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THE SOCIAL ORGANIZATION AND ADAPTATIONS OF EARLY HOMINIDS TO VARIOUS ENVIRONMENTS DURING THE PLIO-PLEISTOCENE

ABSTRACT: This article uses insight from social ecology to model the evolution of and changes in the social structures of ancestral hominids during the Plio-Pleistocene. It argues that while changing climates had an acknowledged effect on ancestral lifeways and behaviour, to understand the social organization of hominids we need to consider both historic and demographic factors as well. I argue that the hominid range expansion in evidence during the Pleistocene resulted from socio-ecological solutions adopted by the hominids.

KEY WORDS: Hominid evolution – Evolutionary socio–ecology – Social organization – Sexual selection

INTRODUCTION

The reconstruction of early hominid social structure and social relationships is one of the most interesting and, at the same time, most difficult problems in studies of human evolution. Numerous researchers proposed to use modern hunter-gatherers, various primates, and even some predators as analogues for hominid behaviour (Campbell 1979, Thompson 1975, Wrangham 1987). Such, however, can hardly be applied to the reconstruction of hominid evolution since they are based on the analysis of data derived from established social systems. Such data can provide little insight into the evolution of behaviour (Potts 1987). Because of this, many scholars have recently suggested models for the evolution of hominid social structure based on complex relationships between behaviour and natural environment, demographic and morphological characteristics, the length of the life spans and male and female reproductive strategies (Lee 1988–89, Tooby, de Vore 1987).

INSIGHTS FROM PRIMATE SOCIAL ECOLOGY

Studies in social ecology have demonstrated that primate social structures in general, and group size within different populations of a species in particular, depend on primate reproductive rate and on the intensity of inter-group competition for food resources. These variables, in turn, depend on subsistence types, the spatial distribution of the resources, competition with neighbouring groups and predators (Strum, Western 1982, Terborgh 1983, van Schaik, van Noordwijk 1986). The relationships between the individuals within the same species are the results of complex interaction of multiple factors which include the 1) energetic needs and metabolic rates, 2) spatial distribution of males and females within a population, 3) reproductive need for mates, and 4) the social dynamics within a population (Lee 1988–89).

The theory of sexual selection shows that the factors limiting male and female reproductive success differ from

each other. An access to the resources constitutes the limiting factor for females whereas male reproductive success is limited by their access to fertile females (Trivers 1972). Sexual selection results in territoriality (Krebs, Davies 1987). It has long been assumed that competition for resources located within a defended territory is the major factor causing territoriality. In this case, individuals of both sexes participate in territorial defence, and it is the females who play the most active part in intergroup conflicts (van Schaik 1989). Such intergroup relationships can take a form of offensive hostility but can also be of a more neutral aggregating – dispersing pattern. It has also been argued that when resources within a territory are scarce and the costs of territorial defence are lower than its benefits, the degree of overlapping of the group territories is low (Mitani, Rodman 1979). However, some primate studies show that competition for resources can also occur within species living in groups who exhibit no definite territorial behaviour. In species with significant overlap of group territories, females can be actively involved in the intergroup conflicts (Cheney 1987).

Mating defence is the second factor causing territoriality (Dunbar 1988). In this case, intergroup relationships are, as a rule, antagonistic and carried on mainly by males. This type of territoriality has been recently found, for example, among six langur species of South-eastern Asia (van Schiak *et al.* 1992). It has also been noted that a degree of intergroup conflicts arises as the number of mature males within the groups increases. Recent studies have also shown that primates living in open terrains, and who are thus more vulnerable to predation, are likely to form larger travel parties.

Finally, we also need to consider bonds between females – something rarely done for the reconstruction of early hominid lifeways. Primate studies show a tendency to individual bonds and stable friendly alliances between both related and unrelated females – noted in captive common chimpanzees and well marked in the bonobos (Badrian, Badrian 1984, Chapman *et al.* 1995, de Waal 1982, 1987, 1995, Nishea 1979). In immigrating to new groups, young bonobo females initiate intensive affiliative interactions with the senior resident females, using frequent genital rubbing as well as grooming. These actions enable them to establish close bonds with group females and to make the first step for integrating into the group. After giving birth to her first offspring, the female's position in the group becomes more central and constant. Female-female bonds in bonobo communities are much closer and more stable than among the chimpanzees. Bonobo communities are female centered and female dominated (de Waal 1995, Kano 1980, 1992).

Thus, in evolutionary terms, it seems that the females may have been the first to benefit from social ties with each other. In this light, bipedality would have been a powerful factor promoting the further strengthening of hedonic female bonds. Since Eibl-Eibesfeldt (1989) has characterized human society as exhibiting close bonds between females, we clearly need to include these insights into evolutionary scenarios as well (Butovskaya, in press).

THE MODELS

The following are tentative models for the social organization of various ancestral hominid species. They incorporate data on palaeoclimates, palaeoecology, and palaeoanthropology, and are grounded in basic concepts of evolutionary ecology.

The origin of *Homo* appears to have been stimulated by climatic changes (climate forcing hypothesis). As Vrba and colleagues (1988–89) note, three out of four critical periods in hominid evolution coincide with global climatic cooling episodes, aridity, and the expansion of the open landscapes throughout Africa.

The oldest hominid remains found in Kenya (Tabarin) point to cooling. During this time (4–4.5 Mya), several modern antelope species appear (Vrba *et al.* 1988–89). Extant *Australopithecus afarensis* at the time still retained some morphological traits related to tree-climbing. This suggests that, although displaying bipedal locomotion, this taxon heavily depended on proximity to the trees (Senut 1991). Their diet was likely based on diverse terrestrial resources including roots and seeds as well as meat of various small vertebrates and invertebrates. Thus it is possible that the first tools were designed for gathering rather than for hunting (Tanner 1987, Stanford, Allen 1991). Data on modern chimpanzees (Boesch, Boesch 1981) suggest that females were likely more successful than males in gathering activities. Males likely engaged in sporadic small game hunting. They could have taken prey away from predators either driving them off with sticks and stones or by looking for places where predators (e.g. leopards) stored their prey (Cavallo, Blumenshine 1989). Under conditions of abundant animal resources, some early hominid populations could turn to scavenging as a most efficient and less energetically costly subsistence practice (Blumenshine 1989, Speth 1989). The availability of plentiful ungulate species insured that large parts of prey bodies remained untouched by predators.

Mature males likely played an important part in protecting the group from predators and thus the survival of the group depended on their sufficient number. Feeding on carnivore leftovers permitted the *africanus*-like forms of Australopithecines to survive in seasonal environments. The high caloric value of their foods would have permitted them to economize time in subsistence pursuits. This, in turn, could have facilitated intensification in intragroup social contacts, in individual exploratory activities, and time spent on educating the young.

The other Australopithecine populations evolved towards robust forms. They likely specialized in low-calorie diets (Potts 1988–89). Under these circumstances, the spatial distribution of their food resources made intergroup female competition disadvantageous. The social structure

of these groups, however, could include a reduction in the proportion of mature males within multi-male groups, as well as enhanced territoriality due to male competition for females. Such feeding specializations could result in more rigid hierarchical intragroup relationships between the males, the elimination of matrilineal ties, the deterioration of relationships between the males and the females, and the transition from matrilocal to patrilocal residency. The ensuing monopolization of females by males also reduced females' individual freedoms and their exploratory activities. Such constant social control over females may have selected against technological innovations among the males.

The different thermoregulatory needs which appeared in the course of the evolution of robust and *africanus*-like Australopithecines caused them to occupy different ecological niches (Falk 1988). The further evolution of bipedal locomotion among the Australopithecines ancestral to *Homo* was accompanied by increasing cranial capacity (first, in the surface area of the brain) and in a more ramified circulatory system feeding the brain. The robust Australopithecines did not experience these transformations but increased the massiveness of their dentition. Different subsistence and social strategies facilitated a further evolutionary divergence of these two lines.

Hill (1987) argues that the replacement of tropical rain forests by savannahs had a mosaic pattern. He notes that 3–4 Mya extensive tropical forests grew in the vicinity of Lake Turkana whereas savannahs dominated at Laetoli. The early hominids appear to have favoured open landscapes and tropical forest and savannah ecotones. Anthropoid primates, on the other hand, preferred tropical forests.

Vrba and colleagues (1988–89) suggest that the evolutionary separation of the hominid lineage into *Homo* and robust Australopithecines occurred roughly 3–2.8 Mya and coincided with climatic changes. The evolution of the genus *Homo* was accompanied by more prolonged maturation period and extended life spans (Smith 1988–89) – factors which affected all other aspects of their lives. They likely intensified exploratory activities among the young and stimulated an extension of time spent educating the young. Furthermore, this likely resulted in the emergence of closer relationships between both sexes as well as individuals of the same age and sex.

Individual preference in choosing a mate and friendly relations between specific individuals of the opposite sex led to an increase in paternal investment. This can be clearly observed in multi-male groups of lower catarrhines (particularly, among the Macaque). The enlargement of cranial capacities could also have generated the males' capability to recognize their own offsprings. Finally, the likely disappearance of the formal signs of ovulation further reduced male intragroup competition for females (Lancaster, Lancaster 1983).

About 2–1.5 Mya there occurred transformations in the African carnivore guild. About 70 % of hunting (not scavenging) carnivore species became extinct (Potts 1988–89). This appears to have been the time when hominids first might have turned to the medium game hunting. Males played the major part in hunting while females concentrated on gathering.

At this evolutionary stage, proficient hunting skills and sharing meat with a female and her children likely helped to establish successful sexual bonds. The capability to cooperate with other males in hunting would have increased chances of high social status. Furthermore, social integration could also have been improved through the exchange of individuals between the neighbouring groups.

During this stage of hominid evolution it is unlikely that the males monopolized females within groups because such behaviour would lead to the aggravation of intragroup competition and to unnecessary conflicts. The latter could result in 1) group fragmentation into smaller subgroups, 2) decrease in the proportion of males in multi-male groups, and 3) the formation of mobile groups of single males frequently raiding heterosexual groups to capture females. In such a case, cooperative hunting would become less successful and be simply discontinued. Individual hunting, such as documented for the Efe (Bailey, Aunger 1990), for example, would have been impossible due to insufficient technology.

It also appears that during this stage infanticide did not occur on a regular basis. Such a practice would constitute a real threat for population growth because of the extended maturation periods and the low fertility among females. Lee (1988–89) has shown that the number of offsprings produced by human, chimpanzee, and gorilla females during their lifetime averages four children. These data suggest that we can use the same estimates for the hominids as well. Because of the availability of vast unoccupied areas and the inherent interests of each population to enlarge its habitat, we would expect child care to have been provided not only by relatives but also by other members of the group.

The hominid ecological expansion, which occurred roughly 1–0.9 Mya, was associated with *Homo erectus* (Vrba *et al.* 1988–89) who expanded into various environments including steppes, savannah-forests, semi-deserts, and forests. Their spread was apparently limited by the availability of drinking water.

There are several possible reasons for hominid expansion at this evolutionary stage. The first is population growth due to expanded life spans, advanced child care, and altruism which insured the survival of elderly and wounded individuals. Second, food procurement and processing were greatly improved through the use of fire. These permitted hominids to occupy climatically less favourable areas. In addition, fire likely served as protection for the females and the elderly members of the groups when males left camps to hunt. Third, increased size of group territories and more pronounced territoriality with rudimentary property rights to hunting territories,

compared to the cases for *Australopithecus* and *Homo habilis*, also might have facilitated the expansion of *H. erectus* populations. We know that feeding territories of carnivores considerably exceed those of the herbivores. Property rights may also have applied to water sources and to locations of fruit trees in accord with the accessibility of the resources at a particular point of time permitted *Homo erectus* to occupy highly seasonal environments.

Population growth likely led to the division of core groups into several daughter groups. Such a process is documented among other primates and shows that the dominant group remains in its original territory while subordinate groups leave in search of new habitat (Chepko-Sade 1979).

The heterogeneity of intellectual skills extant within a population served as an essential prerequisite for successful hominid evolution as well as for their high adaptability. Recent studies show that there are some individuals within primate populations who exhibit more developed social intellects which provide them with higher social statuses and with related benefits (Welker, Schafer-Witt 1992). These more skilled social actors are likely to have had advantages during stable ecological conditions. The less socially skilled individuals spend more of their time exploring the natural environment – all to the ultimate benefit of the more skilled and higher ranked individuals. It is these low-ranked individuals who leave their original territories when the core group divides. These same individuals also possess a high ecological intellect and take advantage in advanced food procurement strategies, adopt new diets, and better educate their children. My research on the brown macaques amply documents such behaviour (Butovskaya 1995, in press). Data presented by other scholars support these findings and suggest that high-ranked individuals are less successful in experimental situations where it takes them much more time to chose appropriate strategies and solutions (Bunnell *et al.* 1980). The sum of this evidence indicates that it is the low-ranked individuals who probably had better chances to survive under conditions of sharp environmental changes which accompanied global cooling.

The final division of labour between males and females occurred when *H. erectus* began hunting co-operatively. This period saw a significant increase in the length of child dependency. At this time more active child care became a vital strategy – one which ensured reproductive success of both sexes. By now sexual selection played a minor role while parental investment and partnership increased significantly (Lancaster, Lancaster 1983). The trend towards serial monogamy, which took its final form at the later stages of human evolution, could have also appeared during that time period (Mansperger 1990, Fisher 1989). Under such conditions, matrilineal ties became less important and the social ties transformed into male-female, male-child, and male-relatives ones (Reynolds 1976). The patrilocal social structures gradually replaced previous matrilocal ones.

CONCLUSIONS

Although environmental conditions greatly affected the evolution of hominid social organization, I suggest that it is the original type of social relationships extant in ancestral form which were of prime importance in both hominid social relationships and social structures. I argue that the history and demography of the original hominid groups played an important role in their subsequent evolution (see also Datta 1989). Specific spatial social structures could undergo significant changes through time and result in variability even on the level of a taxon. At the same time, the evolution of social relationships within the *Homo* lineage tended to increase intragroup sociability and tolerance to other members of the group, and to develop mechanisms for reducing social tension and aggressiveness while favouring complex forms of cooperation and altruism. The *Homo* lineage evolved in the direction of more rigid social organization and increased competition for mates adapted to changing environments. These were built on prior strategies of avoiding competition with other hominid forms who diversified by shifting to low quality diets. Different hominid forms are likely to have coexisted within the same territory and to have been periodically in contact with each other – as is the pattern with modern primates. Finally, it is possible that such contacts could have facilitated the transfer of technologies from one form to another.

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