Meat-Sharing as a Coalition Strategy by an Alpha Male Chimpanzee?

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INTRODUCTION

Wild chimpanzees kill or scavenge mammals and often share meat (Boesch and Boesch, 1989; Goodall, 1986; Hasegawa *et al.*, 1984; Takahata *et al.*, 1984; Teleki, 1973). Meat-sharing is puzzling insofar as it appears to be altruistic, and is the only pattern of food sharing that is regularly observed among adult chimpanzees in the wild.

Two non-mutually exclusive hypotheses have been proposed to explain the function of meat-sharing. First, Wrangham (1975) suggested that meat-sharing occurs when an individual has more than he needs, particularly after eating a lot. In such a case, it is pointless to keep avoiding or threatening others who are eager for portions of meat. Meat-sharing is the least costly strategy that minimize time, energy, and risk of injury. This hypothesis provides a theoretical basis for why food-sharing can occur in even selfish chimpanzees. However, Wrangham did not interpret the function of meat-sharing in terms of positive benefits to the meat-owner, although he did mention the selective release of meat to family members and estrous females. Second, de Waal (1989) proposed a hypothesis for chimpanzee food-sharing based on reciprocity. In his captive colony consisting mostly of adult females, he showed that if individual A shared foliage with individual B, then B reciprocated. Moreover, grooming between two individuals during the morning affected the probability of food-sharing later in the day.

During our long-term study of M Group chimpanzees in the Mahale Mountains, we have observed an adult male, Ntologi, the alpha

male for more than 10 years, sharing meat selectively with other individuals. He gives certain middle- or low-ranking males disproportionately large portions. In this paper we examine meat-eating episodes to assess whether or not Ntologi follows a consistent rule regarding with whom to share. These data along with observations of grooming, associations, and other social interactions between Ntologi and others, lead us to propose a new hypothesis for the function of sharing: It may be a political strategy, used to establish and to reinforce alliances.

METHODS

Chimpanzees were observed in the Mahale Mountains National Park, Tanzania (Nishida, 1990). The data presented here are based on observations made of M Group chimpanzees over nine years, from 1981 to 1989. From meat-eating episodes recorded during this time, we extracted all the cases (N=47) when the alpha male, Ntologi, had possession of the carcass at least temporarily and distributed meat to at least one other chimpanzee.

Following Wrangham (1975) and Kawanaka (1982), we defined the "meat-eating cluster" as the group of chimpanzees that closely gathered around the meat possessor to take or to beg for part of the carcass. "Meat-recipients" were defined as participants in such clusters who were permitted to take a portion of meat directly from Ntologi.

Observations reported here were divided into seven periods, within each of which more than one researcher were present. Each period began in July or August and ended in January or February of the next year. For example, the '81 period covered the months from July 1981 to February 1982. Male rank relationships did not change considerably within each period. Male rank was determined by the directionality of pant-grunting and by the result of dyadic agonistic confrontations. In addition, published and unpublished reports were available (for 1981, Takahata *et al.*, 1984; for 1983, Kawanaka, 1990; for 1985, Hayaki *et al.*, 1989; for 1986, Kawanaka, 1990 and Hunt, 1989; for 1987, Hunt, 1989). When ranking could not be determined between several competing males, the same rank was assigned to them all (Table 1).

We analyzed correlations between meat-sharing by Ntologi and grooming with and proximity to him. Data on grooming with Ntologi were available from published sources for 1981 (Takahata, 1990), 1983, and 1986 (Kawanaka 1990) and from unpublished data for 1985, 1987, 1988, and 1989. Table 2 shows total duration of grooming between Ntologi and other adult and old adolescent males in the seven study

Table 1. Male Age and Dominance Rank

	Names of individuals	Year of birth	Age rank	Periods of study by year '81	'83	'85	'86	'87	'88	'89
Adult males (≥15 yrs)	KL (Kalindimya)	late 1930s	(1)	6	6	5.5	–	–	–	–
	RA (Rashidi)	late 1940s	(2)	7	–	–	–	–	–	–
	KI (Kagimimi)	late 1940s	(3)	3	3	4	5	–	–	–
	BA (Bakali)	early 1950s	(4)	2	2	2.5	3	5	4.5	7
	NT (Ntologi)	mid 1950s	(6)	1	1	1	1	1	1	1
	LU (Lubulungu)	mid 1950s	(6)	5	5	8	7.5	6	10	–
	MU (Musa)	mid 1950s	(6)	4	4	7	7.5	8	9	9
	DE (Kalunde)	?1963	(8)	8	7	5.5	3	2	2	2
	LJ (Lukaja)	?1965	(9)	9	8	2.5	3	7	4.5	5
Old adolescent males (12–14 yrs)	SM (Kasulamemba)	?1967	(10)	10	9	9	–	–	–	–
	KZ (Kasangazi)	?1968	(11)	11	10	10	9	3	4.5	6
	SU (Shike)	?1970	(12)	12	11	11	6	4	4.5	3
	BE (Bembe)	?1972	(13)			14		11	11	10
	NS (Nsaba)	1973	(14.5)			12		9	7	4
	AJ (Aji)	?1973	(14.5)			13		10	8	8

periods.

We defined a grooming reciprocity index between Ntologi and others as $(a-b)/(a+b+2c)$, where a is the duration for which Ntologi grooms individual B, b is the duration for which B grooms Ntologi, and c is the duration of mutual grooming between Ntologi and B (Nishida, 1988).

The proximity index between individuals A and B was defined in 1981 as $\{DP(A,B)+DP(B,A)\} \times 100/\{DT(A)+DT(B)\}$, where $DT(A)$ is the observation duration on individual A, and $DP(A,B)$ is the total duration during which individual B was within 3 m of the focal animal A

Table 2. Data on Grooming of Adult Males with Ntologi

			81*	83#	85A+	85B	86#	87A	87B	88	89
Adult males	KL	*a*	–	0	1	36.4	–	–	–	–	–
		c	–	0	0	2.4	–	–	–	–	–
		b	–	0	0	2.3	–	–	–	–	–
	RA	*a*	167	–	–	–	–	–	–	–	–
		c	–	–	–	–	–	–	–	–	–
		b	154	–	–	–	–	–	–	–	–
	KI	*a*	57	2.8	1	0	1.5	–	–	–	–
		c	–	0.3	1	0	0.3	–	–	–	–
		b	104	1.3	3	0	1.7	–	–	–	–
	BA	*a*	54	0.4	2	4.8	1.8	13.4	5.6	5.3	11.1
		c	–	0.2	0	13.7	0.4	8.4	8.1	9.3	8.0
		b	59	0.5	0	0	4.0	30.1	11.1	16.8	25.5
	LU	*a*	470	3.4	3	32.1	4.6	16.6	3.2	16.6	–
		c	–	0.6	2	20.7	0.9	8.7	12.1	2.6	–
		b	70	2.8	3	16.0	1.6	29.2	7.2	4.9	–
	MU	*a*	9	2.2	1	1.1	1.2	34.7	5.6	3.3	30.0
		c	–	0.2	0	0	0.1	9.1	0	0.5	6.5
		b	0	2.4	0	0	0.3	38.8	0	2.6	25.7
	DE	*a*	0	0.2	0	0.7	0.7	5.9	18.0	0	0
		c	–	0.0	0	0	0.9	0.7	22.5	0	0
		b	0	0.2	0	6.7	1.9	5.0	33.9	0	0.4
	LJ	*a*	0	0.7	1	1.3	1.8	0	0.7	0	0
		c	–	1.1	0	7.4	1.0	0	0	0	23.6
		b	0	1.7	0	1.9	2.7	0	0	0	19.5
Old adolescent males	SM	*a*	0	0.0	0	0	–	–	–	–	–
		c	–	0.0	0	0	–	–	–	–	–
		b	0	0.1	0	0	–	–	–	–	–
	KZ	*a*	0	0.1	1	0	0.4	0	0	0	0
		c	–	0.1	0	0	0.1	0	0	0	0
		b	0	0.4	1	0	1.5	0	0	0	0
	SU	*a*	–	0	0	0	0.4	0	0	0	0
		c	–	0	0	0	0.0	0	0	0	0
		b	–	0	0	0	0.4	0	0	0	0
	BE	*a*	–	0	0	0	0	0	0	0	0
		c	–	0	0	0	0	0	0	0	0
		b	–	0	0	0	0	0	0	0	0
	NS	*a*	–	0	0	0	0	0.6	0	0	7.6
		c	–	0	0	0	0	0	0	0	0
		b	–	0	0	0	0	0	0	0	0
	AJ	*a*	–	0	3	0	1.2	0.7	0	1.0	7.3
		c	–	0	2	0	0.3	0	0	0	2.9
		b	–	0	2	0	2.5	0	0	0	5.4

Figures are shown in minutes except *, #, and + below. *a*: Ntologi grooms, *c*: mutual grooming, *b*: Ntologi is groomed.

81* : Duration of grooming between focal males in observation unit (10sec). Mutual grooming was allocated to each participant (Takahata, 1990).

83# : Focal sampling (293 h) of Ntologi. % time spent grooming in Ntologi's total resting time (Kawanaka, 1990).

85A+: Ad-lib sampling of Ntologi. One-zero samples per observation day (Hayaki, unpublished).

85B : Ad-lib sampling (Nishida, unpublished).

86# : Focal sampling (60 h) of Ntologi. % time spent grooming in Ntologi's total resting time (Kawanaka, 1990).

87A : Focal sampling (31.6 h) of Ntologi (Uehara, unpublished).

87B : Ad-lib sampling of Ntologi (Nishida, unpublished).

88 : Focal sampling (21.4 h) of Ntologi (Hasegawa, unpublished).

89 : Ad-lib sampling of Ntologi (Nishida, unpublished).

(Takahata, 1990). It was defined in 1983 and 1986 as the percentage of time spent within 10 m from Ntologi (Kawanaka, 1990). Proximity data were not collected while chimpanzees were feeding on meat.

An old male, Kalindimya, was shy, and data on his relations with Ntologi were undoubtedly underrepresented.

RESULTS

The age-sex class of the captor was confirmed on 60 of 130 meat-eating occasions, and Ntologi's contribution was only 8%, although he was one of the three best hunters that were observed to capture prey on five occasions during the period (Table 3). Nevertheless, most opportunities for meat-eating were ultimately under Ntologi's control, as he seized the meat shortly after capture. Ntologi held the carcass in almost a third of 183 observations in which the identity of the holder was confirmed. Ntologi also performed almost half (20 of 39) of the forcible takeovers of carcasses.

Table 3. Process of Meat Acquisition by the Alpha Male

Meat-eating episodes	Identity of hunter confirmed	First carcass -holder confirmed	Second carcass -holder confirmed	Third or fourth holder confirmed	Total
130	60	119	48	16	183
Alpha's contribution	5	30	21	6	57
(%)	(8)	(25)	(44)	(38)	(31)

Table 4 shows the number of times each adult male received meat from Ntologi. The frequency of receiving meat was consistently positively correlated with age, and statistically significant correlations were observed in four of the seven observational periods (Table 5).

However, the frequency of receiving meat was not always positively correlated with dominance rank; a statistically significant correlation occurred only in 1983 and 1985 (Table 5). The correlation between meat

Table 4. Frequency of Getting Meat from the Alpha Male

Period		'81	'83	'85	'86	'87	'88	'89	Totals
No. of episodes		8	8	6	1	8	3	13	47
Adult Males (≥15 yrs)	KL	3	1	1	–	–	–	–	5
	RA	1	–	–	–	–	–	–	1
	KI	5	4	4	1	–	–	–	14
	BA	1	1	1	0	2	3	9	17
	LU	6	5	3	1	8	3	(1)[1]	27
	MU	0	1	2	0	4	3	8	18
	DE	0	0	0	0	0	0	0	0
	LJ	0	1	3	0	3	3	12	22
Old adolescent males (12–14 yrs)	SM	0	0	0	0	–	–	–	0
	KZ	0	0	0	0	0	0	0	0
	SU	0	0	0	0	0	0	0	0
	BE	0	0	0	0	0	0	0	0
	NS	0	0	0	0	0	0	1	1
	AJ	0	0	0	0	0	0	1	1

–: Died or missing.

[1]LU became sick in 1989 and mostly moved alone, and was excluded from analysis, although he was once observed to get meat.

Table 5. Spearman's Rank Correlation Coefficients among Age, Dominance, and Meat-getting

Periods	'81	'83	'85	'86	'87	'88	'89
Number of adult males excl. Ntologi	8	9	10	8	8	10	9
Age v. meat	+.58	+.69 *	+.63 *	+.65 *	+.71 *	+.98 **	+.40
Dominance v. meat	+.47	+.72 *	+.61 *	+.10	−.42	+.50	−.16
Age v. dominance	+.40	+.82 *	+.66 *	+.26	+.07	+.21	+.02
#	+.41	+.63 *	+.61 *	+.29	+.20	+.30	+.16

#: Including Ntologi. * $p<0.05$ ** $p<0.01$

acquisition and dominance rank was negative in 1987 and 1989 because young adult males, who rarely obtained meat, rose in rank.

Total Amount of Grooming

If grooming and meat-sharing are parts of an alpha male's alliance strategy, we would expect the amount of grooming exchanged between

Table 6. Correlation of Frequency of Meat-receiving with that of Grooming with the Alpha Male

Year	Spearman's r_s	Number of adult males	Sampling methods	Source of data on grooming
1981	0.91 *	7	Focal (21.8 h)	Takahata (1990)
1983	0.85 *	7	Focal (293 h)	Kawanaka (1990)
1985	0.70 *	10	Ad-lib	Hayaki (unpub.)
	0.42 NS		Ad-lib	Nishida (unpub.)
1986	0.53 NS	8	Focal (60 h)	Kawanaka (1990)
1987	0.65 *	10	Focal (31.6 h)	Uehara (unpub.)
	0.64 *		Ad-lib	Nishida (unpub.)
1988	0.78 **	11	Focal (21.4 h)	Hasegawa (unpub.)
1989	0.90 **	9	Ad-lib	Nishida (unpub.)

* $p<0.05$ ** $p<0.01$ NS: Not significant at 5% level.

Ntologi and other males to be positively related to the frequency with which he shares meat.

The frequency of meat acquisition was significantly positively correlated with the total amount of time spent grooming with Ntologi during six of the seven observation periods (Table 6). In 1985 meat sharing data were significantly correlated with grooming data from one source, but not with another. In 1986 a positive relationship between these two variables existed, but did not reach statistical significance.

Grooming Reciprocity

We predicted that the alpha male would not only maximize grooming bouts with allies, but also would groom them at least as often as they groom him. The grooming reciprocity index was calculated for comparison only in 1983 and 1986, when Ntologi was followed for more than 60 hrs and the numbers of samples exceeded 7. The index, which increased with the alpha's grooming activity, was positively related to the frequency with which others received meat, although the correlations did not reach statistical significance (1983: $r_s=0.57$, $N=7$, $p>0.05$; 1986: $r_s=0.48$, $N=8$, $p>0.05$).

Ntologi showed favoritism toward a particular male, Lubulungu. He groomed Lubulungu more than Lubulungu groomed him in all study periods except 1987. By contrast, Ntologi was groomed by Bakali, a former adversary, more than vice versa in all study periods except in 1985, when Bakali's beta status was threatened by Lukaja and he apparently began to seek Ntologi's support (Table 2).

The reciprocity index was positively correlated with the ages of the males, although the correlations did not reach statistical significance (1983: $r_s=0.56$, $N=7$, $p>0.05$; 1986: $r_s=0.16$, $N=8$, $p>0.05$).

Proximity

Allies were expected to remain nearby to support each other against other males, and the proximity index was significantly positively correlated with the frequency with which individuals obtained meat in two years (1983: $r_s=0.84$, $N=7$, $p<0.05$; 1986: $r_s=0.69$, $N=8$, $p<0.05$). The relationship between the two variables approached significance in an additional year (1981: $r_s=0.69$, $N=7$, $p<0.10$). Lubulungu and Kagimimi had the highest proximity indices with Ntologi, and appeared to have special relationships with him. Proximity data for other periods were not available.

Mean Durations of Proximity Bouts

We expect the alpha to socialize with his allies most frequently, and

therefore to remain near them for the longest periods. The mean duration of proximity bouts between Ntologi and others was positively related to the frequency with which others received meat (1981: $r_s=0.74$, $N=7$, $p<0.05$). Data on proximity duration for the other periods were unavailable.

Aid in Combat

Ntologi tended to support male members of his meat-eating cluster against other males when they were involved in conflicts. For example, in the 1985 study period, Kagimimi beat violently with both hands on the back of Bakali, who was dominant over him, when Ntologi was nearby. Bakali screamed without retaliating. Kagimimi continued to threaten Bakali, who grimaced. Then Ntologi chased Bakali.

Ntologi has been a powerful alpha male, and successive second-ranking males of M Group have not challenged him. Therefore, it is unknown whether Ntologi's suspected allies would support him against any adversary. There are, however, suggestive episodes. For example, in 1989 Ntologi injured his right hand and limped while travelling. Once, when Ntologi was sitting alone, the second-ranking male, Kalunde, i.e., Ntologi's present rival, appeared. Ntologi did not move initially, but as soon as Bakali and Lukaja, the current regular members of his meat-sharing cluster, approached, Ntologi began a violent display, in which he was joined by the two. Seeing this, Kalunde ran away.

Separating Intervention

Some episodes suggest that Ntologi actively attempts to keep certain individuals away from his allies. For example, in 1983 Ntologi separated Kagimimi and Bakali, who was then second-ranking, when the former was grooming with the latter. Similarly, in 1990 J. C. Mitani (unpublished data) observed Shike, the young, third-ranking male, grooming Musa, who is currently a frequent companion of Ntologi. Ntologi then drove Shike away by approaching and starting to groom Musa. He groomed Musa for less than 30 seconds, however, before moving away himself.

Female Beneficiary

Table 7 shows the females who obtained meat most often from Ntologi. From 1981 to 1985, there were five females who acquired a substantial amount of meat more than five times. Three were females much older than Ntologi, of whom one was his presumed mother. The two other females had been monopolized by Ntologi during their estrus

Table 7. Frequency of Female Beneficiary

1981–85		1987–89	
um	10	SL	10
ng[1]	9	CH	7
SL	7	WD	4
gp	5	WO	4
GK	5		

ab : Old females.
AB: Females sexually "possessed" by Ntologi.
[1]Alpha's presumed mother.

periods.

From 1987 to 1989, there were four females who obtained meat at least four times. Only one from the previous period, Silafu (SL), was permitted to share frequently again. Three other females obtained meat frequently; all had been monopolized sexually by Ntologi. The two old females with whom Ntologi shared meat previously had died, and his mother was moving alone frequently because she was too old to keep up with others during travel.

In summary, Ntologi preferred to share meat with his presumed mother, his current consorts or mothers of his offspring, and very old, infertile females.

DISCUSSION

The alpha male, Ntologi, appeared to follow consistent rules that dictated with whom to share meat. These rules were:

1) "Don't share with young males who are rising in the dominance hierarchy."

Late adolescent and young adult males below 20 years of age were rarely observed in meat-eating clusters. When Ntologi controlled access to meat, these males usually watched from a distance, and never approached, despite the fact that these males had successfully captured many monkeys recently. The potential rise in status of these males may threaten the alpha male.

2) "Don't share with the beta male."

Beta males are the most likely usurpers of the alpha's status. After being defeated, two alpha males at Mahale, Kasonta of K Group (Nishida, 1983) and Kajugi of M Group (Takahata, 1986), were

ostracized and lost mating privileges. Even if not ostracized, once he is defeated by the beta, the alpha male may be defeated by the third-ranking and even other lower-ranking males, as was the case with Mike of Gombe (Goodall, 1971) and Yeroen of Arnhem (de Waal, 1982). Given the threat posed by these males, Ntologi has not shared meat with two successive beta males, Bakali and Kalunde. Kalunde, an extremely large male, has never been permitted to enter the meat-sharing cluster in the presence of Ntologi. Kalunde became the beta male in 1986 and since then has become Ntologi's major rival in M Group. Although he is usually observed not far from Ntologi, Kalunde typically disappears from the scene during meat-eating episodes when Ntologi controls access to the carcass. Kalunde has never been seen to beg for meat from Ntologi. The former alpha male of M Group, Kajugi, did not share meat with Ntologi when he was the beta male (Kawanaka, 1982 and unpublished data).

3) "Share meat with non-threatening, middle-ranking males."

Some young males and agemates do not pose a threat to the alpha's position because of their small body size or emaciated condition. Four males were consistently permitted to join the meat-eating cluster by Ntologi, and none of them appeared to threaten his alpha status.

Ntologi shared meat most often with Lubulungu, a middle-to-low-ranking, small-bodied male. For over eight years, until mid-1987, Lubulungu had been consistently Ntologi's most frequent associate and grooming partner. He gradually dropped in rank as he aged; after 1988 he often traveled by himself and the frequency of meat-sharing with Ntologi sharply dropped. He disappeared in 1990. What is interesting is that in the late 1970s he had an intimate relationship with the former alpha male Kajugi and often received meat from him (Kawanaka, 1982, 1990). Thus, even the apparently strongest bond between two adult males seems to be based on opportunistic male coalition strategies.

Lukaja, another small male, has had a unique relationship with Ntologi. Unlike other males, and in contrast to Kalunde in particular, Lukaja was permitted to share meat with Ntologi even when he was only 20 years old. In 1985 he competed for beta status with Bakali, but Ntologi continued to allow him to enter the meat-eating cluster (probably because Bakali was Ntologi's major rival then). In 1986 Lukaja became seriously ill and dropped to the bottom of the adult male hierarchy. In the following year he recovered and rose in rank, but could not regain his original position because two younger males, Shike and Nsaba, firmly occupied the third and fourth ranks. It is interesting to note that since that time Lukaja's relationship with Ntologi has become even more relaxed. He has become one of the most conspicuous

members of the meat-eating cluster. During the most recent observation period in 1989, Lukaja ranked fifth and received meat from Ntologi more often than any other individual.

Bakali, Ntologi's agemate, was never permitted to share meat during the period when he occupied the second-ranking position in M Group. He fell in the hierarchy when challenged by Lukaja and Kalunde and, more recently, by three younger males, Shike, Nsaba, and Kasangazi. These events have caused Bakali to seek more contact with Ntologi, and as a result, Ntologi's former major adversary has become one of his favored partners in meat-sharing, grooming, and association.

Like Bakali, Musa is Ntologi's agemate, but rose no higher than fourth in the hierarchy even in his prime. Changes in his relationship with Ntologi was similar to those seen with Bakali. Musa was not given meat often when he was in his prime, but as he grew older and was defeated by younger males, Ntologi began to share meat with him consistently.

4) "Share meat with old but influential males."

This is a corollary of the third rule. Between 1979 and 1987 Kagimimi, the second-oldest male, obtained meat often and was a frequent associate and grooming partner of Ntologi. Like Lubulungu, Kagimimi was also one of the favorite partners of the former alpha male, Kajugi (Kawanaka, 1990) and received meat from him most often (Kawanaka, 1982). During the period of study reported here, Kalindimya, the oldest male, was shy and not habituated to human observers. As a result, he was rarely observed to interact with other chimpanzees. Nevertheless, he was among the few who obtained meat from Ntologi, which suggests that he may have obtained a disproportionate share when human observers were absent.

Despite these observations, old age did not always lead to favored status during meat-sharing episodes. Rashidi, who was as old as Kagimimi, was not often observed in the meat-eating cluster (Takahata *et al.*, 1984). The exclusion of certain old individuals may be related to the influence they wield. For example, Kalindimya and Kagimimi were very high-ranking males in their prime. As they aged, they continued to influence group movements as they were followed by others frequently. By sharing and thus strengthening alliances with old, influential males, Ntologi may have enhanced his leadership role in the group.

Do the data presented here accord with previous observations of sharing? Wrangham (1975) showed that the frequency with which animals obtained meat at Gombe was positively correlated with age but was less closely related to rank. He noted that two old, low-ranking males acquired meat from others most frequently, and suggested that

this was due to differences in the costs of competition. Old males compete more assertively because their reproductive potential is low, and they thus have less to lose. Since Wrangham (1975) did not provide information on the exchange of meat between individuals, we cannot evaluate with his data our hypothesis that meat-sharing provides coalition benefits to the sharer.

The hypothesis that food sharing is a coalition strategy does not necessarily conflict with the reciprocity hypothesis, but in the case of meat-sharing, as outlined here, reciprocal exchange through the same "currency" seldom takes place because the alpha male usually controls access to the carcass. From the currently available data it is difficult to ascertain whether Ntologi's policy is better explained as "favoritism of coalition partners" or as "give and take". What is apparent is that Ntologi's reciprocity, if any, is limited to prime adult males. For example, when he plundered a carcass from a prime adult male, he always permitted that male to take a substantial portion. This was not the case for young adult males and adolescent males (Table 8).

Table 8. Relationships of Capturing, Snatching, and Sharing

Name of male captors	No. of episodes NT took meat from		No. of episodes NT "returned" portion (share with captor)	No. of episodes NT shared meat from the carcass he had taken from others	No. of episodes NT shared meat from the prey that he captured	Total
Old or prime adult	LU	2	2	7	3	12
	LJ	3	3	5	2	10
	KI	3	3	4	1	8
	BA	2	2	5	1	8
	MU	1	1	5	2	8
	KL	1	1	1	0	2
Young adult	KZ	1	0	0	0	0
	SU	1	0	0	0	0
Adolescent	TW	1	0	0	0	0
	TB	1	0	0	0	0
	BB	1	0	0	0	0

The alpha's meat-sharing cannot be considered solely in terms of the alpha's standpoint. Older males and non-promising males may capitalize on their opportunities of taking the lion's share, because an alpha always faces as his major adversary a second-ranking male who will challenge him for alpha status in the future. When the alpha male

does not assert his higher status by forcibly taking the meat from some old possessors (Takahata *et al.*, 1984; Teleki, 1973), perhaps the latter are taking advantage of the alpha's weakness.

Holding and controlling meat may be important for an alpha male, because he permits or denies others access to a highly favored resource. In so doing, he may reinforce his already acquired high social status (Moore, 1984; Teleki, 1973). Ntologi was twice seen to secure a big carcass that he scarcely ate, once a bushbuck fawn (*Tragelaphus scriptus*), and once an adult red colobus monkey (*Colobus badius*). In both cases he continued to hold the carcass only to let other chimpanzees nibble meat from it until it was all consumed. In Arnhem Zoo, during the period that Luit, the second-ranking male, was challenging the alpha's position, he suddenly developed a strong motivation to get into the live trees. He would try to climb up a tree in order to distribute most of the leaves to the waiting colony on the ground. De Waal (1982, p.109) interpreted this "Santa Claus" behavior as part of Luit's strategy to become popular in the colony and perhaps to gain female support. Goodall (1990, p.72) stated that once the alpha male Figan gave the entire carcass of a colobus to his ally Humphrey only to join in another hunt, seizing and killing another colobus that he consumed himself.

In conclusion, although our thesis that meat-sharing by an alpha male acts as a coalition strategy is admittedly speculative, we believe it is a promising hypothesis to be tested in future field studies.

SUMMARY

1. The functional significance of meat-sharing among adult chimpanzees has heretofore been little understood. On the basis of long-term data on a particular alpha male, this paper proposes a promising hypothesis that meat-sharing can be used as a coalition strategy by alpha males.

2. The alpha male, Ntologi, of M Group has shown a consistent tendency to share meat with only particular members of the group during his 10-year tenure of alpha status.

3. The frequency of receiving meat from Ntologi was consistently positively correlated with the ages of adult males. The amount of grooming exchanged between Ntologi and other males and the extent of proximity with him were both significantly positively correlated with the frequency with which he shared meat.

4. Ntologi often shared meat with some old males and some middle-ranking males, but not with beta males and young adult males. He

tended to groom often and reciprocally, and to stay in proximity, with those males with whom he shared meat. A few episodes of aiding in combat and intervening to separate tend to favor the hypothesis of meat-sharing as a coalition strategy.

5. Ntologi also often shared meat with an old female who was presumed to be his mother, with previous and current consort females (mothers of his current and future offspring), and with other females as old as his mother.

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