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M. L. BUTOVSKAYA, O. N. LADYGINA

SUPPORT AND COOPERATION IN AGONISTIC ENCOUNTERS OF STUMPTAIL MACAQUES (MACACA ARCTOIDES)

ABSTRACT — The investigations on two groups of stumptail macaques, located in 600 m outdoor corrales were carried out in Sukhumi Primate Research Center in June and September of 1986. The types and structure of support and cooperation in the groups of stumptail macaques are discussed. The dependence of frequency and direction of support and cooperation with basic ranks of individuals and kinship relations in the groups are analysed. Irrespective of what form it is shaped, aggressive contacts of affiliative patterns, the interference in agonistic encounters presented the sufficient base for group integration and stability.

KEY WORDS: Agonistic aids-reciprocal — Non-reciprocal support — Kinship bonds — Active helpers.

It appeared quite evident, that it's impossible at present to treat the intragroup relations strictly in terms of dominance-subordination on the basis of individuals strength and aggressiveness (Bernstein, 1981; Bernstein, Williams, 1986). Animals in the group practically never remained indifferent to the conflicts happened nearby. They help each other in agonistic interactions. Due to that fact individuals, usually treated by investigators as subordinate in the situations of pair conflict, gained the dependent preferences over sufficient number of animals with higher basic ranks (Lancaster, 1973; Takahata, 1982). Such relations are described in terms of dependent hierarchy. In general, this phenomenon perhaps characterize the attitude of the group to its members. The relations among kins, inter-individual sympathies and antagonism play an important role in keeping up the group stability. Quite possible, that they may also be an important stimulus in the choice of the object of support and cooperation in agonistic situation among the group members. Such examples were already given for rhesus macaques (Kaplan, 1977;).

The aim of our investigation was to check the general regularities of individual and kin support in the groups of stumptail macaques. We discuss the following questions:

1. What types of support in agonistic conflicts can be met in the groups of M. arctoides, and what is the structure of this phenomenon?
2. Does the frequency and the direction of aids and cooperation depends of the basic rank of the individual and the factors of kinship?
3. Can the agonistic aids be estimated as an important factor of intragroup stability for M. arctoides?

OBJECTS AND METHODS

The investigations were carried out in Sukhumi Primate Research Center in June and September of 1986. The general time of observations — 250 hours. Two groups of M. arctoides were investigated. Each of them was located in 600 m² outdoor corrales. Both groups were formed in 1983 from animals,

transported earlier from Thailand and those born in Primatological Center. Analogically to the periodization of ontogenesis proposed by V. Vančata and co-workers (1986) the following age groups of animals were distinguished: infants (0—12 months), subadults (1—3 years), youngs (3—4 years), adults (elder than 4 years). The first of our groups consisted of 40 animals, the second had 36 animals. The general information about the animals (age, kinship relations, sex) is presented in *Table 1.* All of the adults and young animals and most of subadults were individually recognised. The investigations were carried out daily always in the same time synchronically by two observers phocally by 30-min time frequency matrices and ad libitum (Deriagina et al., 1984).

TABLE 1. *The general information about individuals in two groups of stumptail macaques*

a) group 1					b) group 2				
sex	zootechnical number	code	age	physiological state	sex	zootechnical number	code	age	physiological state
♂	17,114*	C-1	7	adult	♂	14,173*	1	12	adult
					♂	18,857*	N-1	4.5	adult
♀	13,062*	F-1	15	adult	♀	12,264*	O-1	15	adult
♀	13,601*	A-1	13	adult	♀	12,909*	Q-1	14	adult
♀	13,702*	G-1	13	adult	♀	13,056*	R-1	13	adult
♀	13,708*	D-1	18 5	adult	♀	13,218*	P-1	10	lactative
♀	14,553*	I-1	11	adult	♀	13,694*	M-1	19	adult
♀	15,131*	E-1	16.5	adult	♀	13,703*	S-1	12	adult
♀	15,201*	B-1	10.5	lactative	♀	13,984*	T-1	18	lactative
♀	15,481*	A-2	10	lactative	♀	14,491*	V-1	11	adult
♀	15,560*	H-1	10	lactative	♀	14,567*	M-3	11 5	lactative
♀	15,979*	B-4	9	lactative	♀	15,486*	2	10	adult
♀	16,203*	C-2	9	adult	♀	15,555*	V-1	9.5	lactative
♀	16,536*	1	8	lactative	♀	15,716*	N-2	9.5	lactative
♀	16,593*	F-1	8	adult	♀	17,161*	W-1	6.5	adult
♀	17,503*	K-1	6.5	lactative	♀	17,472*	X-1	6.5	lactative
♀	18,344*	F-2	5	lactative	♀	17,927*	3	6	adult
♀	18,345*	L-1	5	lactative	♀	18,006*	O-3	5.5	lactative
♀	18,934*	D-3	4	lactative	♀	18,141*	4	5	pregnant
♀	57*	G-2	3.8	young	♀	58*	N-3	3.5	young
♀	106*	A-3	3.5	young	♀	108*	R-2	3	young
♀	142*	E-2	3	young	♀	119*	S-2	3	young
♀	174*	I-2	3	young	♀	150*	O-2	3	young
♂	434*	B-5	1.5	subadult	♂	473	V-2	1	subadult
♂	634*	E-4	1	subadult	♀	257	M-4	2.5	subadult
♀	248*	B-2	2.5	subadult	♀	363	Q-2	2	subadult
♀	281*	E-3	2.5	subadult	♀	382	P-2	2	subadult
♀	314*	A-4	2	subadult	♀	449	M-2	1	subadult
♀	385*	H-2	2.5	subadult					
♀	401*	G-3	3	subadult					
♀	423*	C-3	1.5	subadult					
♀	486*	D-2	1	subadult					
♂	743*	K-2	0.5	infant	♂	625	W-2	0.8	infant
♂	763*	A-5	0.42	infant	♂	635	M-5	0.75	infant
♂	824*	D-4	0.25	infant	♂	642	T-2	0.67	infant
♂	827*	F-2	0.25	infant	♂	657	X-2	0.67	infant
♂	828*	H-3	0.17	infant	♂	665	N-4	0.75	infant
♂	857*	B-3	0.08	infant					
♀	(16,203)	C-4		newborn					
♀	790*	L-2	0.75	infant	♀	709	O-4	0.42	infant
♀	(18,344)	F-3		newborn	♀	(15,555)	V-2		newborn
					♀	810	P-3	0.08	infant

* the individually investigated animals
( ) — the number of newborn's mother

RESULTS

The basic ranks of animals R were established in accordance to the quantity of difference ΔR between the number of individuals over which the investigated animal dominate and to whom they are subordinate (Hausfater, 1975; Hausfater, Altmann, 1982). The highest rank (α) was equivalent to the maximal difference between the numbers, and the lowest rank (w) — to the minimal difference. The basic agonistic ranks of individuals in both groups of M. arctoides are presented in *Table 2* (*a, b*).

The aids between individuals in agonistic interactions were widely spread phenomenon in both groups of M. arctoides. The agonistic conflicts

TABLE 2. *The basic ranks of individuals in the group of stumptail macaques (R) and the meaning of differences between the number of victories and losses in agonistic encounters (ΔR)*

a) group 1

adults	C-1	A-1	G-1	C-1 D-1 E-1	H-1	K-1	B-4	B-1	A-2 1 D-3	F-1	T-1	F-2	young and subadult animals	B-2	A-4 B-5 G-2	C-3 D-2 I-2	E-2 G-3 H-2	A-3 E-3	E-4
R	1	2	3	4	5	6	7	8	9	10	11	12	R	1	2	3	4	5	6
ΔR	20	11	7	6	4	2	1	−1	−2	−3	−4	−8	ΔR	0	−2	−3	−5	−6	−8

b) group 2

adults	1	V-1	W-1	T-1	3	Q-1 R-1	O-1	R-1 M-1	2	O-3	V-1 N-2	S-1	M-3 X-1	N-1	4	young and subadult animals	O-2	R-2	S-2	N-3
R	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	R	1	2	3	4
ΔR	17	15	8	7	5	4	3	1	0	−1	−2	−3	−6	−8	−9	ΔR	4	−3	−8	−10

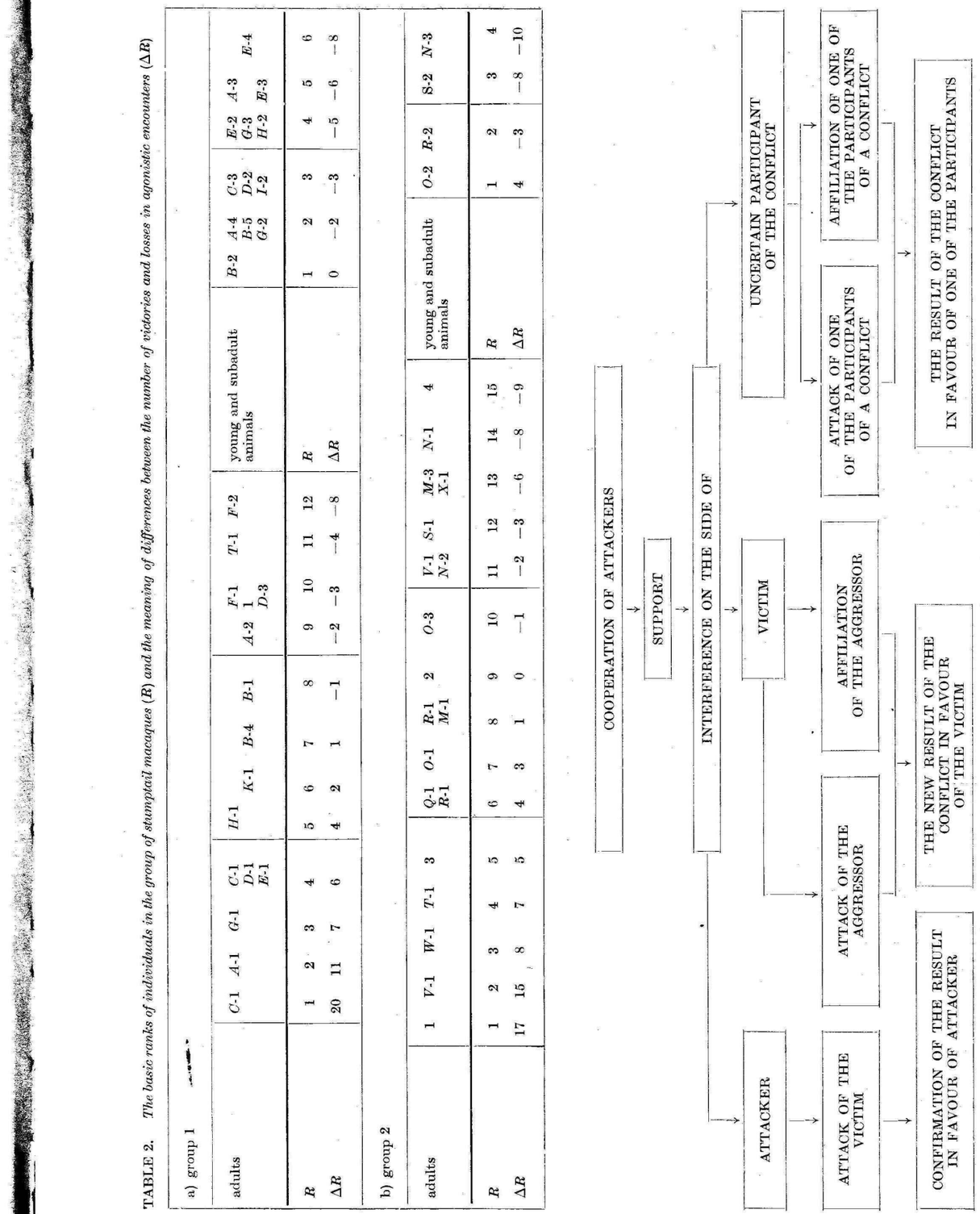

FIGURE 1. *The structure of behaviour "the support in agonistic encounters".*

accompanied by support and cooperation (189 cases) prevailed over the pair agonistic contacts without interference of other group members (80 cases registrated). Out of 189 cases of help in agonistic episodes two types of actions were distinguished: interference (external aids) and cooperation (internal aids). The function of interference consisted in rendering assistance for attackers or their victims. The actions in the case of interference were of aggressive or affiliative character. The latter corresponds to agonistic buffers by terminology of Itani (1959). Our classification of the types of aids in agonistic encounters is much in common with those proposed by Massey (1977).

The aids for the attacker consisted of aggressive actions that intruder adressed to victim. The expected results of the conflict in this case never changed, but simply were fixed by external support. The interference on the side of victim was expressed both in the form of aggression directed towards the attacker and affiliative actions. As a result the initial conflict either finished or regenerated into the cooperative attack of the supporter and victim against the aggressor. In both cases, the victim gained the dependent advantage over the attacker. The interference happened also in the cases where the initiator of the conflict and victim weren't identified and the animals attacked each other with the changing success. In those cases due to the affiliative and aggressive actions of the helper the results of the conflict were decided in favour of one of the participants (*Fig. 1*). As an agonistic cooperation we marked the cases of simultaneous attack by two or more individuals directed to the same target.

The observed groups of M. arctoides had much in common in frequency of agonistic aids and in correlation of different types of the pattern (*Table 3*).

TABLE 3. *The ratio of different types of agonistic support in the groups of stumptail macaques*

the correlation	1 group	2 group
support of victims / support of attackers	4.59	4.67
aggressive support of victims / affiliative support of victims	2.06	1.93
interference / cooperation	3.80	1.95

The members of both groups supported the victims 4 times more frequently than attackers. The aggressive interference on the side of victims took place exactly 2 times more frequently than affiliative. Interference in both groups was more common event than cooperation. The directions and frequences of support in agonistic encounters were marked in both groups under study (*Table 4a, b*). It was found that adults were the most frequent helpers, they directed their support most commonly towards the young females and subadults. The frequency of such type of aids was 2.1 times higher in the 1st group in comparison with the summarized frequency of support directed towards adult group members from the side of adult and subadult animals. In both groups more than half of individuals neither supported the other animals nor received support from the others. Only a small part of a group members fulfilled the function of helpers and received the help from the other animals quite frequently (6 and more times during the period of observation). Adult males-leaders from both groups were the most active animals-helpers judging by the frequency of support and the number of favoured individuals (*Table 4*). In each group there were also active helpers among adult highly ranking females (*A*-1, *E*-1), (*Table 5*).

Subadult and young individuals were the most frequent objects of support by the most of group members (*Table 5*). For example, *H*-2, *O*-2, *Cr*-3. Only one adult female, favoured by a great number of helpers — *H*-1 was marked. In the I group, the leader (*C*-1) simply preferred to help this female and her daughter (*H*-2). In the same group the close interrelations between 3 non-kins were observed. Two of them — adult high ranking females (*A*-1, *I*-1) frequently protected the same subadult female *G*-3. Female *A*-1 actively supported female *I*-1

In the second group only one case of selected aids was marked: the male-leader frequently protected the young highly ranking female *O*-2. It is necessary to mention, that the mother of this female (*O*-1) was the low ranking animal and never was chosen as an object of active support by other individuals. On the contrary, the young female (*O*-2) was actively protected not only by the leader but also by the most of adult animals in the group

We differentiate between two types of interactions: reciprocal and nonreciprocal. As reciprocal bonds we considered those in which individuals mutually supported each other, and nonreciprocal — those, in which the help was directed only in one side- the frequencies of the mentioned types of interactions were calculated as a percentage from the whole number of pairs, participated in support and cooperation totally (*Table 6*). Two groups differed according to these indexes. In the first group the nonreciprocal type of support prevailed, and in the second — both types of support were presented practically with equal frequency.

The rank correlation coefficient between the basic ranks of individuals and the frequency of their agonistic aids towards the other animals were calculated. In both groups the reliable values were obtained, testifing about the existence of the positive correlation between the indexes mentioned above: 1. $p^s_1 = 0{,}81/N = 18$, $p^s_{0.5} = 0{,}47$; 2. $p^s_{\cdot} = 0.71/N = 19$; $p^s_{0.5} = 0.46$. This results means that adult individuals with high basic ranks protected the other animals more frequently in comparison with low-ranking individuals. The rank correlation coefficients were also calculated between the values of individual's basic ranks and the frequencies of the support received by them. For adult individuals the following

TABLE 4a. *The frequencies of agonistic support in the groups of stumptail macaques*

a) group I

	A-1	A-2	A-3	A-4	B-1	B-2	B-4	B 5	C-1	C-2	C-3	D-1	D-2	D-3	E-1	E-2	E-3	E-4	F-1	F-2	G-1	G-2	G-3	H-1	H-2	I-2	I-2	J-1	K-1	L-1	1
A-1	—			1																											
A-2		—		2																											
A-3			—																												
A-4				—																											
B-1					—	1																									
B-2						—																									
B-4							—																								
B-5								—																							
C-1									—																						
C-2										—																					
C-3											—																				
D-1												—																			
D-2													—																		
D-3												1		—																	
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J-1																												—			
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L-1																														—	
1																															—

TABLE 4b. *The frequencies of agonistic support in the groups of stumptail macaques*

b) group II

	M-1	M-2	N-1	N-2	N-3	O-1	O-2	O-3	P-1	Q-1	R-1	R-2	S-1	S-2	T-1	U-1	V-1	W-1	X-1	1	2	3	4
M-1	—	1																					
M-2		—																					
N-1			—																	1			
N-2				—																1			
N-3					—															2			
O-1						—	2													4		1	
O-2						2	—					1		1		1						1	
O-3								—												1			
P-1									—	2													
Q-1									1	—	1					1				1			
R-1										1	—	1	—							1			
R-2											1	—	1										
S-1	1												—	1									
S-2													1	—			1						
T-1															—					1		1	1
U-1										1					1	—				1			
V-1																	—			1			
W-1																		—		2			
X-1																		1	—				1
1			1			1	2		1	1	1	1		1	1	1	1	1		—		1	1
2			1			2	—													1	—		1
3																				1		—	1
4																			1	1	1	1	—

TABLE 5. *The objects of the most active support and the most active helpers in the groups of stumptail macaques*

	active helpers		the object of active support	
	by frequency	by the number of individuals	by frequency	by the number of individuals
group 1	*C*-1, *A*-1, *E*-1, *I*-1	*C*-1, A-1, *E*-1, *C*-2, *G*-1	*G*-3, *H*-2, *H*-1	*G*-3, *H*-2, *H*-1
group 2	1, *V*-1	1, *V*-1, 3, 4	1, *O*-2	1, *O*-2, *Q*-1, *S*-2

TABLE 6. *The frequency of occurence of reciprocal and nonreciprocal pairs in the groups of stumptail macaques*

group	recipr.	non-recipr.	recipr + non-recipr.	recipr. (%)	non-recipr. (%)
1	3	33	36	8.3	91.7
2	16	19	35	45.7	54.3

TABLE 7. *The frequency of agonistic support between the members of the same matriline (p) and non-kins (q)*

a) group 1

matriline	p	q	n	$n_o - n$	r
A	3	12	4	27	2.25
B	1	9	4	27	1.00
C	—	22	3	28	—
D	—	9	3	28	—
E	—	12	4	27	—
F	—	4	2	29	—
G	1	22	3	28	0.64
H	2	19	2	29	3.05
I	—	15	2	29	—
	Total:				6.94
	N = 9				r = 0.77

b) group 2

matriline	p	q	n	$n_o - n$	r
M	1	1	2	21	21.00
N	—	7	3	20	—
O	4	13	3	20	3.08
R	1	7	2	21	3.00
S	—	6	2	21	—
	Total:				27.08
	N = 5				$\bar{r}$ = 5.42

n — the number of individually observed members of matriline
n_0 — the general number of animals in the group

results were obtained: 1. $p_1^s = 0.44/N = 18$, $p_{0.5}^s = 0.47$; 2. $p_1^s = 0.63/N = 19$; $p_{0.5}^s = 0.46$. This result means that differential support in connection with the basic ranks among the adult animals of the first group was completely absent, and in the second there was a tendency to help the individuals with high basic ranks. In order to estimate the proportion of internal support (between the individuals of the same matriline) and external support (between the animals non-kins) in agonistic encounters, we proposed to use the special coefficient, *r*, calculated by formula:

$$r = \frac{p}{q} \cdot \frac{n_o - n}{n - 1}; \text{ where:}$$

p — the frequency of internal aids;
q — the frequency of external aids;
n — the number of individually observed members of matriline;
n_o — the general number of individually observed animals in the group.

The frequencies of agonistic aids between the number of the same matriline (p) and non-kins (q) are presented in *Table 7*.

Judging by the coefficient the following intergroup differences existed: the external aids prevailed in the I[st] group over internal ones. In the matrilines *A* and *H* the kins actively supported each other. The aunt and mother helped the subadult *A*-4, and mother *H*-1 actively assisted the subadult *H*-2. Necessary to stress, that the aids between kins were active only in direction of subadults.

Judging by the value of correlation coefficients in the IInd group the situation was quite opposite: the internal help prevailed over external (*Table 5b*). Mothers *M*-1 and *R*-1 actively supported their adult daughters and young female *O*-2 protected her low-ranking mother *Q*-1.

The comparison of intensivity of kin's support with the frequency of non-kin's support allowed us to make the following conclusion: these two phenomena compensated each other. In the I[st] group the members of matriline actively help each other, but only occasionally received an external aid. The members of matriline *B*, on the contrary, frequently received an external help and rarely supported each other, among the members of matriline *C* any kin's support was absent, nonkins never supported these animals; mother *H*-1 actively supported her daughter and both of them were the objects of intensive agonistic aids from the side of non-kins.

It was marked, that some mothers preferred to support the offsprings not of their own. For example, adult female *E*-1, with 3 own offsprings preferred to support actively only non-kins. The offsprings of this female were actively supported by nonrelatives, among which the members of matriline *D* were the most active. The high-ranking female from matriline *G* — *G*-1 supported preferentially nonrelatives, and her daughter was an object of support by most adult group members. The closest aid interrelations were observed between the members of matrilines *G* and *I*.

DISCUSSION

The interference in agonistic conflicts undoubtedly can be treated as an important mechanism of gaining the intragroup stability and order (Massey, 1977). Irrespective of what form it is shaped in — aggressive or affiliative, the interference in agonistic conflicts undoubtedly presented the sufficient base for group integration.

Gaining the support from the dominant individuals animals manage to avoid the danger of destructive forms of aggression. The group members in the groups under study helped victims of aggression more frequently than attackers. Similar results were obtained earlier by Kaplan (1977) for rhesus monkeys. Thanks this patterns the original compensational balance was achieved in the group as a whole: the animals with low basic ranks aquired the dependent advantage over the high-ranking individuals. Our results witnessed also the important mission of high-ranking animals in keeping up the group unity. The realization of the role of control animal was frequently shaped in the form of victim's support in agonistic encounters. In our case the most active supporters were α males and the highest ranking adult females. It's possible to conclude, that situation in the Ist group was more perfect, than in the IInd group, that the Ist group was potentially more stable. This statement is supported by the information about the agonistic individuals status in each group: evidently expressed differences in agonistic behaviour of animals with different basic ranks were practically absent in the Ist group like the absence of aggression in the context of sexual behaviour, the low frequency of cooperation in aggressive attacks. The leader of the Ist group fulfilled the role of controlling animal evidently more frequently, than the leader of the IInd group; the leadership in the Ist group was never disputed.

The support of adult animals directed towards subadults and young individuals was the most widespread type of aids in both groups of M. arctoides. Among the young and subadult animals the individuals with high basic rank gained support more frequently. These results conforms with the ideas of Loy and Loy (1974) about the close correlations between the dependent ranks of subadults, and their future basic ranks. It is known that infants and subadults who stayed more time nearby the high ranking females, may receive the support of the latter independently of the rank of their own mothers (Berman, 1983). We witnessed one such young female in the IInd group (*O*-2). This type of behaviour of the offsprings of lowranking mothers can be explained as a special strategy, which enabled those animals to aquire in adulthood higher hierarchical status. At the same time, we found that the offspring (*G*-3) of high-ranking mother, was actively supported practically by all the group with the exception of the own mother. These data agree with the idea, that high-ranking mothers had passed the rank to their offsprings not helping them actively in the conflicts with other animals, but by forming the stereotype of subordinance among the subadults of low-ranking females (Horroks, Hunter, 1983). We suppose, that the establishment of hierarchical relations by means of forming the stereotype of subordinance among low-ranking animals, but not by the cultivation of higher aggressiveness among the dominant individuals during their ontogenesis can be treated as one of the progressive factors of increasing the intragroup stability.

Females from some of the matrilines (especially from the Ist group) preferred to protect unrelated subadults (even females with sufficient number of offsprings practicise this strategy), but not of their own. In this case their offsprings received the support from other non-kins. Necessary to mention the existence of a number of females which mutually assisted the offsprings of each other (*D*-1 and *E*-1; *G*-1 and *I*-1). The results aquired allow to conclude that the support from the side of non-kins may appear more effective and suitable type of aids directed towards young and subadult animals because it practically never evoke the negative reaction from the side of other group members. Usually, agonistic cooperation and aids were unreciprocal in the groups of M. arctoides, both among kins and non-kins. Analogic conclusions were made earlier for M. radiata by Silk (1982).

Only one pair of animals-kins which mutually supported each other was marked in the IInd group (*O*-1 and *O*-2). The animals from the Ist group preferred to help non-kins more frequently than the members of their own matriline. The latter is strictly in the contradiction with Hamilton's hypothesis (Hamilton, 1964), that relatives must support each other more frequently and actively than nonrelatives. As a rule, the relatives in our study supported different group members. Such strategy, most probably enabled each matriline to widespread the maximal sphere of support and due to this fulfilled the function of strengthening the intragroup stability. This served as an additional compensational factor of certain closeness of matrilines in other aspects of social behaviour.

The analysis of the structure of support in agonistic conflicts in the groups of M. arctoides enables to judge in the whole about the number of ethological mechanisms ensuring the group stability and to estimate the relations between the members of the same and of different matrilines. This information can be useful while discussing the corner-stone problems of anthroposociogenesis, connected with the constructions of correct models of the origin of maternal family, exogamy and while discussing the problems of regulation of the social life in early hominid's societies.

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M. L. Butovskaya,
O. N. Ladygina
Institute of Ethnography
AN SSSR
ul. Dmitrija Uljanova 19
SU — 117036 Moscow
U.S.S.R.