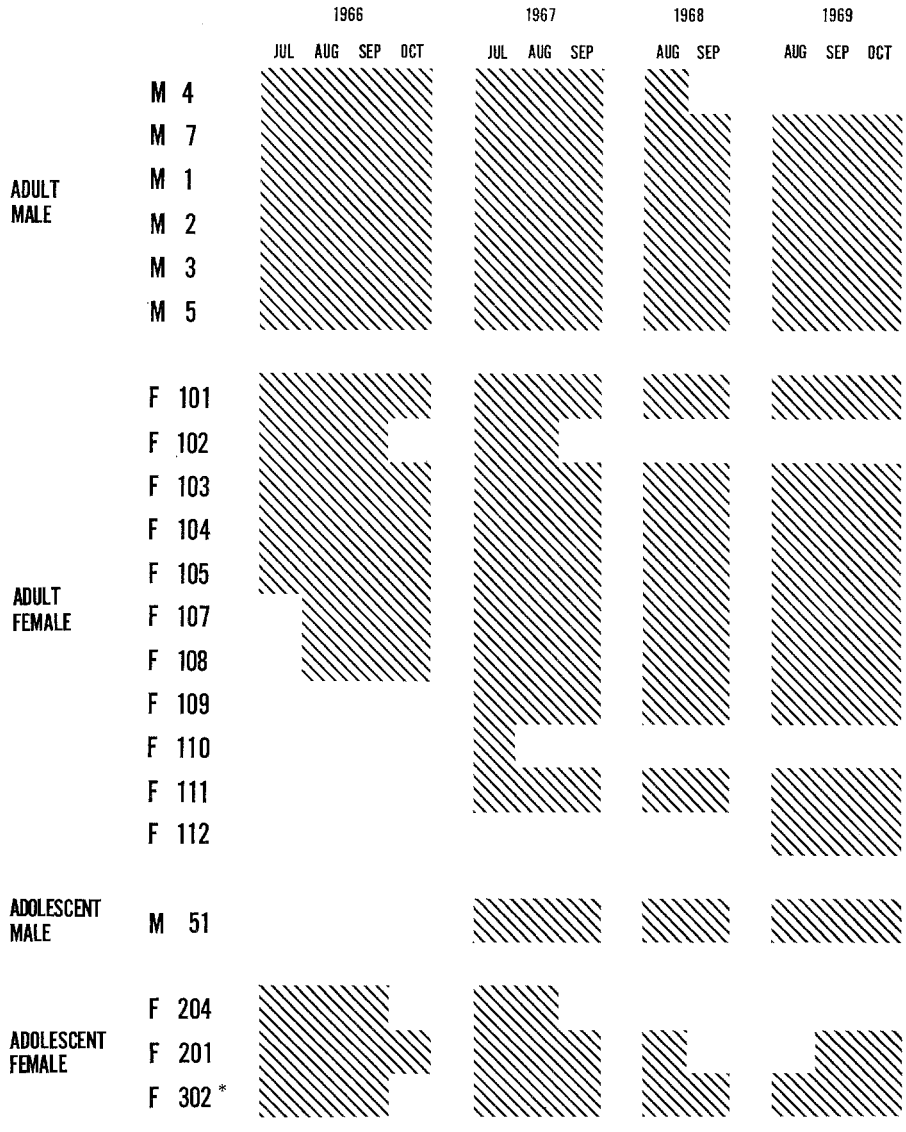

Fig. 1. Attendance records of the members of the Kajabara group in the main observational periods (adults & adolescents only). The shadowed parts indicate that the individual was observed at the feeding place during the period. Blank spaces mean that the individual had not yet been individually identified, had not yet joined the Kajabara group, or was missing at that time. *F 302 has become adolescent since 1969.

frequented the feeding place. The Kajabara group contained 6 adult males, 10 adult females and 13 immature animals in July, 1967 (Fig. 1).

GENERAL INTERACTIONS

1. Agonistic Interaction

This interaction consists of attacks and threats by the subject against the object and the submissive expressions of the object. Expressions of attacks and threats are indicated in the following ways:

i. swinging one arm sideways, up or down;
ii. shaking the body;
iii. standing on all fours with head down and with one hind leg often kept raised for some moments.
iv. glaring fixedly (often with the mouth open);
v. slapping with one hand at the ground, drumming on tree trunks, or hitting the ground with a stick;
vi. swinging or throwing sticks;
vii. aggressive vocalization;
viii. chasing, often with barking;
ix. seizing the object and hitting or rolling him/her with one or both hands;
x. kicking or stamping on the object.

Submissive expressions are as follows:

i. defensive facial expression, grin (Fig. 3);
ii. defensive vocalization;
iii. presentation posture;
iv. escape;
v. embracing the subject from behind.

What is characteristic of chimpanzees' aggressive behavior is that it has a great tendency toward demonstration, namely, that it is focussed on threats rather than on true attacks.

Case 1. Aug. 3, 1966. 11: 32. An adolescent female (F 204) made her appearance at the feeding place, and an adult male (M1), who had been sitting there, immediately sprang up with great vigor and pursued her bipedally[1)], swinging a sugar cane stick which he had been chewing. F204 ran off screaming, but M1 kept pursuing her, hitting the ground with the stick. F204 succeeded in escaping.

Case 2. July 27, 1967. 19: 08. An adolescent male (M51) made his appearance at the feeding place. An adult male (M2), who had been sitting there, looked back, stood on all fours, and raised his right hind leg as if he were about to spring upon M51. M2 threatened M51 vigorously by swinging his right arm down. M51 was surprised and ran off into the bush.

Agonistic interactions are accompanied by great noise and clamor. The object

1) As has been pointed out by Kortlandt (1962), when a male chimpanzee becomes aggressive, he often stands bipedally with a stick in his hand to threaten or attack.

Table 1-a. Frequency of combinations of adult and adolescent individuals between which agonistic interactions occurred.

One attacked		One attacking																				
		M 4	M 7	M 1	M 2	M 3	M 5	F 101	F 102	F 103	F 104	F 105	F 107	F 108	F 109	F 110	F 111	F 112	M 51	F 201	F 204	F 302
Adult Male	M4																					
	M7																					
	M1		2																			
	M2		2																			
	M3	2	3	2	1						1											
	M5	2	2	4	2					1	1											
Female	F101		1	1							1											
	F102						3			1	1											
	F103		1	1																		
	F104		1																			
	F105																					
	F107		1		1																	
	F108		1		1		1			2		1										
	F109		1	4	1					1	1											
	F110																					
	F111																					
	F112																					
Adolescent Male	M51			1	3																	
Female	F201		1	3	2			1			1											
	F204		1	4	2						2											
	F302*				1																	

* F302 has been an adolescent since 1969. An adult male is placed, in a procession, in accordance with the position he occupies in the dominance-rank order.

Table 1-b. Summary of Table 1-a.

One attacked		One attacking						
		M	F	AM	AF	JF	I	Total
Adult male	(M)	22	3	0	0	0	0	25
Adult female	(F)	19	8	0	0	0	0	27
Adolescent male	(AM)	8	1	0	0	0	0	9
Adolescent female	(AF)	15	4	0	1	0	0	20
Juvenile female	(JF)	15	2	2	0	0	0	19
Infant	(I)	2	0	0	0	0	0	2
Total attacks		81	18	2	1	0	0	102

is sometimes actually caught. There were 15 cases where the attackers caught and hit the objects with one or both hands. In one of the cases M7 came upon an aggressive episode in which M2 was hitting M3, and M7 joined in the attack. This was the only observed case of co-operative attack.

Since the subject is always dominant over the object in the interaction, it is possible to determine the dominant-subordinate relation of individuals between whom agonistic interactions occurred. The total number of agonistic interactions, including the Type A Interaction (see p. 63), amounted to 102. The combinations of individual members are shown in Table 1-a. Adults are obviously dominant over immature individuals. Generally adult males dominate adult females, but it must be noted that this is not always the case.

2. Friendly Interactions

Behavioral group contributory to strengthening familiarity among group members is to be called friendly behavior.

1) Greeting Behavior

Greeting behavior was first recognized in chimpanzees by Goodall (1965). This is most frequently observed when a subgroups meets another one which has been ranging apart for several hours or days, or when individuals who formed a subgroup the previous night before going to sleep meet each other for the first time the following morning. Greeting behavior of a simple form is seen among members of the same subgroup when they meet again after resting apart for an hour or so. This type of behavior seems to have the function of mutual recognition and tolerance among individuals in the "extensible" (Nishida, 1968) social group of wild chimpanzees.

This type of behavior is shown by the subject toward the object in the following manners:

i. the subject approaches the object, near the side of whom he stands on all fours for several seconds;

ii. the subject approaches and sits down behind or by the side of the object. In both i and ii, the approach is frequently accompanied by a series of low panting calls "gwo-gwoho-gwoho. . " or "gwa-gwa- gwa."

iii. grooming or presentation posture is sometimes seen in instances of ii. In a few cases the subject licked the face of the object;

iv. the subject directs his mouth, with lips pushed forward, to the face, head,

back, genital area, or other part of the object's body. This behavior is sometimes accompanied by the friendly panting call "hwa-ach-ach-ach." The subject often bites the arm or leg of the object softly (mock-bite) (Figs. 4 & 5);

v. the subject reaches out one hand toward the object;

vi. the subject touches, with one hand, the head, face, shoulder, belly, thigh, genital area, or other part of the object;

vii. the subject embraces the waist of the object from behind;

viii. mounting. The subject embraces the object's waist with both arms, standing bipedally on the ground. Pelvic thrusts may or may not be made.

ix. combinations of two or more of the above.

When the object responds instantly to any of these behavioral types, or when both of them greet each other at the same time, it is called reciprocal or mutual greeting respectively.

Reciprocity is expressed by,

x. kissing, in correspondence to iv (Fig. 6);

xi. shaking hands, in correspondence to v; and

xii. mutual embracing, in correspondence to vii.

It appears that the greeting behavior of chimpanzees has the function of continuing and strengthening social bond among group members who do not always range together. By greeting they will confirm that each is an acquaintance of the other. A subordinate chimpanzee receives the tolerance of a dominant one. Greeting interactions may also be the mechanism which facilitates the formation of a new subgroup.

An incipient form of greeting behavior may be seen in baboons (HALL & DEVORE, 1965), but among chimpanzees greeting is not only much more varied as to behavioral types, but much more frequently seen. These respects clearly make a qualitative difference. This may perhaps show that greetings among chimpanzees are inseparably connected with the extensibility of the chimpanzee social unit. Several cases from the author's field notes are cited below:

Case 3. Aug. 16, 1967. 12: 05. A subgroup consisting of five males and two pairs of mother and infant appeared at the feeding place. 12: 09. The males suddenly got excited and started emitting a panting bark "gwa-gwa-gwa- - - ." Both M1 and M7 ran towards the bush, out of which M4 made his appearance. M4 approached M1 and M7 and brought his face near each of them one by one.

Case 4. Sept. 4, 1967. 17: 02. When M1, M2, M3, and M5 were gathered together at the feeding place, F103, who had been traveling alone during the day, appeared. She went directly toward M1, who was sitting. F103 approached quite near and put her muzzle to the face of M1, and then bit his right arm with her mouth wide open. Then she began foraging for food at the feeding place. F103 did not greet the other males. (When a chimpanzee who has been ranging on his/her own meets his/her companions, he/she does not greet all of them; he/she always *chooses* some few of the dominant animals to greet.)

Case 5. July 31, 1966. 15: 45. M5, F103, M2, M1, and M3 appeared at the feeding place. 16: 30. Under the shade of a tree in one corner of the feeding place, M5 held F103's head down with his left hand and repeatedly licked her right cheek from the head down to the chin. The licking lasted for about 10 seconds. Then M5 groomed the right hand, right part of the head, and the back of F103. She let him have his own way, but she did not reciprocate the grooming.

Case 6. July 27, 1967. 18: 30. M7 took five sticks of sugar cane at the feeding place and was going to the bush with them. On his way, he sat down beside M1, who was eating in a sitting

posture. M1 instantly reached out his right hand with a piece of sugar cane toward M7, who showed no response, but started chewing his own sugar cane.

The examples cited above are called "one-sided" greetings. One-sided greeting behavior is tinged with some kind of submission, in that the object does not show any apparent response and in that the object is dominant over the subject, as a general rule (*vide post*), whereas mutual greeting gives a strong impression of mutual familiarity, which seems one of the most characteristic behavioral types of chimpanzees. A tendency for greeting to be often mutual between individuals who had been separated for a long time was recognized.

Case 7. Aug. 28, 1967. 16: 32. M7 appeared at the feeding place. M1, who had been there, got excited, uttered panting sounds, ran toward M7, and reached out one hand toward him. At once M7 covered the hindquarters of M1, but with no thrust. Then both M1 and M7 put their muzzles near each other. Though their mouths were wide open, no contact of muzzles was observed. This state lasted for about 10 seconds.

Case 8. Sept. 2, 1967. 18: 51. M2 appeared alone at the feeding place. 10: 00. A group of chimpanzees was approaching the place from the west and uttering sounds. There was a frequent exchange of calls between M2 and the group, which proved to consist of M3, M51, F101, and F201. First, M51 and M3 came out of the forest. M2 was looking toward M3 from up in a tree. M3 approached M2, who got down from the tree and went toward M3, who made grimaces at M2. As soon as they were face to face, they stood upright and embraced each other, with each one's arms flung around the other's waist. This posture lasted for about 2 seconds, and they put their muzzles near each other as if kissing. Though their mouths were wide open, there was no contact of muzzles. After that both of them began eating bananas. There was no greeting observed among individuals other than the mentioned pair.

Case 9. July 31, 1967. 16:12. M2, M1, F111, and M3 appeared at the feeding place. 16:15. M7 came down to the feeding place, whereupon M1 immediately approached him and groomed his right leg for a little time. M3 approached M7, who had a stick of sugar cane in his hand. M3 reached his right hand out toward M7 and instantly M7 put out his hand with the stick of sugar cane towards M3, who grasped the stick and M7 let it go. Though M3 thus got hold of the stick, he threw it away a little later and picked up another stick.

Case 8 is an example of mutual greeting. In Cases 7 and 9, those who took the initiative in greeting were M1 and M3, and the one who responded was M7. Generally speaking, even in reciprocal greeting it is often the case that the subject or the initiator of the greeting is subordinate to the object or the recipient. Case 9 is analogous to the food-sharing interaction (*vide post*) as far as form is concerned. However, if we look into the content of the interaction, the stick of sugar cane which M7 offered is no less than a substitute for his right hand. What is important here is not the giving and receiving of the stick, but the fact that M7 offered his right hand and that M3 responded.

A look into combination of individuals who were involved in one-sided greeting will reveal that in the case of greetings between adult and immature animals, it is always immature animals who are the subjects of the interaction (Table 4). In 10 combinations of adult males among whom dominant-subdominant relationships have been definitely ascertained (Table 1-a), the subordinate ones are always the subjects

Table 2. Frequency of combinations of individuals between which greeting or appeasement behavior was seen.

One greeting or appeasing	One greeted or appeased																				
	M 4	M 7	M 1	M 2	M 3	M 5	F 101	F 102	F 103	F 104	F 105	F 107	F 108	F 109	F 110	F 111	F 112	M 51	F 201	F 204	F 302
M4		1	1																		
M7																					
M1		4(3)																			
M2		1(2)	2						1												
M3		1	2(1)																		
M5		1(2)	2	1	1				1												
F101																					
F102																					
F103		(1)	2(1)		1																
F104		(6)	(6)			1(1)							1								
F105			(1)																		
F107		1(2)	1(2)																		
F108																					
F109		(3)	(1)		(2)																
F110											(1)										
F111			(1)																		
F112																					
M51		(1)	(1)		1																
F201	(1)	(1)	(1)								1										
F204				(1)																	
F302			1(1)	1	(1)																

Figures in parentheses represent the frequency of appeasement behavior.

Table 3. Frequency of combinations of individuals between which mutual or reciprocal greeting bahavior was observed.

	Combination		Frequency
M-M	M4	M1	1
	M1	M7	2
	M1	M2	1
	M3	M7	2
	M3	M2	2
F-M	F101	M1	1
	F103	M3	1
	F104	M3	1
	F104	M2	2
	F107	M4	1
M-F	M1	F104	1
	M1	F107	1
	M3	F103	1
	M5	F110	1
F-F	F101	F103	1
	F101	F104	1
F-AF	F110	F204	1
	F110	F302	1
	Total		22

Table 4. Summary of Table 2 (greeting behavior).

One greeting	One greeted					
	M	F	AM	AF	JF	Total
M	17	2	0	0	0	19
F	6	1	0	0	0	7
AM	1	0	0	0	0	1
AF	0	1	0	0	0	1
JF	3	5	0	0	0	8
Total	27	9	0	0	0	36

of greeting interactions (Table 2). From this it may be concluded that the subject of a one-sided greeting interaction is generally subordinate to the object.

A comparison in terms of age/sex classification shows that greeting behavior is seen overwhelmingly among adult males (Table 4).

One-sided greeting interactions were seen on 17 occasions among adult males, on 8 occasions between adult males and females, but only once among adult females. Mutual or reciprocal greeting interactions were seen almost exclusively between adult males and females and among adult males (Table 3).

2) Appeasement Behavior

This behavior, which resembles one-sided greeting, takes the form of diverting beforehand any possible attacks by a dominant animal. As behavioral types it contains i. running to the other animal, ii. grinning, iii. presentation posture (Fig. 7), iv. touching part of the other's body with one hand, v. grasping the scrotum with one hand, vi. short-time grooming, vii. biting the ear softly, viii. biting one or both arms softly, ix. inserting one hand under the arm, x. reaching out one

hand towards, xi. grasping the face of the reacter with both hands, xii. embracing the hindquarters from the rear (Fig. 8), and xiii. screaming. There is almost no apparent difference between appeasement and one-sided greeting behavior except the behavioral situation. However, fear on the part of the subject seems to exist. Self-possession or calmness on the part of the subject recognized in greeting behavior is lacking in this type of behavior, as may be seen from the fact that the subject, on sighting the object, *runs* toward him, sometimes accompanied by a scream. The object generally shows no apparent response to the appeasement gesture of the subject, but a male object often put his muzzle down to the genital area or his index finger into the vagina of a female subject after the female appeasement presentation. Sometimes a male object bites one hand or arm of the female subject softly, or in contrast to this, a dominant male object may stretch his hand towards the subordinate chimpanzee and *let the latter bite* his hand or fingers (Fig. 9). This behavior on the part of the dominant male may be categorized as "reassurance" behavior (*vide* GOODALL, 1968).

Case 10. July 17, 1967. 11: 37. An adolescent female (F204) appeared at the feeding place and looked around. She fell on her buttocks with surprise as M2 appeared from the left. F204 hastened to M2 and touched him on the right side of the waist with her right hand. After a while she left with a stick of sugar cane in her hand.

Case 11. July 18, 1967. 10: 06. F110, in estrus, came into the feeding place, when F105, an old female, appeared at the edge of the feeding place. F110 did not take food, but ran back toward F105 and touched her on the waist with one hand. Then F110 took a stick of sugar cane and started eating.

Appeasement is, needless to say, shown by a subordinate individual toward a dominant one. On 50 of 54 occasions of appeasement episodes, adult males were the objects of the interactions (Table 5).

Table 5. Summary of Table 2 (appeasement behavior).

One appeasing	One appeased					
	M	F	AM	AF	JF	Total
M	8	0	0	0	0	8
F	26	1	0	0	0	27
AM	2	0	0	0	0	2
AF	6	1	0	0	0	7
JF	8	2	0	0	0	10
Total	50	4	0	0	0	54

3) Friendly Behavior During Rest

During rest chimpanzees often indulge in social grooming. A groomer, sitting on a tree, holds an upper twig with one hand to sustain himself and reaches out the other hand to the groomee, who is often lying on the bough. Grooming is also seen in 1) and 2). In these cases grooming is done very briefly and in a situation accompanied by a certain tension. During a rest period, however, grooming is performed leisurely for a comparatively long time (sometimes lasting more than an hour) and grooming *per se* is an object of behavior.

Table 6. Frequency of grooming relationships among different age-sex classes.

	M	F	AM	AF	JF
M	18	12	0	0	0
F		0	0	0	1
AM			0	0	0
AF				0	2
JF					2

Grooming during rest was observed on only 35 occasions (Table 6), but it does not necessarily mean that this type of grooming is rarely performed. On the contrary, the chimpanzees spent their most peaceful time resting in the bush near the feeding place, where it is presumed that they groomed each other with a considerably high frequency. The writer refrained from approaching the Kajabara group resting in the bush near the feeding place lest observations at the open feeding place should be disturbed, which accounts for the very scanty records of observation of grooming during rest.

The longest recorded instance of grooming was seen among three adult males (M1, M2, and M5). It lasted for 105 minutes. They groomed one another by turns. The total amount of time during which one of them was groomed was correlated with his rank order among them (Table 7 & Fig. 10).

"Kissing" during rest was observed only once. M1 and M2 embraced and kissed each other on a tree and continued to do so for 2 minutes.

Table 7. Grooming relationships among three adult males. Figures represent minutes during which a chimpanzee is groomed or grooming.

One grooming	One groomed			
	M1	M2	M5	Total min.
M1		52	10	62
M2	30		1	31
M5	59	5		64
Total min.	89	57	11	

4) Friendly Behavior Connected with Dominance Display

There are at least two behavioral types by which an adult male chimpanzee shows his dominance over other individuals. These types of behavior have a certain nuance of demonstration, and in response to such behavior the object of the interaction often grimaces, screams, or runs off.

i. Mounting. This behavioral type is the same as that already mentioned in greeting behavior. But unlike its occurrence in greeting behavior, where mounting is an element in a behavioral sequence, dominance-display mounting is often performed *per se*. On 8 of 14 occasions mounting of this kind was performed between an adult male and an adult female (Table 8); pelvic thrusts accompanied the mounting on six occasions.

Table 8. Frepquency of combinations of individuals between which dominance-display behavior was observed.

	Subject	Object	Mounting	Strutting	Penis-gripping
M-M	M4	M1	1		
	M4	?	1		
	M7	M1	1	2	1
	M1	M3			2
	M1	M5	1		
	M2	M5			1
M-F	M4	F104		1	
	M7	F105		1	
	M1	F107	1		
	M3	F102		1	
	M3	F105	1		
	M5	F103	2		
	M5	F105	1		
	M5	F107	1		
	M5	F109	2		
M-JF	M1	F302	1		
AM-F	M51	F104	1		
Total			14	5	4

ii. Strutting. Adult males often strut in a haughty manner, with arms thrown out. This behavior is most conspicuously seen among mountain gorillas (SCHALLER, 1963).

iii. Penis-gripping. A mature male sometimes grips the penis of his subordinate companion with one hand. Penis-gripping was observed on five occasions, four of which interactions occurred among adult males.

5) Friendly Behavior of Unclear Function

There are several types of friendly behavior whose function remains unclear or unresolved.

i. Lip smacking. This behavior was observed only twice.

Case. 12. July 25, 1967. 11: 09. F110, in estrus, appeared at the feeding place and started chewing sugar cane. 11: 10. M5 came out and sat down besides F110. He reached his hand toward the swelling sexual skin of F110, who crouched and assumed a presentation posture. M5 smacked his lips, approached F110, and groomed her head a little. 11: 12. M5 went into the bush with a stick of sugar cane in his hand, followed by F110.

Lip smacking in this case may be interpreted as an expression of friendliness connected with sexual concern, since it was a response to the presentation of a female in estrus and he groomed the female immediately afterwards. Another case of lip smacking was seen when F101 snatched two sticks of sugar cane from M2 (*vide* p. 63 for snatching). Then M2 smacked his lips at F101. Just after that, M2 made a redirective attack towards F201 (F101's daughter).

ii. Touching the other on a part of the body with one hand.

It has already been stated that this behavioral type appears also in greeting and appeasement. Cases were observed, however, in which this behavior had apparently no function of greeting or appeasement.

Case 13. Aug. 3, 1966. 10: 50. A subgroup of 18 chimpanzees, including M1 and F201,

appeared at the feeding place and continued to stay at or near the place. 15: 55. When M1 and F201 came into the place side by side, M1 touched F201 lightly on the waist with his right hand. F201 screamed, but did not try to run off. Both then took sugar cane.

In case 13, touching occurred between two individuals who had been together for over 5 hours, so that it can not be regarded as greeting behavior, nor should it be regarded as appeasement, since the subject of the interaction was dominant over the object; moreover, it was not sexual behavior, since F201 did not show any sign of swelling of the sexual skin.

It was often observed that when a mother with an infant-two late was near another female, the infant on its mother's back reached out its hand to touch the other female on the head or face. This behavior may show the exploratory tendency of infants. The touched female showed no response at all.

Case 14. Oct. 1, 1966. 07: 20. A subgroup of 13 chimpanzees, including F104, appeared at the feeding place for the first time for that day. 07: 45. F108 came into the feeding place on her own. F104, who was already there, approached F108 and touched her on the face, head, and jaw with one hand. At that time F104's infant, while clinging to its mother's back, reached out one hand and touched F108 on the face.

iii. Putting the muzzle down to the genital-pelvic area.

Chimpanzees, especially adult males, often put their muzzle down to the genital-pelvic area of females. The female object stands on all fours without showing any expression of fear or submission (Fig. 11). This behavior has been recognized as a behavioral type of greeting. However, several cases were observed in which it was impossible to interpret this type of behavior as having a greeting function, considering the circumstances under which it occurred.

iv. Penis-grip. An adult female (F104) was once observed to grasp the penis of an adult male (M3) with her right hand as they passed each other at the feeding place. What this behavior implied remains unknown.

v. "Pseudo-sexual" (?) behavior. An adult male often stretches his hand to the genital area of a non-estrous mature or immature female. He may poke his index-finger into her vagina and moreover he may sniff or lick the finger. He sometimes repeats this several times. He may, though rarely, lick the vagina directly with his tongue.

An adult male was observed twice to copulate with a female who did not show any sign of receptivity; he inserted his penis into her vagina and repeated many thrusts. This behavior may have had sexual meaning, but if so, it is very curious that the behavior was directed toward non-estrous females; the author failed to find any other possible explanation (redirection, reassurance or dominance-display etc.), considering the situations in which they occurred.

3. Behavior in Uncertainty

Chimpanzees show physiological reactions expressive of uncertainty or tension and/or perform a set of behavior designed to dissolve that uncertainty or tension when they see an observer near at hand or when they see a more dominant animal approach or show attack-threatening behavior.

1) Yawning, Erection of the Penis, and Incontinence of Urine and Faeces

Chimpanzees often showed the physiological reactions of yawning and the erection of the penis when they were in a state of psychological uncertainty. Yawning was often observed when a chimpanzee was on a tree and an observer was under it. When a subgroup of chimpanzees appeared at the feeding place for the first time for the day and the subgroup was headed by a young adult male (M3 or M5), that young adult male often erected his penis in addition to making grimaces. When they felt great fear or high tension, they often loosened their bowels or discharged urine involuntarily.

2) Scratching

When a chimpanzee feels a slight uncertainty or a slight tension, he scratches his belly, back, or arm with one hand while standing on all fours. This behavior seems to show a kind of hesitation about doing something and was seen among both adult males and females, but was seen particularly often in males (Fig. 12). Scratching was often observed when a chimpanzee was about to come out of the bush into the open space or before he approached a dominant individual.

3) Redirection

This is compensative behavior by which an individual tries to dissolve uncertainty or tension caused by the approach or aggression of a more dominant individual by redirecting that uncertainty or tension onto a more subordinate animal or something else.

Case 15. Aug. 6, 1967. 07: 10. M7 approached M1 from behind, M1 instantly became aware of the approach and screamed with a defensive facial expression. Then M1 immediately approached and mounted M5, who made grimaces and kept screaming.

When surprised by an observer in the forest, chimpanzees in trees threw down withered branches or vines ("branch-throwing display," GOODALL, 1965). This behavior was often accompanied by the shaking of trees and/or the hitting of tree trunks. At the feeding place an excited animal was often observed to pick up dead branches or sticks of sugar cane lying on the ground at random and to throw them. This was seen exclusively among adult males. Once chimpanzees gathered around the author when he showed them bananas in the forest 2 miles away from the feeding place. Males were very excited, and M1 was observed to keep biting the fingers of M2 while emitting panting grunts. M2 did not show any submissive facial expression.

4) Gathering

When chimpanzees are in strong psychological uncertainty or astonishment, they, particularly the males, often gather together and embrace each other.

Case 16. Aug. 8, 1967. During the morning the bush was cut in an area of about 100 m^2 so that the area of the feeding place was extended. 17:13. A subgroup of chimpanzees approached the feeding place for the first time for the day. M1 first reached the entrance of the feeding place from the track, but upon seeing the changed condition of the feeding place he hurriedly retraced his way into the track. After a short while, M5, M1, and M7 came out side by side at the entrance to look into the feeding place, where they embraced each other in a state of great excitement. After that the subgroup came down into the feeding place with M7 leading and both M1 and M5 following him.

Embracing one another or contacting one's body with another's apparently has the function of alleviating and dissolving tension in wild chimpanzees, and it is presumed that it has some connection with the fact that greeting and appeasement behavior include physical contact or approximation in their content. It may be certain that physical contact can bring psychological stability to chimpanzees. An interesting response was observed when chimpanzees at Kasoge were first presented with bananas, a food unknown to them until then[2].

Case 17. July 31, 1966. 15: 45. M5, F103, M2, M1, and M3 approached the entrance of the feeding place in the order mentioned. M5 entered the feeding place alone, and the other four remained at the entrance and stood jostling one another under a shrub from a branch of which a bunch of bananas was hung. They were gazing at the bananas. At the head of the four was M2, closely followed by F103, behind whom were M1 and M3, all four closely packed together. F103 first started eating a banana, and then M2, M1, and M3 followed suit.

5) Explosive Display

It sometimes occurs that an adult male chimpanzee suddenly goes wild without any apparent reason. He may suddenly begin to run about. He may slap at the ground, beat tree trunks with both hands, pick up and throw fallen leaves or sticks, roll stones, try to drag a large fallen tree, stamp on the ground or tree buttresses, and/or climb a tree very rapidly (Fig. 13-a & b). This behavior cannot, in behavioral types, always be discriminated from redirection already mentioned, which is, however, to be "understood" in the cotext of the interaction.

This behavior is sometimes *infectious*: when an adult male behaves furiously, another male may join him in going wild. Another chimpanzee was infected on five of the 19 occasions of such kind of behavior (Table 9).

Table 9. Frequency of explosive display in adult male chimpanzees.

	M4	M7	M1	M2	M3	M5	Total
Initiating explosive display	0	6	9	1	3	0	19
Joining explosive display	1	2	1	1	3	1	9
Total	1	8	10	2	6	1	28

Case 18. Aug. 8, 1967. 17: 17. M1 suddenly went wild at the feeding place. He ran across the place from right to left, hitting tree trunks on the way and ran back from left to right, picking out sticks of sugar cane planted in the ground so as to toss them up one after another. M5, M2, and M3 made grimaces while sitting at the feeding place.

2) July 31, 1966. 11: 45. A bunch of bananas was hung from a branch at the feeding place for the first time. 12: 20. F103 appeared alone and after hesitating alittle, took a banana and peeled it and began eating. She ate all the bunch by 13: 10. 15: 00. Another bunch was put up. As can be seen from Case 17, therefore, all the other individuals except F103 had never seen bananas before.

Case 19. Sept. 1, 1967. 15: 36. M3 suddenly went wild. Brandishing a stick of sugar cane in his hand, he kicked a tree trunk with vigor and stamped on the tree buttress. He climbed up the tree very fast, while hitting the trunk with both hands, but he calmed down while in the tree. M2 was astonished and retreated toward the bush.

It is generally the case that when a male shows violent behavior those around him scream or run off with grimaces. In case 19, M2, who was dominant over M3, ran off. In another case, not mentioned here, M4, who was dominant, was observed to make grimaces when M1 went wild.

6) Mass Excitement

When many chimpanzees congregate in a certain limited area, a great deal of calling occurs. There is an uninterrupted exchange of calling between subgroups which are located within earshot of each other. On such an occasion calling is often made simultaneously by all the members of a subgroup (unisonous outburst), and it is often the case that this excercises mutual attraction over the subgroups. As several subgroups approach each other, chimpanzees become greatly excited. Some engage in a series of chasing and running, and several adult males indulge in all sorts of wild displays. Sometimes this lasts for more than 2 hours. It is, however, not clear what meaning this group behavior accompanied by great excitement has. GOODALL (1963) seemed to term such group behavior as the "rain dance" and REYNOLDS and REYNOLDS (1965) as "carnival." REYNOLDS suggested that it seemed to be associated with the meeting at a common food source of bands that may have been relatively unfamiliar with each other, but this mass excitement occurs as intra-social-unit group behavior in Kasoge.

INTERACTIONS CONCERNING FOOD

Social interactions among wild chimpanzees in connection with food are not so simple as those seen in other subhuman primates. For instance, it is a common phenomenon that a Japanese monkey in the wild intercepts a piece of food which some other individual is going to take, and in such a case it is known that the one who intercepts is almost always dominant over the latter. From this fact, the "peanut-giving test" can be utilized as a means of fixing ranking relationships among Japanese monkeys (ITANI, 1954).

In chimpanzees, however, it is not always the case that when a piece of food is placed between two individuals the dominant one takes it. Moreover, a subordinate individual has been seen to snatch a piece of food already in the possession of a dominant one. Begging and sharing behavior has also been observed among chimpanzees (KORTLANDT, 1962; GOODALL, 1965). Thus, it cannot be denied that a new social relation which had never been acquired in the stage of the Old World monkey has been established *in connection with food* in the society of wild chimpanzees. It follows that it will be proper to treat social interactions concerning food separately from other social interactions.

According to the behavioral types of the subject of the interaction, interactions concerning food can be classified into four categories.

Table 10. Frequency of combinations of individuals between which type-A interactions occurred.

	Subject	Object	A-1	A-2	A-3 & 4	Total
M-M	M4	M5			1	
	M1	M3	1			5
	M1	M5	1		1	
	M2	M5	1			
M-F	M1	F101	1			
	M1	F103	1			
	M1	F109		1		6
	M2	F109	1			
	M5	F102	2			
F-M	F103	M5			1	
	F104	M3	1			3
	F104	M5	1			
F-F	F103	F108	1			
	F104	F101	1			4
	F104	F102	1			
	F104	F109	1			
M-AF	M1	F204	1	1		3
	M2	F201		1		
F-AF	F101	F201			1	2
	F104	F204		1		
M-JF	M1	F302			2	3
	M2	F302		1		
F-JF	F104	F302		1		1
Total			15	6	6	27

1. TYPE A.

The subject makes attacking or threatening expressions.

(1) A-1: When the object is going to take a piece of food, the subject comes running out and snatches it away.

(2) A-2: When the object is going to take a piece of food, the subject threatens the object, whereupon the object shows a submissive reaction, such as grimacing or presentation, and eventually the piece is taken by the object.

(3) A-3: The subject attacks or threatens the object, who has a piece of food. The object throws the piece away, and the subject takes it.

(4) A-4: The subject takes food in the hands of the object away by main force. The object makes submissive expressions.

Type A interactions are not essentially different from the agonistic interactions which have already been descrided, in general interactions, so the author will not go further. Type A interactions were observed 27 times (Table 10).

2. TYPE S.

The subject *tries* to take a piece of food from the hands of the object *without* any apparent attacking or threatening expressions. The object makes *no* submissive expressions.

(1) S-1: The subject succeeds in snatching. Neither the subject nor the object makes submissive expressions.

(2) S-2: The object refuses, and the subject makes no submissive expressions.

(3) S-3: The subject makes submissive expressions, and the object lets a piece of food go. The subject takes the food (Fig. 14-b, c).

(4) S-4: The object refuses and the subject makes submissive expressions.

S-1 interactions were observed on 30 occasions, S-2 on six occasions, S-3 and S-4 twice each (Table 11). In S-1 interactions, the subject was dominant over the object on 14 occasions, but the fact that the object does not show any submissive expression in the interaction may mean that no aggressive element is contained in the subject's act of snatching. When the subject is subordinate, as on many occasions, it will be natural that there should be no submissive expression on the part of the object.

It is worthy of note that the cases in which females snatched food from males accounted for 53% of the total S-1 interactions. Many of these cases gave the author the impression that males let females carry the food away rather than their being robbed of it. In this sense the attitude of the male object in the S-1 interaction greatly resembles that of the male object who shows food-sharing behavior, which is to be referred to later.

Table 11. Frequency of combinations of individuals between which Type-S interactions occurred.

	Subject	Object	S-1	S-2	S-3	S-4	Total
M-M	M4	M7	1				
	M4	M2	1				4
	M4	M3	1				
	M2	M7	1				
M-F	M4	F103	1				
	M4	F104	1				
	M7	F103	1				6
	M1	F101	1	1			
	?	F104	1				
M-AF	M4	F201	1				1
F-M	F101	M1		1		1	
	F101	M2	3		2		
	F101	M3	1				
	F101	M5	1				
	F102	M2		1			
	F103	M5	1				
	F104	M1	1	1		1	25
	F104	M2	2				
	F104	M5	3	1			
	F105	M5	1				
	F109	M2		1			
	F111	M2	2				
	F111	M3	1				
F-F	F101	F102	1				1
F-AF	F101	F201	1				1
JF-F	F309	F109	2				2
Total			30	6	2	2	40

In the S-2 interaction the subject was dominant over the object on two of the six total occasions; that is, the object could refuse to give up its food in spite of its subordination. Moreover, when the object refuses to give up food, the object may not only refuse to let the food go but may also positively show certain symbolic behavior which eventually causes the subject not to snatch it away:

Case 20. Aug. 7, 1968. 18: 37. F201 took two sticks of sugar cane and began to walk to the bush with them when M4 appeared and approached her. F201 put one stick on the ground, but M4 reached out his hand and got hold of the other stick in her possession and tried to snatch it away. F201 refused to give it up, putting her muzzle down to the arm with which M4 grasped the stick. After a while, M4 abandoned the idea of trying to snatch it and was satisfied with getting the only stick that F201 had previously put on the ground.

We shall now examine some combinations of individuals who were frequently involved in Type S interactions.

Between M1 and F101, M1 snatched food from F101 once (S-1) but on another occasion F101 did not hand over any food when M1 tried to snatch it (S-2). On the other hand, F101 twice tried to snatch food from M1. On both occasions M1 refused, on one occasion of which F101 made grimaces upon meeting refusal (S-2 & S-4). M1 was known to be dominant over F101, so that attention should be called to the fact that snatching behavior, including that which is unsuccessful, can occur irrespective of dominance order between subject and object.

Between M2 and F101, M2 was never seen to snatch food from F101. On the other hand, F101 snatched food from M2 on three occasions (S-1). On the other two occasions, M2 would not let go of his food, and F101 made grimaces and screamed, as a result of which M2 was made to let go of his food (S-3). In this S-3 interaction, M2 let go of his food[3] because F101 showed a submissive expression, so it must be said that this interaction, though passive, is very close in nature to food-begging and food-sharing interactions.

Though both M1 and M2 are dominant over F101, their attitudes toward her are very different. This may probably result from differences in the quality of their dominance over F101, from the existence or non-existence of a special relationship with F101 (for instance, a blood relationship between M2 and F101 may exist), from differences in personality, or from the physiological and psychological condition of the object.

All S-type interactions are basically the same in the point of one individual's attempting to snatch food from another. If we think that no attempt will be launched unless the subject is confident of success to some extent, giving and taking of food by means of snatching is an interaction attempted irrespective of dominance order between the subject and the object, which may therefore be said to be characteristic of chimpanzee society and is never seen in higher primates other than man. As a matter of fact, the S-1 interaction is nothing but one which is successful. Although the probability of success in snatching would naturally be very high if the subject were

3) Among Japanese monkeys, a dominant individual, who is trying to snatch food from a subordinate one, sometimes gives up his attempt when the latter shows a submissive facial expression. However, no interaction similar to S-3 has been observed.

dominant over the object, what matters is the fact that snatching is often successful even when the subject is subordinate.

3. TYPE B.

The subject "begs" food from the object; he reaches out his hand palm uppermost. Begging is sometimes substituted by some other behavioral types of greeting, i.e., the subject may show the presentation posture, put the muzzle down to the object, or touch the thigh or arm of the object; the subject may bite softly the wrist of the object.

(1) B-1: The object gives part of his food to the subject. The subject obtains the food.

(2) B-2: The object does not give up his food.

(3) B-3: The object tries to avoid the subject and runs off.

Sometimes the subject hangs about the object importunately. Begging behavior is mentally higher than snatching in that the former takes a detour in obtaining food, whereas the latter is a direct attempt. This behavior is performed almost exclusively by adult or adolescent females, who begged food of adult or adolescent males on 28 (87.5%) of the 32 total occasions of begging interaction (Table 12).

Because of the long-term contact with human observers, the Japanese monkeys on Koshima islet beg men for food (KAWAI, 1965), which is, however, completely different from that of chimpanzees, in posture in that the former begs men, not con-

Table 12. Frequency of combinations of individuals between which Type-B interactions occurred.

	Subject	Object	B-1	B-2	B-3	Total
M-M	M1	M4		1		
	M5	M4	1			2
M-F	M3	F103		1		1
F-M	F101	M7	1		1	
	F101	M1	1	1		
	F102	M1		1		
	F102	M2	1	1	1	
	F103	M1	1	1		
	F104	M7	1	1	1	
	F104	M2	1			
	F105	M4	1			24
	F105	M1	1			
	F107	M7	2			
	F109	M1			1	
	F111	M7	1		1	
	F111	M2			1	
	F111	M3			1	
	?	M7	1			
AF-M	F201	M1	1			
	F204	M7		1		2
AF-F	F204	F107		1		1
F-AM	F111	M51	2			2
Total			16	9	7	

specifics, in that the former seems to be a rather reflexive reaction to food, and in that the former has no corresponding sharing behavior.

On 16 occasions a chimpanzee willingly gave part of his food to his companion upon being requested to do so (B-1). The percentage of B-1 in the Type B interactions, that is, the rate of successful begging, reached 50.0%. It will be appropriate to call the B-1 interaction "begging and sharing interaction." Typical cases of B-1 interaction will be given below from the author's field notes.

Case 21. Aug. 24, 1967. 15: 04. M7 appeared at the feeding place, took three sticks of sugar cane (one of them being short) and sat down besides F104. Seeing this, F107, with a newborn baby, came out of the bush, ran to M7, faced him and reached out her hand with palm up. M7 placed the short stick on the outstretched hand of F107, who would not leave but kept on reaching out her right hand towards M7. After a short while, M7 broke one of the remaining sticks into halves with both hands and gave one half to F107, who then disappeared into the bush with the two pieces of sugar cane.

Case 22, July 5, 1966. 08: 30. M1 came into the feeding place to take four sticks of sugar cane. He retired with them under a tree near the bush and started eating one of them, placing the other three sticks in front of him. F105 came from behind M1 and reached out her hand from behind him. M1 kept chewing, ignoring her. F105 approached him still closer and pulled one of the three sticks in front of him. Thereupon, M1, in order to prevent her attempt at theft, grasped one end of the stick and a sort of tug of war ensued. M1 succeeded in drawing the stick closer to him by main force and then broke it into two pieces at a point nearer to him so as to give the greater part to F105.

Case 23. July 14, 1966. 08: 00. M1, M2, F101, and others appeared at the feeding place. 08: 30. F102 came out of the bush, directly approached M2 and begged him for sugar cane. M2 immediately broke a stick of sugar cane he was chewing into two roughly equal parts, one of which he gave to F102.

As will be clear from the cases mentioned above, it is worthy of particular note that the object does not merely give but sometimes gives a part of the food after halving[4] it. This is to be called "halving behavior."

In case 22, F105 first begged but did not receive, so she tried to take the food away. In response to her attempt, M1 showed halving and sharing behavior. If M1 had allowed F105 to take the stick of sugar cane, the case would have been very similar to the S-1 interaction. Thus, the S-1 interaction in many cases can be said to be, psychologically, a phenomenon very similar, apart from actual patterns of behavior, to the B-1 interaction.

Attention must be paid to the fact that adult or adolescent males gave food to adult or adolescent females in almost all B-1 interactions. In other words, begging behavior is peculiar to females, while halving and sharing is peculiar to males.

That a subordinate chimpanzee has a means of communication in receving food from a dominant one and that the latter has the mental ability to give and/or share should be considered an epoch-making event in the social evolution of subhuman primates.

B-2 and B-3 are cases in which begging for food is met with refusal, and B-3 is of particular interest in that the male runs about trying to shake off the female who is

4) Bananas were never seen to be halved. One or several fingers were placed on the outstretched hand of the begger. Therefore, for food to be halved, it seems, it must be large enough to be broken into two substantial parts.

begging for food, as he does not want to share his food. In particular it is worthy of note that even M7, the most dominant male, ran off when F104, F111, and F101, each on different occasions, begged him for food. Therefore, it is this B-3 interaction that most clearly shows the symbolic function of begging behavior; F101 tried to snatch food from M1 twice in vain, but when she begged, M1 once gave her food and at another time ran off; F102 once attempted to snatch food from M2 in vain, but when she begged for food at three different times, she was able to obtain it on one occasion, but on another occasion M2 ran off.

Food sharing occurred most frequently when food was fairly abundant but not sufficient for all visiting chimpanzees to have their share. Although agonistic interactions increased when baits were very scarce, it must be noted that food sharing occurred at least several times on such occasions.

4. TYPE O.

This includes all those interactions that could not be classified into any of the types enumerated so far.

(1) O-1: The subject comes close to the object and together they eat the food in the possession of the object.

(2) O-2: The subject comes close to the object, and the former carries away, without any show of expression, the food the object placed near it. The object shows no response whatever.

(3) O-3: When the subject comes close, the object either places his hands on the food he placed in front of himself or draws the food nearer, or the object moves to other places with the food.

O-1 interactions occurred on four occasions between males, on four occasions

Table 13. Frequency of combinations of individuals between which Type-O interactions occurred.

	Subject	Object	O-1	O-2	O-3
M-M	M4	M7	1		
	M4	M1	1		
	M1	M7			1
	M1	M2			1
	M3	M4	1		
	M3	M1	1		
F-M	F101	M2			1
	F103	M7		2	
	F103	M1	1		
	F103	M2	1		1
	F104	M7		2	
	F104	M1	1		
	F104	M2		1	
	F107	M1		1	
	F107	M2			1
	F108	M7	1		
	F111	M1			1
AF-F	F204	F104	1		
	F204	F107		1	
Total			9	7	6

between a male and a female, and once between a female and an adolescent female (Table 13). This is an interaction very commonly observed between mother and her offspring younger than juveniles (such instances are excluded from Table 13). Therefore O-1 shows familiarity between the subject and the object. On two of the four occasions of the interaction observed between males, a subordinate individual went near a dominant one and together they ate the latter's food. Judging from this, the interaction occurs unrelated to dominance rank between subject and object (Fig. 15).

O-2 interaction was observed on seven occasions, on six of which adult females carried food away from males: F104 and F103, high-ranking and relatively old females were the subjects on three and two occasions respectively, and F107, who was in estrus, once. If this point is taken into consideration, O-2 may be said to be a modified form of the B-1 interaction where begging and handing over are omitted with particular females.

O-3 may be regarded as behavior shown by an individual in possession of food in order to avoid a possible S or B interaction. This interaction occurs unrelated to dominance rank between subject and object.

SOCIAL RELATIONSHIPS

1. Dominance

A total of 22 cases (10 combinations) of overt agonistic interactions among males were observed, from which it has been ascertained that M4, M7, M1, and M2 are all dominant over M3 and M5, and that M7 is dominant over M1 and M2. Moreover, dominance rank among males can be inferred from the fact that in appeasement and one-sided greeting behavior the object of the interactions is usually dominant over the subject. In this way, in 14 of 15 combinations of six adult males, dominance order has been made clear. M4 and M7 are dominant over any of the other four males whose ranking order makes the linear hierarchy: M4, M7>M1>M2>M3>M5. As to physical constitution, M7 is the largest and M2 is slightly smaller than any of the other five. Except for these, there are no great differences of physique among them. It was presumed that, as to relative age, M4 was especially old, followed by M7, M1, and M2. M3 and M5 were regarded as the youngest. It follows that ranking relationships among males are fairly directly correlated with age. Between M4 and M7, however, it was impossible to determine which was dominant.

Dominance display behavior peculiar to males is considered not unrelated to the existence of a dominance hierarchy among males. It is clear that chimpanzee males have a definite dominance hierarchy, which differs, however, in many points from the rigid ranking system seen in macaques or baboons, as Goodall (1965) has pointed out. For instance, when a low-ranking male shows "explosive display" (p. 61), other higher-ranking males sometimes run off or make grimaces. Assuming that it is the subordinate who shows submissive expressions, it may be said that a particular male showing explosive display is dominant over all others *at that instant*. This may be called "situation-specific" dominance. Such a kind of inversion is not seen in

macaques or baboons. GOODALL (1966) cites a case of an adult male whose ranking moved up as a result of his self-demonstration by slapping or throwing away an empty kerosene can, so explosive display may sometimes serve to raise the ranking.

As has already been stated, overt agonistic interaction was observed only in 10 of 15 combinations among adult males. Moreover, the subordinate animals of the 10 combinations were M5, M3, M2, and M1, who were involved in the interaction ten times, eight times, twice and once, respectively. It should be noted, therefore, that almost all of the interactions centered around M3 and M5, the youngest or lowest-ranking males. It was inferred that not many years has elapsed since these two males had become mature. Thus, generally speaking, overt agonistic interaction among mature males may be said to be rather rare, in spite of the existence of a ranking order.

It has already been stated that in one-sided greeting the one who greets is subordinate, as a rule, to the one who receives the greeting. But it must be noted that the subject of the greeting does not show any submissive expression and that the dominant individual sometimes greets his subordinate companion. From this it may be said that greeting behavior is an interaction based on a principle of equality rather than on dominance-subordination. In particular, mutual greeting may be based solely on the principle of equality. It is a great feature of dominance in chimpanzees that there are the two principles mentioned above, and that one works strongly in one situation and the other in another: namely, that each principle has a flexibility and that one can be switched over to another.

Thus, though we can recognize the existence of a linear hierarchy among chimpanzee males, the modes in which dominance-subordination is expressed may be said to be vague in the extreme. This may be related to the "extensibility" (NISHIDA, 1968) of a chimpanzee group. In macaques and baboons, who keep closely-packed groups at all times, a rigid ranking system has developed in order to decrease social conflicts. In chimpanzee groups, which repeat joining and parting, familiarization among members is a much more important matter than decreasing conflict. Thus, social interactions in which the principle of dominance-subordination functioning in avoiding conflict is entwined with the principle of equality with emphasis on familiarization have developed among wild chimpanzees.

Agonistic interactions were observed among females on only eight occasions. It was known from this that F103 was dominant over F102, F108, and F109, and that F104 dominated F101, F102, and F109 and that F105 dominated F108. Although it is evident that dominance rank exists among females in some combinations, it should not be presumed that a clearly defined linear hierarchy, as seen among males, exists among them. In addition, almost no greeting interaction was observed among females. Therefore, it may be safe to say that among females both the principle of dominance-subordination and that of equality are still in a state of underdevelopment. In other words, females have only a low degree of socialization.

Generally speaking, males are dominant over females[5]. High-ranking males,

5) GOODALL (1965) and REYNOLDS and REYNOLDS (1965) state that males are, without exceptions, dominant over females.

such as M7, M4, and M1, in particular, have been ascertained to be dominant over all females. It was, however, certain that F103 was dominant over M5 and F104 over M3 and M5. F103 and F104 are old-aged females, while M3 and M5 are the youngest of the mature males. Relative age may, therefore, be at least one great factor in making a female dominant over a male. However, not all old females are dominant over M5 and M3. For instance, F102, another old female, was known to be subordinate to M5. The reason why M5 has different dominance relations with F104 and F102 remains unknown. The problem will be looked at from the standpoint of the personalities of each individual, possible special relationships between individuals (such as blood relation), and/or the personal histories of each individual.

2. Tolerance

The concept of tolerance may be defined as the phenomenon of a dominant individual tolerating a subordinate one after the dominance-subordination relationship between them has been clearly established. According to this definition, tolerance is seen clearly only between adults and immature individuals, and among adult males.

A great degree of tolerance underlies relations between adult males. This applies to sexual as well as to feeding activities, as Goodall (1965) has pointed out. Between adults and immature individuals, adults, particularly adult males, are not so tolerant of adolescents and juveniles, but very tolerant of infants (up to 3 years of age). It goes without saying that there exists a good deal of tolerance between a mother and her offspring.

3. Leadership

Chimpanzees generally move in subgroups, and there is an individual who regulates the movement of the subgroup. As Goodall (1965) pointed out, the leader in a small subgroup is the most dominant individual in that subgroup and generally heads the progression. For instance, with the subgroup consisting of F104, F204, F102 and F302, F104 started the movement of leaving the feeding place towards evening, followed by the other individuals. With the subgroup consisting of F201, M51, M3 and F101, M3 was the third individual in the order of progression, but when he halted, the others followed suit.

With large mixed subgroups it is very difficult to know whether or not there is a leader and who the leader is, if there is one. It was often observed, however, that in leaving the feeding place, as soon as a certain individual started moving, several other members followed suit. Those who most often had influence upon other individuals in this way were M4, M1, and M7. In this respect M2, M3, and M5 apparently had almost no influence upon others.

A chimpanzee subgroup is of a temporary nature, so that its leader must necessarily be temporary. Since chimpanzees are endowed with an ability of independent movement (Nishida, 1968), any adult individual is considered able to lead a subgroup. Moreover, a chimpanzee leader has almost no function in regulating relations among the members of the subgroup. From this it is apparent that the leader of a chimpanzee group is evidently very different in nature from the leaders of a troop of Japanese monkeys (*vide* Itani, 1954).

However, when the entire Kajabara group starts on a long journey, there arises a phenomenon which cannot be understood without supposing the existence of a so-called leader. Every year the Kajabara group starts on a migration on a certain day towards the end of the dry season or at the beginning of the wet season, moving from the feeding place to the savanna woodland area (NISHIDA, 1968). On this occasion every member of the group goes on the journey, no single individual staying behind at the feeding place. In 1966, the migration occurred on November 2, and in 1967, on September 5, and after those dates no single member returned to the feeding place. It seems that this phenomenon is not to be understood well unless we suppose the existence of a so-called leader who regulates, on specific occasions, the movement of the entire Kajabara group. Observations at the feeding place, however, failed to determine who might undertake this kind of leadership. The problem remains to be solved in the future.

4. MOTHER AND OFFSPRING

Individuals who are in a mother-offspring relationship were inferred from the facts that they often come together to the feeding place, that they placed themselves near each other when feeding, and that the offspring often followed its mother. From these observations it was established that at least five pairs, F101 and F201, F102 and F302, F104 and F204, F105 and F107, and F111 and M51, were in a mother-offspring relationship (except those cases in which the offspring were younger than the Juvenile-I stage).

Mother and offspring are generally affinitive to each other, but agonistic interactions were observed twice between F104 and F204, and once between F101 and F201. Concerning food, S-1 or O-1 interactions are usually the case between a mother and her offspring; the subject may be the mother in one interaction and the offspring in another. Food sharing was observed twice between M51 and his mother, F111. On both occasions M51 gave her food.

Case 26. Jul. 31, 1967. 16:18. M51 came down to the feeding place, took a stick of sugar cane, and was going into the bush when suddenly F111, who had been in the bush, came into the feeding place and approached him trying to snatch the stick from him by main force. M51 would not let go, but drew it toward himself, broke it into two and handed one, about two-thirds of the original, to F111, who immediately disappeared into the bush with it.

This attitude of M51 towards his mother is different from that of an adolescent female towards her mother. When an adolescent female has a stick of sugar cane in her hand and her mother tries to snatch it from her, the young female does not show halving behavior. Her mother always succeeds in snatching it without meeting any strong resistance. It is certain that F111 was already losing dominance over her son, although she showed no begging behavior toward him on either occasion. It is presumed that a mother stays dominant over her daughter even after the latter has become a grown adult, but it is doubtful whether a mother stays so over her son[6].

6) According to GOODALL (1966), an identified male became dominant over his mother after his full maturation.

There are some interactions peculiarly seen between individuals who have a blood relationship. In 1966, F107 was observed three times, before giving birth to her first child, carrying her infant sister. On one occasion F107 was carrying her infant sister on her belly in a procession of a large subgroup. On another occasion she was observed carrying her infant sister on her belly, with F105, their mother, following about 3 meters behind them. On this occasion she carried the infant for at least 2 minutes. On the third observed occasion F107 was in estrus and her sister jumped onto her back. F302 was often seen holding her infant sister in her arms in a tree or running after her in play.

Examples cited above seem to show that the analysis of the mother-offspring and sibling relationship is indispensable to the elucidation of the social organization among wild chimpanzees. This point has long since been pointed out by GOODALL (1963).

DISCUSSION AND CONCLUSION

1. CHARACTERISTICS OF THE SOCIAL BEHAVIOR OF CHIMPANZEES

Chimpanzees in the wild have many behavioral characteristics some of which seem to be shared by human beings, but which are absent in the other subhuman primates. These will be summed up in the succeeding discussion.

1) Agressive Behavior

One of the characteristics of social behavior among wild chimpanzees is the decrease of true attacks and the corresponding increase of threats in aggressive behavior. Aggressive chimpanzees depend far more strongly upon threatening display than upon true attacks as their aggressive expression in agonistic episodes. The behavioral repertoire concerning threats is more abundant among chimpanzees than among other subhuman primates. In correspondence with the various threat displays, the subordinate individual often responds to the threat by showing various types of submissive behavior, not by mere escape. Man is the animal who expresses his aggression or submission more often by language than by a true attack. Threatening displays are often a substitute for true attacks in chimpanzees as language is in man.

2) Dominance

Agonistic interactions have been said to be infrequent (GOODALL, 1965; REYNOLDS & REYNOLDS, 1965). Although this does not necessarily mean that chimpanzee society lacks dominance rank among adult males, it is obvious that dominance is far from being the determinant which prescribes social relationship among adult chimpanzees. It is impossible to use the "peanut test" (ITANI, 1954) to decide dominance rank between two chimpanzees; the author has determined dominance relationships by observing which individual makes submissive expressions in an agonistic interaction.

Adult males are not always dominant over adult females. In reality some adult females were seen to be dominant over two adult males. Since much depends upon the personality and combination of the individuals concerned, male-female relationships among chimpanzees are so variable that they cannot be generalized by a simple

formula. The dominance system mentioned above seems to be more comparable to that of man than to those of baboons or macaques, though the dominance concept must be reexamined.

3) Leadership and Individual Independence

Temporariness of leadership and the lack of a superordinate leader or leaders is one of the characteristics of chimpanzee society. Although there are some adult males who often take the leadership, it seems that any adult animal can lead its subgroup if it has the opportunity. SERVICE (1966) writes: " . . . But despite the obvious significance of leadership in such activity, a hunting-gathering society is . . . distinctive in that it has no formal leadership of the sort that we see in later stages of cultural development. There is no permanent office of headman; leadership moves from one person to another depending on the type of activity that is being planned." The analogy between primitive hunter-gatherers and chimpanzees concerning leadership is obvious.

4) Physical Contact

Chimpanzees show behavior accompanied by physical contact in a great many social contexts; physical contact is seen together with such various types of behavior as submissive, appeasement, and greeting behavior, behavior in uncertainty, dominance display behavior, and others. It is one of the features chimpanzees share with human beings that physical contact plays an important role in many social contexts. No one who has experienced great fright, grief, astonishment, or delight will deny the psychological stability brought about by physical contact with another person.

5) Greeting Behavior

It seems evident that greeting behavior originates from submissive behavior; many patterns of greeting are the same as those of submission, with only a difference in the social contexts in which they occur. In spite of this, there are some cases, as is seen in mutual greeting interactions, where it is not always proper to regard the subject's behavior as one of submission and the object's as one of reassurance; it is worth noticing that mutual greeting behavior apparently lacks the submissive or reasurance nature of both subject and object, so the observer cannot help having the impression that the two individuals concerned are of an equal status. Such a type of greeting interaction, with a possible change of motivational aspect, seems to be shared also by human beings. But one more aspect must not be overlooked in the variety of greeting and appeasement behavior among wild chimpanzees. The open nature of the chimpanzee social unit has already been discussed (REYNOLDS, 1966; NISHIDA, 1967, 1968). Though observational data have not yet been made available, it is very probable that patterns of greeting and/or appeasement behavior really function as a means of inter-troop communication, when a chimpanzee who belongs to one social unit tries to enter another one. Therefore, the open nature of chimpanzee society, as well as group extensibility, might favor the development of greeting and appeasement behavior.

6) Sharing

Patterns of begging gestures are also found in greeting and submissive behavior. Moreover, there are some cases where greeting interactions are not discernible from a begging and sharing interaction in behavioral pattern. There is found clear-cut

psychological coincidence between the object's reaction in reciprocal greeting, namely the "giving" of one hand towards the subject and the giving of food on the part of the object in begging and sharing interaction. Sharing behavior can thus be reagarded as a response of the dominant animal to the greeting stimulus of the subordinate, that is, reassurance behavior with motivational change. This motivational change is to be inferred from the fact that a chimpanzee, when begged, often divides his food and gives part to the begger (halving). The evolutionary significance of sharing will be discussed in the succeeding section.

The behavioral characteristics listed above are more or less related to the "loose social structure" (GOODALL, 1965) of chimpanzee society, which has been qualified as "non-concentrativeness" in grouping (ITANI & SUZUKI, 1967), or as "group extensibility" (NISHIDA, 1968).

2. BEGGING AND SHARING BEHAVIOR

Besides true sharing interactions, we have seen many patterns of interactions which are accompanied by the giving and receiving of food (for example, the snatching interaction). In spite of this fact, food-sharing is neither seen frequently nor is it indispensable when food is abundant. However, the sharing behavior might have an adaptive value when food is scarce. Therefore, we must examine what kind of food can be shared among chimpanzees when fruit, their main food, fails to ripen in the wide range of their habitat. The chimpanzees were observed to chew the bark of *Brachystegia* or *Stelluculia* or stalks of *Aframomum* spp., etc., during the off-crop season in the study area. Grasses or barks cannot, however, be considered to be shared, for the object shared must be large and valuable enough to them, so we must take into consideration that savanna-living chimpanzees sometimes eat meat.

GOODALL (1963) often observed chimpanzees taking meat and sharing it with their companions, but up to now no correlation has been recognized between meat-eating and the change of food-supply. Chimpanzees seem to hunt and eat animals only sporadically. Efficient hunting cannot be expected even if chimpanzees find it necessary to get meat during the off-crop season because hunting is not done in groups except in rare cases and because chimpanzees have no hunting weapons at all. Thus we have no evidence that food-sharing behavior may be very *adaptive* in chimpanzee society.

What characterizes the begging and sharing interaction among wild chimpanzees is that adult males usually give food to adult females and not vice versa. In other words, the incipient differentiation of roles by sex in the interaction is recognized. This may be considered to offer a psychological basis towards the division of labour which may have developed in proto-hominid society.

It goes without saying, however, that sharing behavior has more negative aspects in chimpanzees. It highlights the difference between the sharing behavior of chimpanzees and that of primitive hunters or wolves in that the former has no connection with organized hunting. Qualitative differences which discriminate the food-sharing behavior of chimpanzees from that of primitive hunter-gatherers are (i) no reciprocity, (ii) no voluntariness: chimpanzees will not voluntarily (namely, without being begged) give food to other individuals, (iii) relatively low frequency and sporadic

occurrence, and (iv) no home base or camp site where sharing occurs periodically.

Sharing behavior among wolves lacks the first point of above list. This is because non-omnivorous wolves, being entirely dependent on meat, do not exploit vegetable food at all; otherwise, the sharing behavior of wolves is more or less comparable to that of hunter-gatherers. Thus we cannot but conclude that human type sharing behavior occurred only after the proto-hominid penetrated into the savanna terrain to begin true systematic hunting.

3. COMPARATIVE STUDY

Patterns of social behavior of chimpanzees in the Mahali Mts. were described briefly in this report. Although the data obtained are not yet complete, it will be useful to compare the behavioral repertory found in the Mahali Mts. with that found at the Gombe Stream Reserve about 170 km away from the former. It can be safely said that all major types of social behavior found at Gombe Stream were found in the author's study area as well, with apparent coincidence in details of patterns; "dialect" differentiation has not been noticed, though further observation may be needed. ITANI (1959) described in detail one behavioral pattern of Japanese monkeys living in Takasakiyama, which he called "paternal care." He stated that paternal care was not observed among all the local populations investigated so far, and concluded that paternal care was "cultural" behavior. But now this statement, it seems, has become doubtful in the light of subsequent data. The author (unpublished data) recognized paternal care in all of the three populations which he investigated intensively and which are located far from Takasakiyama. So it seems that paternal care is not cultural behavior, but rather the species characteristic behavior of Japanese monkeys. The results obtained among wild chimpanzees also suggest that their social behavior is not cultural, but species-specific behavior. The suggestion is very interesting that even human social behavior "seems to be programmed innately to a great extent" (EIBL-EIBESFELDT, 1969).

Compared with subhuman primates, however, human social behavior may be qualified as follows: all the local populations (or ethnic groups) in the world may have *in common* all repertories of elementary patterns of social behavior (e.g. aggressive behavior, greeting behavior, etc.), but human beings can be discriminated from other subhuman primates in that each pattern of human social behavior is not identical *in detail* but has some variability among local populations. It may be one of the characteristics of mankind that there exists variability to some extent in the province of social behavior, namely, that there is a culturally-determined part in its patterns. This variability, however slight, may be one of the elements which are related to the differences of social organization among human local populations.

Acknowledgments. This study was financed mainly by the Scientific Research Fund of the Ministry of Education and partly by the Wenner-Gren Foundation for Anthropological Research; the report is a part of the results of the Kyoto University Africa Primatological Expedition, which began in 1961.

I should like to express my thanks to the following persons and institutions: Dr. J. ITANI, the director of the expedition, for his guidance, ideas and encouragement; Professor J. IKEDA, Dr. Y. SUGIYAMA, and Mr. K. KANO for their advice and instructive suggestions; The Uni-

versity-College of Dar-es-Salaam and the District Office of Kigoma for the facilities they provided for me; my African helpers, Messrs. RAMADHANI, OMALI, KAHASO, KAPAMA, SALUMU, and SADI for their assistance and advice; and the people of Kasoge and Katumbi villages for the friendship and kindness which they showed me.

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—Received *October 20, 1969*; Accepted *November 29, 1969*.

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EXPLANATION OF FIGURES

Fig. 2. The Kajabara group which appeared at the feeding place.

Fig. 3. An adult male (M5) screaming, being attacked by a dominant male.

Fig. 4. M2 putting his muzzle to the face of dominant M1.

Fig. 5. M2 putting his muzzle to the face of M7, who responds with his mouth wide open.

Fig. 6. Two adult males embracing and kissing each other.

Fig. 7. A juvenile-I female making grimaces and showing presentation posture towards M1.

Fig. 8. M2 embracing the hindquarters of dominant M7 from the rear.

Fig. 9. M1 stretching his hand towards and appeasing juvenile-I female and letting her bite his hand.

Fig. 10. Grooming parties at the feeding place.

Fig. 11. M1 putting his muzzle down to and sniffing the genital area of F104, who also sniffs the genital area of M1.

Fig. 12. M1 coming out of the bush into the feeding place, scratching his buttocks.

Fig. 13-a. An adult male kicking the tree buttress.

Fig. 13-b. An adult male stamping on the tree buttress.

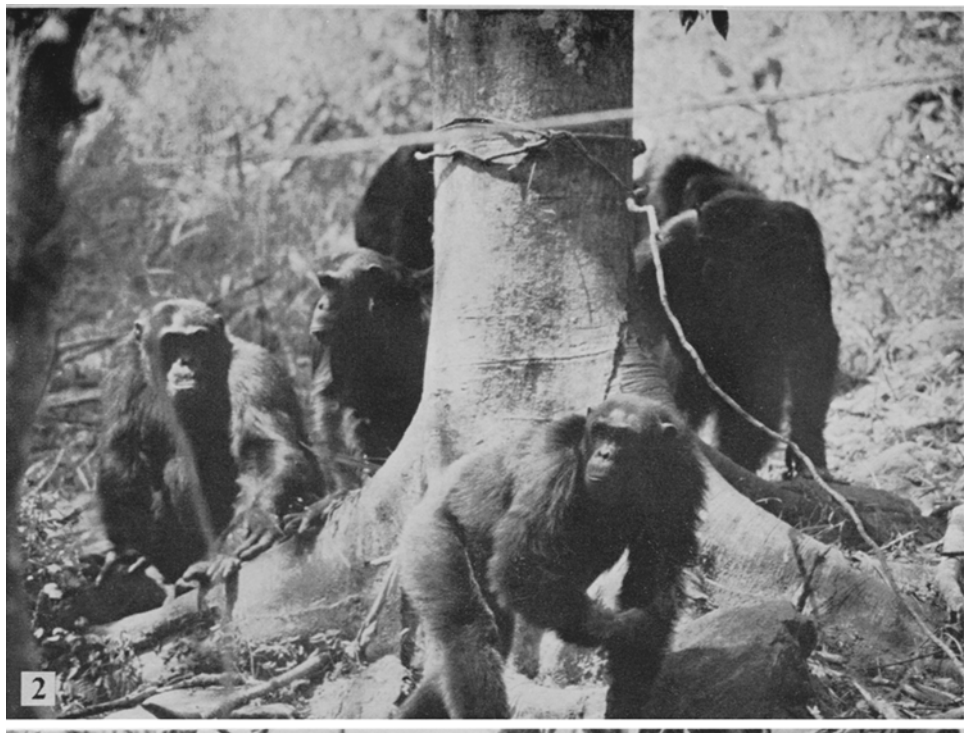
Fig. 14-a. An old female (F101) stretching her right hand towards M2, who is eating bananas.

Fig. 14-b. F101 grasping the banana which M2 holds with his right hand, trying to snatch it away. M2 does not let it go at first. F101 makes grimaces.

Fig. 14-c. F101 succeeding in snatching the banana.

Fig. 14-d. M2 retains only the banana peel. F101 goes away.

Fig. 15. M4 (left) and M7 are eating bananas on good terms in a corner of the feeding place. These two are the most dominant among the males in the group.



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