

Dominance Among Male Chimpanzees in the Mahale Mountains National Park, Tanzania: A Preliminary Study

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ABSTRACT. Dominance relationships among male chimpanzees in the Mahale Mountains National Park, Tanzania, were analyzed. Although all adolescent males were unequivocally subordinate to all adult males, dominance relationships within the age classes were much less clear. Especially among adolescent males, few pant-grunts or agonistic interactions occurred. While adolescent males frequently pant-grunted at adult males, these latter males, except the alpha and the youngest, rarely pant-grunted to one another. This suggests that a difference of social status exists between adolescent and adult males. Adult males rarely display overt dominance to one another probably because the presence of other males affects their interactions. Moreover, they seem to try to keep their dominance relationship ambiguous when making it overt is not advantageous to them. This may be a political way for males to coexist with one another in a unit-group.

Key Words: *Pan troglodytes schweinfurthii*; Dominance; Pant-grunt; Aggression; Coexistence.

INTRODUCTION

In a fission-fusion society of chimpanzees, adult males are more sociable than adult females (NISHIDA, 1968). Males spend more time with one another than do females, and have frequent interactions in a variety of contexts (NISHIDA, 1979). Male-male relationships may play an important role in maintaining integration of the unit-group. However, the dominance rank system of chimpanzees is not so clear as that of macaques or baboons (ITANI, 1984).

This study describes dominance relationships among males over a 6-month period in 1985-1986. This is a preliminary one because historical analyses such as reported by RISS and GOODALL (1977), DE WAAL (1982), and NISHIDA (1983) are necessary to understand the dominance relationships in detail.

METHODS

This study was conducted on the M group chimpanzees (*Pan troglodytes schweinfurthii*) of the Mahale Mountains National Park, Tanzania. This group has been studied since 1965, and provisioned periodically from 1968 to 1975. Since then artificial feeding has been reduced, and now the chimpanzees depend entirely on natural foods. For a detailed description of the habitat, research history, and the demography, see NISHIDA (1979) and HIRAIWA-HASEGAWA et al. (1984).

The study period was from August 1985 to January 1986. During this period, M group consisted of about 100 chimpanzees. Data were collected mainly by *ad lib* sampling method, but focal sampling method (ALTMANN, 1974) was also employed for three adult males (KI, LJ, and SM) by M.A.H. and for one adult male (KZ) and five adolescent males (SU, NS, AJ, TW, and TB) by H.H. Names and estimated ages (see HIRAIWA-HASEGAWA et al., 1984 for age estimation) of adult and adolescent males are shown in Table 1.

Table 1. Adult and adolescent males in M group.

Name (abbr.)		Birth year	Age class
Kalindimya	(KL)	1930s ¹⁾	Old adult male
Kagimimi	(KI)	1940s ¹⁾	
Bakali	(BA)	1954 ¹⁾	Prime adult male
Ntologi	(NT)	1955 ¹⁾	
Lubulungu	(LU)	1957 ¹⁾	
Musa	(MU)	1957 ¹⁾	Young adult male
Kalunde	(DE)	1963 ¹⁾	
Lukaja	(LJ)	1965 ¹⁾	
Kasulamemba	(SM)	1966 ¹⁾	
Kasangazi	(KZ)	1968 ¹⁾	Adolescent male
Shike	(SU)	1970 ¹⁾	
Bembe	(BE)	1972 ¹⁾	
Hitto	(HT)	1972 ¹⁾	
Nsaba	(NS)	1973	
Aji	(AJ)	1973 ¹⁾	
Mtwale	(TW)	1975 ¹⁾	
Jilba	(JI)	1975 ¹⁾	
Toshibo	(TB)	1976	
Masudi	(MA)	1977	

1) Estimates (see HIRAIWA-HASEGAWA et al., 1984, for details).

Table 2. Pant-grunts among males.*

Receiver	Utterer												
	Adult										Adolescent		
	NT	BA	LJ	KI	KL	DE	MU	LU	SM	KZ	SU	NS	AJ
Adult													
NT	—	5	17	3	2	12	9	8	9	24	11	8	20
BA		—					2			5	1	1	1
LJ			—				1		4	8	5	3	2
KI				—		1			1	2	1	1	3
KL					—		1						
DE						—				8	3	1	2
MU							—			1	1		5
LU								—	1	6	2	1	3
SM									—		3		3
KZ										—	4		4
Adolescent													
SU											—		
NS												—	
AJ													—
HT													
BE													
TW													
TB													
JI													
MA													
Total	0	5	17	3	2	13	13	8	15	54	31	15	43

*Figures indicate numbers of pant-grunts, combining *ad lib* and focal data.

(continued)

The following two types of interactions were analyzed to determine the dominance rank among male chimpanzees.

PANT-GRUNT

The pant-grunt is usually uttered during a greeting situation, and is always directed by a subordinate to a dominant individual. NOË et al. (1980), DE WAAL (1982), and BYGOTT (1979) showed, when they analyzed the dominance system of chimpanzees, that the pant-grunt was the best indicator of relative status. A chimpanzee, during intense social excitement, particularly when in the presence of an ally, may display toward or hit a superior, but the latter will not pant-grunt toward him (GOODALL, 1986).

AGONISTIC INTERACTIONS

Agonistic interactions included attack, threat, and directed charge (they were called "aggressive behaviors"), and screaming, grin face, avoidance, presenting, touching, kissing, mounting, and embracing (they were called "subordination behaviors"). Usually, within pairs of individuals when one individual performs aggressive behaviors, the other does not perform such behaviors. Conversely, when one individual performs subordination behaviors, the other does not perform such behaviors. In such cases, we can recognize dominance-subordination relationships within the pairs at least when nearby third parties do not influence the pair's interaction. However, interactions in which one individual performed only presenting, touching, kissing, mounting or embracing were excluded from analysis, because a dominant male sometimes performs such behaviors for reassuring himself.

Table 2. (continued)

Utterer														Total
Adolescent					Juvenile					Infant				
HT	BE	TW	TB	JI	MA	FC	UU	HR	HB	BG	IW	NC	LT	
11	3	28	5		2		2	1						180
		4	6											20
3	1	10	5	1										43
2		6	3		1									21
														1
1	1		4	2									1	23
		8	4	1		1	1							22
1	1	7	4										1	27
	4	3	9							1				23
	3	1	2	1								1		16
2	7	4	3	2	1				1					20
1	2													3
														0
—	1													1
	—													0
		—			1									1
			—							1	1			2
				—										0
					—									0
21	23	71	45	7	5	1	3	1	1	2	1	1	2	403

RESULTS

DOMINANCE RANK BASED ON PANT-GRUNTS AMONG MALES

We observed 415 pant-grunts between males, combining *ad lib* and focal data. In 403 pant-grunts, we could clearly identify the individual at whom the pant-grunt was directed. Table 2 summarizes the direction of pant-grunts among males. The direction of pant-grunts was one-sided without exception. Linear rank order based on pant-grunts seems to exist among males. However, it was impossible to determine the rank order exactly among adult males and among adolescent males. Adult males except KZ, the youngest adult, rarely pant-grunted among themselves except toward NT, the alpha male. Also adolescent males rarely pant-grunted among themselves except toward SU, the oldest adolescent, while they often did so toward adult males. Almost half of all pant-grunts were directed toward the alpha male.

The remaining 12 pant-grunts which were uttered toward a gathering made it impossible to identify whom they were directed to. However, in 8 of the 12 pant-grunts, NT was included in the gathering. In the other cases, LJ was included in the gathering (Table 3). These pant-grunts seem to have been directed at NT or LJ whoever was the most dominant in the gathering at the time, because pant-grunts are usually directed at the most dominant individual when a chimpanzee encounters a gathering. The direction of pant-grunts agreed with those in Table 2. Therefore, these pant-grunts were regarded as having been directed at NT or LJ in the following analysis.

One hundred and eighty-seven of the 415 pant-grunts were observed in focal sampling (Table 4). Most pant-grunts were uttered by adolescent and young adult males toward adult males. LJ, KI, SM, KZ, and SU frequently received pant-grunts from adolescent males, while KZ, SU, NS, AJ, TW, and TB frequently uttered pant-grunts toward adult males. With the exception of KZ, the lowest ranking adult male, focal adult males were rarely involved in pant-grunting with other adult males. In fact, only two cases of one adult male pant-grunting at another were observed during tracking, except for NT, the dominant adult male, and KZ, the youngest adult male. Likewise, four adolescents were rarely involved in pant-grunting with other adolescent males. This suggests the difference of males' status between adults and adolescents. KZ and SU, who frequently received pant-grunts from adolescent males and frequently directed to adult males, seem to be situated on this border.

Table 3. Pant-grunts toward a gathering.

Date	Time	Utterer	Gathering ¹⁾
August 21	10:16	AJ ²⁾	NT, KZ, <i>GW</i>
August 29	10:42	TW ²⁾	NT, KI
August 31	13:55	TW ²⁾	NT, KI
October 2	12:23	AJ ²⁾	NT, KI
October 19	13:30	TB ²⁾	NT, MU
November 1	10:13	SM	LJ, MU
November 3	11:05	TW ²⁾	LJ, DE
November 4	10:13	SU ²⁾	LJ, MU
November 4	10:13	AJ	LJ, MU
November 8	11:00	TW ²⁾	NT, LU, <i>NG</i>
November 23	15:21	MU	NT, LJ, BA, LU
December 15	10:30	TB ²⁾	NT, LU

1) Italics indicate female; 2) focal sampling.

Table 4. Pant-grunts data from focal sampling.*

Partners	Focal animals									Total
	Adult				Adolescent					
	LJ	KI	SM	KZ	SU	NS	AJ	TW	TB	
Adult										
NT	1/0		2/0	7/0	5/0	4/0	11/0	18/0	5/0	53/0
BA				2/0	1/0				5/0	8/0
LJ	—		2/0	3/0	5/0	2/0	1/0	3/0	4/0	20/0
KI		—		1/0		1/0	2/0	5/0	1/0	10/0
KL										0/0
DE				5/0	2/0				3/0	10/0
MU					1/0		3/0	6/0	2/0	12/0
LU				6/0	2/0	1/0	1/0	5/0	2/0	17/0
SM			—				1/0		8/0	9/0
KZ	0/1	0/1		—	2/0		1/0		2/0	5/2
Adolescent										
SU	0/1	0/1	0/3	0/1	—			2/0	2/0	4/6
NS						—				0/0
AJ		0/1	0/2	0/3			—			0/6
HT					0/1	0/1				0/2
BE			0/1	0/2	0/5	0/1				0/9
TW	0/2	0/1	0/1					—		0/4
TB	0/1	0/1	0/1						—	0/3
JI				0/1	0/1					0/2
MA		0/1						0/1		0/2
Juv. & Infant										
HB					0/1					0/1
BG									0/1	0/1
IW									0/1	0/1
Total	1/5	0/6	4/8	24/7	18/8	8/2	20/0	39/1	34/2	148/39
Duration of tracking (min)	1820.4	1346.2	1833.9	1631.1	1718.1	1468.9	1738.1	1748.4	1607.8	14912.9

*Figures indicate numbers of pant-grunts which the focal animal uttered / those which the focal animal received.

AGONISTIC INTERACTIONS AMONG MALES

In the combined *ad lib* and focal data (Table 5), we observed 109 agonistic interactions in which only one of the pair performed aggressive behaviors or subordination behaviors, excluding cases accompanied by pant-grunts. Out of these, only 38 interactions (0.15 interactions/hour) were observed during focal sampling. Dominance relationship based on these interactions basically agreed with that based on pant-grunts.

DOMINANCE-SUBORDINANCE RELATIONSHIPS AMONG ADULT MALES

Combining all data from Table 2, Table 3, and Table 5, dominance-subordination relationships among adult males and among adolescent males are shown in Tables 6 and 7.

Adult males can be arranged in linear rank order, although the status of BA and KL were unclear. BA had been the second ranking male as late as 1984 (HIRAIWA-HASEGAWA, pers. comm.). In 1985, LJ rose in rank and became equal to BA. We observed four cases of interactions between BA and LJ which were related to dominance, but it was not possible to determine which was dominant.

In one case, BA ran up ahead of NT while screaming, and approached LJ. BA hugged LJ

Table 5. Agonistic interactions among males.*

Dominant	Subordinate														Total							
	Adult							Adolescent								Juvenile						
	NT	BA	LJ	KI	KL	DE	MU	LU	SM	KZ	SU	NS	AJ	HT		BE	TW	TB	JT	JI	MA	UU
Adult																						
NT	2	4*	2*	1	1	2	1	1	2*	2*	2	2*	4	2	2	1	1					
BA	—	—	—	3*	6*	2	1*	1	2	1*	1*	1*	3*	4*	1	1*						
LJ	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
KI	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
KL	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
DE	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
MU	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
LU	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
SM	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
KZ	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Adolescent																						
SU	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
NS	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
AJ	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
HT	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
BE	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
TW	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
TB	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
JT	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
JI	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
MA	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	0	2	4	3	0	6	8	7	4	9	9	7	9	7	0	19	6	6	6	0	1	2

*Figures indicate numbers of agonistic interactions in which the dominant-subordinate relationship was apparently recognizable, and pant-grunts did not occur, combining *ad lib* and focal data. *including focal data.

Table 6. Dominance rank order among adult males.

Dominant	Subordinate										Total
	NT	BA	LJ	KI	KL	DE	MU	LU	SM	KZ	
NT	—	7	21	5	2	13	10	10	10	25	103
BA	—	—					3			5	8
LJ			—	1		3	7	2	5	9	27
KI				—		3			1	3	7
KL					—		1				1
DE						—	1	1	2	8	12
MU							—	2	1	2	5
LU								—	1	7	8
SM									—	4	4
KZ										—	0
Total	0	7	21	6	2	19	22	15	20	63	175

from the front. NT then approached and chased after BA. BA screamed and moved behind, following NT. In this case, BA seemed to hug LJ in order to reassure himself. However, this type of contact-seeking behavior (GOODALL, 1968) is not always directed at a more dominant individual. This case only indicates that NT was dominant to BA.

In two more cases, LJ displayed near BA. In one case, however, the outcome was not observed, and in the other case, BA quickly climbed up a nearby tree but it was ambiguous whether or not BA had avoided LJ who was displaying. Nevertheless, these cases do show that LJ was able to display near BA. It is frequently observed that clearly subordinate males refrain from displaying in the presence of dominant ones or are attacked or chased for doing so if a dominant male approaches during his display.

In the fourth case, BA chased LJ but both BA and LJ were screaming. This case was observed from a ridge, the interactions occurring in the forest below, so the observer could not confirm the outcome of this interaction. However, this case shows that LJ had become equal to BA. The rise in rank of LJ became evident in another case, in which LJ could display near NT.

Did LJ really rise in rank? We observed a case also in which LJ hugged DE when someone barked nearby. Probably, LJ hugged DE in order to reassure himself, similar to the case previously mentioned. However, this case gave us the impression that LJ was still young and inexperienced. If LJ really did rise in rank, the former male coalition in male-male relationships will be reorganized. Until 1984, BA usually opposed NT and they rarely met each other. This tense relationship might change in the future.

KL was the oldest male in M group. He was considered to have been the alpha male in the past. He has been observed for a long time, but is still shy in the presence of human observers. For this reason, pant-grunts and agonistic interactions including him were rarely observed. We observed MU once pant-grunt at KL. This indicates that he at least was dominant over MU. However, the following case presents a contradiction to this.

Case 1 (September 13, 1985)

13:47 KL is eating meat near NT, KI, LU, and a few females. One of them pant-hoots and displays. KL threatens LU, slapping the ground, screaming. LU erects his hair, but grimaces.

13:48 LU approaches KL. KL again threatens LU, screaming. LU stops.

13:50 LU pant-hoots and displays at KL. KL steps back a little, screaming and grimaces. LU puts a hand on KL's back, and KL calms down.

In this case, LU seems to have been equal or dominant to KL; nevertheless, KL was

dominant to MU who was dominant to LU. MU directed charging display at LU two times, and in both cases LU screamed (Table 5). Is the dominance relationship among chimpanzee males not linear? In interpreting this case, we must take into account the presence of other adult males. LU might have behaved more dominant toward KL because of the presence of high-ranking males, NT and KI. Certainly, LU had always been tolerated by NT, and they had often ranged together. However, KL had been tolerated by NT as well as LU especially in meat eating situations (TAKAHATA et al., 1984). It was our impression that LU was stronger than KL, even when taking into account the presence of other more dominant males. If our impression is correct, however, what may be puzzling is that MU pant-grunted at KL. Old males might be able to behave as if they were dominant, because they are respected by younger males, i.e., they remember the males' younger days as a powerful active individual.

Old males sometimes attacked more dominant males when the most dominant male was nearby. In the following case, KI (old male) attacked LJ and BA in the presence of NT.

Case 2 (January 28, 1986)

8:45 KI attacks LJ in a tree. NT stays under the tree. LJ makes a counterattack and they exchange blows. KI stops attacking, without screaming or grin face. BA comes from the west and pant-grunts at NT. KI approaches BA and strikes BA vigorously on the back, standing bipedally. BA screams and makes no attempt to counterattack. KI threatens BA, who continues to grimace. Afterwards, NT attacks BA.

In a different situation, KI was able to take all the sugarcane thrown experimentally toward LJ in the presence of NT and MU. However, we observed a case in which KI and LU threatened one another while KI grined and screamed. This means KI may have been subordinate to LU. Furthermore, we observed another case in which SU covered KI who present-crouched. Although KI made no vocalization or grin face, he certainly adopted a presentation posture toward SU, a late adolescent male. These cases raise questions about KI's status and shows that KI's rank might actually be lower than it sometimes appears.

DOMINANCE-SUBORDINANCE RELATIONSHIPS
AMONG ADOLESCENT MALES

Dominance rank order among adolescent males was even more obscure than that among adult males (Table 7), because few pant-grunts of agonistic interactions occurred among them. Most pant-grunts and agonistic interactions involved two older adolescents, SU or NS (88%: 29 of 33 interactions). Early adolescent males rarely pant-grunted at one another,

Table 7. Dominance rank order among adolescent males.

Dominant	Subordinate									Total
	SU	NS	AJ	HT	BE	TW	TB	JI	MA	
SU	—		1	3	7	4	4	3	1	23
NS		—	1	1	2	1		1		6
AJ			—							0
HT				—	1					1
BE					—					0
TW						—			1	1
TB							—	2		2
JI								—		0
MA									—	0
Total	0	0	2	4	10	5	4	6	2	33

and were rarely involved in agonistic interactions among themselves. Furthermore, if a dominant adolescent attacks a subordinate, he may be attacked by adults, as screaming of young animals can be dangerous for nearby adolescent males.

Case 3 (November 23, 1985)

13:02 When TB approaches *TM* (estrous female), TW charges at him. TB flees, screaming. Then, he approaches TW while screaming with grin face. At that time, TW quickly runs away.

Clearly, TW was dominant to TB. However, he avoided TB when TB came screaming. In another case, TB who was attacked by TW immediately approached an adult male for reassurance. Adolescent males must pay attention to the presence of adult males.

Young adolescent males sometimes attack a dominant adolescent male when their mothers or brothers are present. They can behave as if dominant to the other in such situations. We observed a case in which NS was attacked by TB in the presence of TB's brother and mother. At that time, his mother supported him, attacking NS, but his brother ignored them. Also in another instance, TB threatened HT, considered to be dominant to TB by their relative body size, in the presence of TB's mother, although HT ignored TB and TB's mother showed appeasement behavior to HT. The dominant young male seems to ignore the subordinate's attempt at trouble making.

DISCUSSION

Although male chimpanzees in small unit-groups form a linear dominance hierarchy (NISHIDA, 1979; SUGIYAMA & KOMAN, 1979), their dominance relationships are less clear in large-sized unit-groups. BYGOTT (1979) distinguished only four categories of adult males (alpha, high-ranking, middle-ranking, and low-ranking) in a 15-male unit-group at Gombe. The present study also shows that dominance relationships among males are more or less unclear in the M group which has ten adult males and nine adolescent males.

However, a difference of social status exists between adult males and adolescent males. Clearly, all adult males dominated all adolescent males. Adolescent males frequently pant-grunted at almost all adult males, especially the alpha male, while adolescent males and adult males rarely pant-grunted to males of their own age class, excluding the alpha, NT, and KZ and SU who were in the border position between adult and adolescent.

Pant-grunts were directed undoubtedly by the subordinates to the dominants. However, it should be noted that most pant-grunts occurred between pairs whose dominance relationships were already apparent from the difference in body size or other agonistic interactions. This suggests that such pant-grunts are not uttered in order to confirm the participants' dominance relationship, although they might have an effect of confirming dominance. It seems more likely that at least adolescent males pant-grunt at adult males in order to make their presence or existence recognized. On the other hand, adult males, except the alpha and the youngest, rarely pant-grunted to one another. This seems to indicate that they try not to show a submissive attitude to one another.

The unclear dominance relationships among males may be caused by the fact that they rarely meet on their own, so most interactions are affected by the presence of others (NISHIDA & HIRAIWA-HASEGAWA, 1987). A dominant adolescent male must pay attention to adults who may support the subordinate. Older adolescent males, who are potentially dominant to younger ones, may run the risk of being injured by adult males if they display overt domi-

nance to younger adolescent males. Younger adolescent males may refrain from showing a submissive attitude to older adolescent males, because it may not confer any advantage by doing so. It seems to be enough for young males to show a submissive attitude to and be tolerated by adult males. Likewise, a dominant adult male must also pay attention to other adult males who may be allies of the subordinate. Adult males seem to inhibit one another from displaying overt dominance because of the complex coalitions formed among them. Considering the results of the pant-grunt data, they may try to keep their dominance relationship ambiguous when making it overt is not advantageous. Therefore, declining old males may be able to act as if in higher status than they really are. While keeping dominance relationships ambiguous, young males wait for a chance to promote their status, and declining old males maintain their status. This is a political way of coexisting with other males in a unit-group, in which adult males must have ambivalent relationships with one another (NISHIDA & HIRAIWA-HASEGAWA, 1987).

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