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Some aspects of hominid socioecology according to primatological data

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Abstract
A reconstruction of social structure and social relations in early hominids is proposed on the basis of modern data on primate socioecology. Relations between predator pressure and within-group structure, between the distribution of resourses and competition within and between the groups is analyzed. General tendencies in the association between social structure (dominance, kin-clans) and the level of within-group cohesion is supposed to be universal for non-hominid primates and hominids. Models of aggression and peacemaking for hominids are proposed. The nature of male-female bonding and parental investment at different stages of hominid evolution appears to be linked with ecological and anatomical changes, as well as with cultural innovations (hunting, emergence of home bases).

Key words: Primates, hominids, socioecology, social relationships

The reconstruction of social structure and social relationships in different species of hominids is one of the most exiting and complicated problems in human evolutionary studies. There has been a large number of attempts at reconstructing the basic features of hominid behaviour. Modern hunter-gatherer societies, various primate species, and even carnivores have been proposed as models (Campbell 1979; Thompson 1975). It is becoming more and more evident, however, that none of the specific analogies is applicable for modeling human evolution since all of them are based on the existing social systems without attempting to understand the origins of behavioural patterns (Potts 1987).

Most investigators propose to model the formation of hominid social structures on the basis of ideas on the relations between behaviour and environment, demographic and morphological patterns, life history, dispersion patterns, and reproductive strategies of both sexes (Lee 1988; Tooby & De Vore 1987).

In-group and between-group competition

According to primate socioecology, group social structure and group size may vary within the same population and even the dispersion patterns may be quite different in conspecifics from different localities. As reported by Starin (1992), various populations of the red colobus, basically a male-phylopatric species, may follow different models of social bonding: in groups from Kibale Forest, Uganda, strong male-male bonds were registered, while female-female relations were noncohesive; in Abuka Nature Reserve, Gambia, small uni- and multimale groups were typical, male-male attachment was virtually lacking, while female-female bonds were strong.

Two basic hypotheses concerning the reasons underlying group formation and the maintenance of within-group cohesion were proposed. According to the first one, high predator pressure is sufficient for the selection favouring a gregarious way of life (Busse 1976; Schaik & Hooff,

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1983; Boinski, 1988). The second one concentrates on the necessity to form cohesive groups in order to successfully compete for food resources with the conspecifics (Wrangham, 1980). Both predator pressure and between-group competition hypotheses agree that the differences between species should exist with respect to within-group social relationships of females.

Thus the level of within-group competition reflects the pattern of resource distribution and the quality of these resources (Noordwijk & Schaik 1987; Schaik 1989).

Dispersal patterns in early hominids

The dispersal patterns and the expression of hierarchical relations may differ in closely related species even if both are subjected to intense predator pressure. One of the examples is provided by two species of squirrel monkeys, *Saimiri oerstedi* and *Saimiri sciureus*, (Mitchell et al. 1991). Direct feeding competition between the groups seems to be absent while that within groups was reported to be low in *S. oerstedi* and marked in *S. sciureus*. As it could be predicted, female relationships were undifferentiated, female hierarchy was lacking, and it were the females who dispersed from their natal groups in *S. oerstedi*. In *S. sciureus*, on the other hand, a clearly expressed female dominance hierarchy was observed, stable within-group alliances were frequent. This species was characterized by female phylopatry .

The type of dispersion pattern in early hominid societies received special attention by a number of authors. Female phylopatry and close bonding between females were proposed as basic patterns of early hominid social structure, because this principle made it possible to maintain within-group cohesion, it also minimized within-group conflicts between and within generations, and provided conditions for the diffusion of cultural traditions at the population level (Butovskaya & Fainberg 1993). The opposite model, that of male phylopatry, was believed to be the most probable one because modern chimpanzees and bonobos, which demonstrate this type of relationships are phylogenetically close to humans (Foley & Lee 1989). It may be asked, however, whether the knowledge about the residental sex is really crucial for understanding within-group social relationships between and within the sexes or the reproductive or parental investment strategies. In most cases, tolerance and affiliative bonding between the males are less easy to establish than those between the females. This is understandable since females compete mostly for food resources, while males compete for both food and mating partners (Wrangham 1980).

For example, both chimpanzees and bonobos are male-phylopatric. But they strikingly differ in the pattern of inter-male and inter-female relationships. In chimpanzees, males maintain close connections with each other. Such associations are tightly associated with formalized dominance hierarchies, and alliances are likely to change following the restructuring of male-dominance relations (Goodall 1986). Grooming is not a reflection of attachment between the male kin, but rather a social tactics to form alliances against other individuals. Another typical pattern is food sharing between the males. In bonobos, on the other hand, male dominance hierarchy is less clear-cut, males show loose associations, alliances in aggressive conflicts are rare (Susman 1987). Grooming relations are correlated with friendly bonds. Food sharing between the males is less common. Female-female relationships in bonobos are characterized by a high level of sociability: females frequently affiliate with each other, and appeasement actions are quite common (Nishida & Hiraiwa-Hasegawa 1987). Although food sharing is more frequent in male-female pairs, it is not exceptional in female-female pairs as well, involving even nonrelated adult females; such cases would be almost impossible in chimpanzee communities (Kuroda 1984).

These differences would be easier to understand if we examine the patterns of competition between males for reproductive females. In bonobo females, the period of pseudo-estrus is much longer than in chimpanzees, and the dominant males' attempts to monopolize estrus females may be less beneficial (Furuichi & Ihobe, 1992). Taking the case with early hominids, we can expect that the absence of visual signs of ovulation might have produced the same effect on the male-male relations as in bonobos, that is, the decrease of within-group competition between the males (Lancaster & Lancaster 1983). Secondly, like in some primate species, menstrual cycles of females from the same group could become synchronized, making the strategy of monopolization of receptive females by the dominant male inefficient.

Close male relations may exist in female-bonded species. Bonnets (*Macaca radiata*) and stumptails (*M. arctoides*) are examples. In these species, males are highly tolerant to each other and spend much time in close proximity, they intervene in dyadic disputes among other males and frequently reconcile after conflicts (Silk 1992; Butovskaya & Kozintsev 1993). Yet, it was shown by us that male stumptailed monkeys can manipulate their affliative preferences in favour of more profitable partners. Kin ties, nevertheless, do exist, and it is seen that males prefer to chose relatives for affiliation if the rank factor is excluded.

In hunter-gatherer societies, dispersal patterns are different; they are highly institutionalized and regulated by social tradition. The origins of various patterns in each case may be unknown at present, but, importantly, such variation seems to indicate that the residence pattern was not the crucial factor in human social evolution.

What appears to be universal for all gregarious primate species, is the importance of kinship relations for the maintenance of group cohesion. Generally, relatives are more predisposed to support and protect each other. They may cooperate in the rearing of infants (females), or protect females from alien males (males). It has been demonstrated that close attachment between relatives is based on familiarity. The familiarity factor is important for both males and females irrespective of the type of migration.

Even in female-bonded macaque societies, close kin relations between the male and its female relatives may be stable over the entire lifespan (Welker & Schafer-Witt 1992). Related females, if they have not emigrated, are usually more attached to each other in male-phylopatric species than the nonrelated females are (Goodall 1986). In gorillas, close female kin preferentially support each other in aggressive encounters (Watts 1992). The degree of intensity of social relations among group members is far from being homogeneous. As demonstrated for a group of rhesus monkeys from Cayo Santiago, the average degree of relatedness among interacting animals is above the level of half-sibs but below that of parents and offspring (Cheverud et al. 1988). Altruistic behaviour under such conditions is basically directed towards close kin. If the model proposed by Cheverud et al. is accepted, it is highly probable that altruistic behaviour, having evolved in the context of close kin, can be redirected towards other group members, for instance, in situations of reciprocal altruism. A model of group selection based on the assumption of the absence of homogeneity in the degree of within-group interactions reflects the real state of affairs in primate societies and appears to be fruitful for the explanation of the origin of altruistic behaviour in hominid evolution.

Co-adaptivenesss of behavioural traits

Recent works by a number of investigators dealing with social relationships in various macaques species have demonstrated a high degree of co-adaptiveness between various behavioural traits. It has been shown that highly intense and severe aggression (high frequency of biting and wounding) is closely related to fleeing and submission, while in situations with a low risk of injuries, high probability of reconciliation is expected (Thierry 1990). Asymmetry in dominance and kinship relations is in close positive correlation with asymmetry of interactions. In species with small rank differences, reconciliatory tendencies are high, interindividual distances are minimal, aggressive interactions are largely bidirectional, affiliative interactions between group members are very common regardless of rank or relatedness between the partners (*Macaca arctoides, M. tonkeana, M. radiata, M. sylvanus*) (Thierry 1988; Butovskaya in press; Silk 1992).

In contast, species with marked hierarchical relations display mostly unidirectional and severe aggression, the choice of affiliative partners is largely limited to kin and groupmates of similar rank, victims and aggressors are less inclined to reconcile (*M. mulatta, M. fascicularis, M. fuscata, M. nemestrina*) (Waal & Luttrell, 1989; Thierry 1990; Butovskaya 1992). The division of macaques species into egalitarian and despotic is not absolute. Generally, these species display different states of equlibrium, varying along a continuum (Thierry 1990). A comparison of four macaque species on the basis of data obtained by other investigators and our own ones is presented to demonstrate this statement (Thierry 1988; Waal & Luttrell 1989; Aureli et al. 1989; Butovskaya & Ladygina 1989) (Table 1).

Table 1. Basic traits of social structure and within-group social relationships in four species of the genus *Macaca*.

Parameters	Long-tailed Macaca	Stump-tailed Macaca	Pigtailed Macaca	Rhesus
Formal biting	present	absent	absent	absent
Risk of injury	low	medium	high	high
Severe injuries	minimal	minimal	high	high
Variability of patterns of non-contact aggression	high	high	medium	low
Level of non-contact aggression	high	high	low	low
Bidirectional aggression	high	medium	low	low
Reconciliation after conflict	high	medium	low	low
Kin-preference in reconciliation	absent	high	high	high
Control of aggression by the male leader	effective	medium	effective	medium to low
Support in aggression on the side of agressors	victims	no preference	victims	aggressors
Kin-preference in support	none	medium	high	high
Permissiveness between group members	high	medium	low	low
Kin-preference in affiliation	medium	high	high	high

Variations similar to differences between species were found within single populations. In rhesus and Japanese macaques, relations between kin generally resemble those seen in egalitarian species, while interactions between non-kin are despotic (Thierry 1990). Social traits could emerge only in close relations to each other, and such correlation is to a large extent the property of the social system itself.

It may be expected that egalitarian social relationships would be more beneficial in situations when large groups of conspecifics are more likely to survive and reproduce. Close within-group alliances irrespective of kinship relations reduce the chances for the development of dominance asymmetry between non-relatives. It is possible to imagine such a situation in populations of early hominids, who entered open territories inhabited by a large number of predators under conditions of low within-group competition for food resources due to their nonpredictable or even distribution in space. Egalitarian relations between group members became even more probable when hominids began practicing big-game hunting.

Demography and life history models

Demography and life history of the ancestral groups are very important for the origin of the behavioural differences between populations (Datta 1989). A situation could be imagined when different populations of the same species developed adaptations to different environmental conditions, started practicing different social patterns and using tools. Despite the fact that different species have various types of aggression patterns, aggression is present in all primate species without exeption. Mechanisms of coping with aggression must have evolved in parallel. Such mechanisms were especially beneficial in situations where high group cohesion was necessary for survival. Several types of conflict resolution have been described in monkeys and apes. The simplest way is the dispersion of conflict partners. Another pattern, mentioned above, is reconciliation. Several types of peacemaking were described as being unique for apes and humans: mediation of conflict by the third individual, opportunism, redirected aggression by previous rivals towards a new joint target, deception (Waal 1990). Humans have many reconciliatory gestures and contact patterns common with great apes: stretching out a hand, smiling, kissing, patting, embracing, touching, sharing. Given the close phylogenetic relationship between humans and apes, it may be suggested that similar peace-making patterns were important in hominid societies.

Diet, tool-making and the evolution of sexual dimorphism

Drawing upon certain findings of primate socioecology, we can make some assumptions concerning the sex ratio in hominid groups. The first factor is the male monopolization potential. Primate groups are multimale if a single male is not able to defend access to the group females. The second factor is the risk of predation. It was demonstrated in two species of capuchin monkeys (*Cebus albifrons* and *C. apella*) that the proportion of males in the group was usually correlated with the risk of predation (Schaik & Noordwijk 1989). Taking into account both of these factors, it is highly probable that early hominid groups were multimale. Because the australopithecines were characterized by a high degree of sexual dimorphism, a conclusion is frequently made that males competed for females, and that the proportion of adult females in the group was usually low.

However, if we admit that hominid ecology was closely associated with woodland or even grassland savanna, another factor, predator pressure, may be expected to be more important. Some shift in the diet of the ancestral forms towards meat consumption may also have played a certain role in the development of sexual dimorphism in early hominid groups. On the other hand, the decrease in dimorphism (primarily in canine size) during the subsequent stages of human evolution could be neither a consequence of a decrease in the sexual competition of males nor a result of a diminished predation pressure, but rather the out-come of the shift from the utilization of natural weapons to the use of artificial ones.

At the early stages of hominid evolution, scavenging was highly probable for a number of reasons: this practice was possible with the smallest energetic costs, the fauna of ungulates was extremely rich at that time, carnivores never fully consumed the carcasses of killed animals, and to gain access to this food, hominids had only to drive away habitual scavengers (it was not very dangerous for them, because they acted jointly and could have used stones and sticks in addition to their canines (Blumenshine 1989; Speth 1989).

Taking into account the patterns of group protection against predators, it is possible to expect that it were mostly males who played the leading role in giving other group members access to meat. The scavenging strategy was highly beneficial after the entrance into the open savanna, because early hominids were unable to compete with habitual predators in speed or strength. Scavenging gave an opportunity to survive under the conditions of climate seasonality. Another positive consequence was the minimization of foraging time; thus additional time became availabe for the intensification of social contacts between group members, investigatory activities, learning and teaching.

Hunting, territoriality and partner's choise

The further aridization of the African continent led to serious changes in the predator fauna. According to Potts (1988), the period of approximately 2-1,5 mio years ago was characterized by the extinction of about 70% of all carnivores. By that time hominids had already possessed all necessary potentials for shifting towards regular hunting: bypedal locomotion, a perfect thermoregulatory system, high intellectual abilities, good memory, a communicative system necessary for coordination of actions during hunting, weapons. And, surprising though it might seem, hunting was oriented towards big game rather than towards middle-sized prey (Schule 1991). A high level of cooperation between males was necessary, and this condition was easily met because of constant pressure towards within-group cohesion of males at all previous stages of hominid evolution.

Parallel with the origin of big-game hunting, the size of group territories increased and between-group competition for territories became sharper. Exactly by that time an increase in both the period of infancy and the total lifespan was registered using skeletal data (Smith 1988). It means that a certain shift towards a greater parental investment might have happened, and there was already some orientation towards a serial pair-bonding (Mansperger 1990; Butovskaya & Fainberg 1993). During that period individual attachments became oriented mainly towards the male-female pair, as well as towards the male-in fant and male-male kin relationships (Reynolds 1976). Female phylopatry, if it had ever existed, was substituted by male phylopatry. This period of human evolution was characterized by an intensive expansion of hominids from Africa to Eurasia. The only limiting factor in hominid dispersion was the availability of fresh water resources.

It seems possible to speculate about the lead-ing principles of partner choice in the period when serial pair-bonding emerged. In many primate species (*Macaca fuscata, M. mulatta, M. radiata, Papio anubis, P. ursinus, Pan troglodytes*), males are generally attracted to elder multiparous females (Anderson 1986). Evident preferences of women in the thirties were mentioned in our own species as well. Under such circumstances high tolerance towards previous off-springs of the chosen female partner should be extremely beneficial under conditions of long periods of infant dependency. Bonobos might provide an example showing how the tendency towards pair-bonding might come into existence through the coincidence in the benefits of both sexes: the female's preference for a male partner who is more inclined to food sharing with her and her previous offsprings, and the male's preference for a multiparous female.

Different species of early hominids might have existed on the same territory. Their contacts could be peaceful like in many primate species, especially if they utilized different resources. According to paleoecological data, robust and gracile australopithecines as well as *Homo habilis* and *Homo erectus* coexisted in some places for more than 0,5 mio years (Potts 1988). It is not clear whether hybridization was a common phenomenon. However, it may be assumed that neighbouring groups used tools left by more progressive forms and subsequently developed similar techniques of tool-making.

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