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THE ROLE OF AGGRESSIVE BEHAVIOUR IN THE EVOLUTION OF PRIMATE AND EARLY HOMINID SOCIETIES

ABSTRACT — A considerable attention is being paid to the investigation of aggressive behaviour of primates, in connection with the development of possible models of social behaviour in early hominids.

KEY WORDS: Aggressive behaviour — primates — early hominids.

Two possible aspects of the role of aggression in the early phases of society are constantly discussed in the special literature. Some researchers accept the idea of the progressive development of altruism and of intragroup co-operation in hominid societies, stressing the necessity of limiting aggression, and its subsequent suppression through natural selection. Others consider that intragroup aggression has a positive function, is an important factor, furthering the selection of the strongest individuals, and they hold that aggression is fully adaptable (Ardrey, 1966, Wilson, 1975).

We investigated and analyzed the aggressive intragroup behaviour of 16 primate species (*Table 1*). The study was realized during the summer and autumn months of the years 1978—1985 in the Moscow and Leningrad Zoos, and at the Primate Research Centre of Sukhumi. The groups of primates were observed in captivity: in cages of sizes ranging from 6 to 20 sq. metres, and in outdoor enclosures of 600 sq. metres. The mean time of investigations amounted to 1500 hours. The methods of focal animal and optional animal were used.

The application of structural-dynamic approach made it possible to treat aggressive behaviour as a dynamic process and divide it into three groups of elements, namely according to the level of activity, according to the degree of qualitative changes and their function (Deriagina, Butovskaya, 1983): aggressive warning (staring, barging the teeth), aggressive conflict (based teeth, running after the object) aggressive contact (biting, beating). In the latter case we should distinguisb a subgroup of contacts resulting in injuries of some of the participants in these clashes. In fact the above elements follow closely, forming chains of actions. The study of dynamics of the aggressive behaviour has revealed that there is a gradual transition between warning elements, warning and conflict in all species subjected to study. It has been also observed that there is a similar gradual process in the relaxation of the aggressive expressions. There is a reverse chain of transitions from contact to conflict, from conflict to warning elements; the process has been called curtailing of the aggressive behaviour (Butovskaya, 1984). The differentiation of aggressive behaviour was determined according to the number of these elements in each group. One of the characteristic features has been the prevalence of warning elements (*Table 1*). In absolute terms they prevailed in chimpanzees and gorillas and they appeared minimally in greyish-brown lemurs. The most variable conflict

TABLE 1. *The main indices of aggressive behaviour in some primate species*

Indices	Tupaia-glis	Lemur fulvus	Ateles-panis-cus	Cercopo-thecus aethiops	Macaca arcto-ides	M. fas-cicularis	M. mu-latta	M. neme-strina	M. fus-cata	Papio hamad-ryas	P. an-ubis	Mand-rillus shinx	Hylo-bates lar	Pan troglo-dytes	Goril-la go-rilla	Pongo pyg-maeus
Frequency of aggressive warning element	22.82	6.95	16.39	34.18	21.57	15.64	19.98	19.91	18.95	36.20	32.16	28.46	7.23	16.26	26.58	10.20
Frequency of conflict	2.91	0.86	2.84	4.66	1.79	2.54	5.04	4.55	6.98	2.60	6.59	3.31	1.40	3.58	7.11	2.80
Frequency of contact × 10	0.11	0.32	0	1.70	0.60	1.09	1.33	0.30	0.74	1.50	0.74	0.24	1.54	0.20	0.99	0
Frequency of olfactory	14.84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Frequency of aggressive contact behaviour with objects × 10	0	0	0	0	0	0	0	0	0	0	0	0	0	0.20	0.99	0
Number of warning elements	17	7	16	11	17	13	17	19	16	14	15	15	17	24	23	12
Number of conflicts	7	5	4	4	7	6	6	7	6	10	8	6	4	8	10	4
Number of contacts	2	3	3	3	5	5	5	3	3	5	5	4	6	1	5	3
Number of postures and movements	8	4	5	7	8	6	6	5	6	8	6	6	3	11	9	2
Number of warning elements with the application of hand × 10	0	1	1	0	3	2	3	1	1	1	2	1	4	4	5	1
Number of the tail × 10	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0
Number of mimic signals	12	6	13	7	19	10	12	15	13	12	14	9	12	19	14	12
Number of olfactory signals	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Number of objects' using	0	0	1	0	1	1	1	1	1	1	1	1	0	2	6	2
F_i 10	0	0	1	0	1	0	2	1	0	1	2	0	0	1	0	0
I_A 100	0.06	0.16	0	0.05	0.21	0.14	0.10	0.22	0.38	0.15	0.18	0.03	0.33	0	0.20	0

where: F_i — *number of injuries in the group*
I_A — *index of aggressiveness*

elements were observed in hamadrias baboons and in gorillas while the least varied conflict elements appeared in green monkey, spider monkey, gibbon and orang-outang. In general lemur and green monkey had the poorest repertoire (*Table 1*), while it was most varied in chimpanzees and gorillas. Another interesting thing is that no substantial difference was observed between monkeys and apes as regards the number of aggressive postures. A great variety of mimics was found in both groups (with the exception of orang-outangs). We found a steady growth of the number of elements, connected with the use of hands in aggressions, along the comparative line ranging from lemurs to monkeys, and further to apes (*Table 1*). The elements of aggressive behaviour growing with the use of objects were marked separately. These elements were constantly used by chimpanzees and gorillas. Especially the latter have been most inventive-minded as regards the use of objects (throwing a stick at the target, beating the adversary with the stick, thrusting the object at the opponent, application of various objects to produce maximum noise effect). Warning patterns predominate in frequency in all species covered by the study (*Table 1*). The maximum frequency of elements of this type was observed in baboons and in green monkeys, and the minimum in lemurs. The latter showed also the minimum frequency of conflict elements, while the maximum number was registered in Japanese macaques and in gorillas. Contact elements were used most frequently by males of green monkeys, and most rarely by spider monkeys and by orang-outangs. The number of injuries inflicted in all studied groups was negligible. The maximum number of aggressive clashes was marked in one of the groups of stumptail macaques (in semi-natural arrangement). Intragroup aggression is practically absent both in the group of chimpanzees and orang-outangs (*Table 1*).

A close link was marked between the level of intragroup aggression and stability (*Table 2*). The stability of the group and its welfare were checked according to the ratio of the infants and juveniles in the group (index of stability). We can say that the greater the share of infants and juvenlies in the group, the lower is the probability of intragroup clashes with injuries. This fact is expressed by the negative rank coefficient between the number of aggressive clashes and the group stability ($Kr_s = -064$) (*Table 2*).

TABLE 2. *The relation between the number of aggressive clashes in the group and between the index of intragroup stability*

Species	x_i	N	I_{stab}	y_i	$x_i y_i$	$(x_i - y_i)^2$
Macaca arctoides	8	6.8	0.11	1	7	49
M. arctoides	7	6.7	0.21	2	5	25
M. arctoides	2	0.6	0.22	3	−1	1
M. malatta	4	2.1	0.57	7	−3	9
M. nemestrina	5	2.4	0.36	4	1	1
M. fascicularis	6	4.4	0.50	6	0	0
Papio hamadryas	3	1.8	0.42	5	−2	4
Papio anubis	1	0.6	0.67	8	7	49

$r_s = -0.64$

The complex of aggressive behaviour indices we have chosen reflects in a complex and objective way the quantitative and qualitative sides of intragroup aggressive behaviour. A phenogram had been worked out, on the basis of 16 indices reflecting the development of aggressive behaviour of the above species. Along the vertical axes was plotted the scale of unsimilarities (the distances according to the sum of indices) while the horizontal lines expressed the levels of difference (Mayer 1971; Sokal, 1968). As starting point the level of aggressive behaviour of tupaias was chosen. The species were grouped according to the significance of unsimilarity coefficient at three levels: I. tupaias (0.00—25.00); II. lemurs, all monkeys and orang-outangs (25.01—50.00); III. apes (50.01 and higher) (*Figure 1*). The results obtained in this way show that in general definite indices of aggressive behaviour are typical of the representatives of each level. There were no sharp dividing lines between the levels according to individual indices. Nevertheless, the limits of each level were defined quite clearly by the sum of indices.

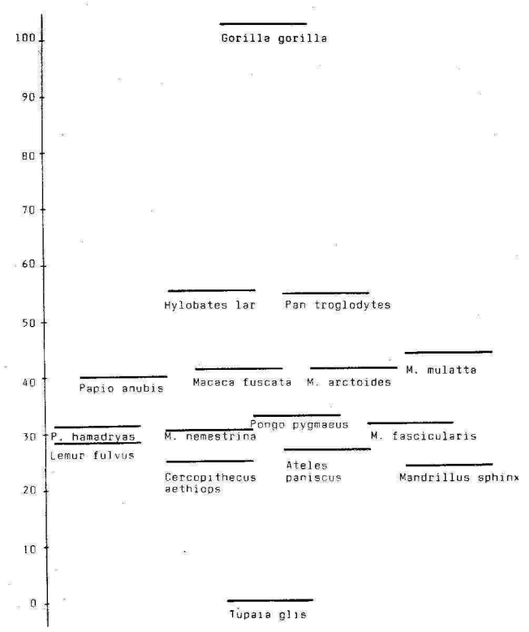

FIGURE 1. *Aggressive behaviour in primates (16 indices).*

Now let us present brief characteristics of each level: I. *Tupaias.* According to the present systematics they are regarded as the most primitive representatives of the order of primates. The results of our investigations confirm this view. In the number of warning elements (including mimic and aggressive

postures) the tupaias exceeded not only the lemurs, but some monkey species as well (*Table 1*). Their typical feature is the irregular development of indices. For instance elements with the use of hands failed. On the other hand there were some other specific features — e.g. the marking of territory with scent, used as warning signal. II. *Lemurs*, Old and New World monkeys, orang-outangs. The species at this level showed some general features of aggressive behaviour. In comparison with tupaias they were characterized by improved and rather intricate warning mechanisms connected with an increase of qualitative differentiation in postural, gestural, tactile and mimical aggressive elements. III. *Apes*. The most typical feature of this group is a general trend towards increasing group stability, tolerance between group members, and consequently a drop in the frequency of aggressive intragroup interactions. An increase in the variability of mimical, gestural and postural elements and the use of objects in aggressive demonstrations and clashes were observed.

The structural-dynamic approach has made it possible to investigate the mechanisms of prevention and buffering the aggression. Under "buffers" we understand mechanisms of stopping the aggression, by any manifestation of the buffering activity by the object of aggression, by the aggressor himself or by a third individual. The buffers have been divided into 2 categories — internal and external ones. Internal buffers represent aggression extinguishing mechanisms belonging to the system aggressor-object of aggression: the "curtailing" of aggression, prevalence of warning elements in the repertoire of the aggressor, the elements of subordination and affiliative behaviour demonstrated by the object of the aggression towards the aggressor — such as grooming, touching by the hand, etc. External buffers — influence one or all participants and stop their interactions. As a rule these actions — both aggressive and friendly — are initiated by the dominating individuals. The passive influence, the mere presence, of a third individual may stop aggression. For example aggressive actions of a male usually stop the fight between females. The grooming of a higher-ranking individual by the object of aggression has the same result. The presenting of infants by a subordinate male to an attacker in barbary macaques (Deag, Crook 1971) and also in stumptail macaques (personal observations). Let us describe a concrete situation with the use of buffers: male A attacked male B in an all-male group of hamadryas baboons. Male B ran to male C (ranking higher than the two participants of the clash) and squatted with bared teeth in front of C, imitating in fact a female behaviour. Male C then shielded the object of aggression, demonstrating his decision to protect him. After that C squatted behind B, put his hands on the latter's hips and bared his teeth against the attacker. Then C turned around. The attacker demonstrated his submission to male C, and ran to another corner of the cage.

The investigations of 16 primate species show the extension of the variety of buffers linked with the actions of the object in rows between primates. These types of buffers are absent in green monkeys. Their maximum number was observed in stumptail macaques (16). Contact buffers appeared to be most effective (grooming, embracing, shielding, touching by the hand). These very elements were used for buffering the most violent forms of aggression. The group of apes was characterized by a decrease of the frequency of the application of typical monkey buffers (such as grooming, submission, shielding), and by an increase of the frequency of touching with fingers, lips, embracing, caressing the face, play of adult individuals, kissing, and stroking in general.

The investigations of general tendencies in the evolution of aggressive behaviour and of the mechanisms of its buffering in primates allowed us to presume that these features were common also in protohominids and in early hominids. Probably they resulted in the development of warning aggressive patterns (especially those connected with mimic and with gestures). Vocal signals began to play an important role. At the same time our data, together with the results of investigations by other authors indicate the existence of links between the group's stability, degree of individual freedoms and their distribution in space, with regards to the frequency of intragroup aggression. The more stable is the group the more frequently occur intragroup interactions (Bernstein, Williams, 1983). The above facts may explain the decrease of frequency of aggressive interactions in big apes, with their unstable and loose organization (Goodall, 1979). Presumably the early hominid societies shared similar peculiarities. The tolerance of individuals to each other must have grown. Our investigations have proved that aggressive clashes prevail between females; fight between males belonging to the group is very rare. The latter may be the expression of a general trend towards a drop in dangerous intermale aggression, and aggression with the participation of males in primates (males can inflict most serious injuries). Evidently in early hominids continued the further development of qualitative variability of warning elements took place, as an extension of the general tendency, registered in primate phylogeny. The decrease in contact aggression associated with injuries could have been achieved not only due to an increase of general tolerance between individuals, but also due to a progressive development of effective complexes, of the visual and vocal buffers of aggression. In connection with these facts it seems that the ideas of the absence of inhibitions to kill intraspecies individuals in man, because of the loss of natural adaptations for the infliction of injuries (teeth, clows) are groundless (Ardrey 1966, Lorenz 1966). We ought to remember that apes are able to use various objects when fighting. In spite of the fact that the frequency of contact aggression in apes is lower than in monkeys, a qualitative development of buffers has taken place. Among the new effective buffers we should mention the play of adults and manipulatory activity. This suggests that there was a further qualitative development of buffers in early hominids, but there occurred no reduction of mechanisms inhibiting aggression. It is quite possible that inconnection with the opportunity to inflict injury from distance, the emphasis had been transferred from the improvement of visual buffers to the development of vocal signals, more effective under these conditions. A selection against superaggressors must have taken place in the early hominid societies (Polis, 1981). Superaggressors destroyed intragroup stability and hindered co-operation inside the group, influenced negatively the process of learning and the transfer of experience to the young generation. Aggressive individuals were expulsed from the primitive societies (Roginskiy, 1978). The high level of intragroup aggression ought to have negative impact on group stability and slowed down its increase (low number of infants), thus it was deprived of the advantages of evolution. Groups with high level of aggression were unable to compete with cohesive and rapidly increasing societies.

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