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Ecological Dominance and the Final Sprint in Hominid Evolution

In contrast to many other models of human evolution the "balance of power" theory of Alexander has a clear answer to the question why a runaway selection process for unique social and moral capacities occurred in our ancestry only and not in other species: "ecological dominance" is hypothesized to have diminished the effects of "extrinsic" forces of natural selection such that within-species, intergroup competition increased (Alexander, 1989). Alexander seems to be wrong, however, in his claim that already the common HUCHIBO (Humans, Chimps, Bonobo's)-ancestor has crossed the ecological dominance barrier. In this paper an adapted version of Alexander's model is presented and several different ways are proposed to make this adapted version testable. A preliminary survey of the available paleontological and paleoecological data suggests that there is some evidence of a less vulnerable position towards predators in early *Homo* and that there are clear signs related to a crossing of the ecological dominance barrier in *Homo sapiens sapiens*.

Key words: Ecological dominance, predation, intergroup competition, paleoanthropology.

Introduction

Many explanations of human evolution fail to explain why evolution of a large brain, language, morality and culture occured only in the human lineage and not in other lineages. Often those models simply assume that all those human characteristics are "adaptive" anyhow - regardless of the specific ecological circumstances - and that their evolution, therefore, is self-evident. However, brain tissue is energetically "expensive" and to explain the threefold brain enlargement and the radical and relatively fast neuro-anatomical revolutions that enabled humans to speak and to create culture we at least will have to invoke very specific and powerful selective forces. Evolution is a "blind" product of natural selection and does not create art for the sake of art (*l'art pour l'art)* nor complicated brains just for the sake of nature-transcending meditations. The relatively fast evolution of human characteristics proove that in the struggle for reproductive opportunities individuals without such characteristics were simply outcompeted by individuals *with* such characteristics. What circumstances would promote a runaway selection of intellectual and moral capacities in which those capacities could become an absolute *sine qua non* for successful reproduction?

Alternative hypotheses

Hunting and gathering.

For several decades hunting and gathering hypotheses about human evolution have competed with each other as favourite explanations of human evolution. But they both are not explanations at all, because they do not explain the increase in brain size nor the unique social and cultural environments that humans create. In short, they do not answer two questions:

1. Why did humans evolve high intelligence in contrast to other hunters (gatherers)? Lions and hyena's do not need language, morality and a capacity for abstract thought to hunt their prey; ants do not need a big brain to gather food.

2. Why do humans, even in primitive societies, tend to live together in groups that are *above* the optimal size required for group hunting (gathering)? Why did not group size *decrease* as hunting weapons and skills improved during human evolution? (Alexander, 1987: 79)?

Sexual selection. Some authors (e.g., Parker, 1987) have also invoked sexual selection to account for the unique runaway selection of human characteristics. But sexual selection would only promote those characteristics to develop in the sex that has to compete for access to the most investing sex (Trivers, 1971). Above that, like so many models, this explanation fails to explain why the process only occured in the human lineage.

What has to explained?

1. Given the fact that humans and great apes are very closely related (for an overview of the evidence, see Tanner 1986), how could (only) the human line evolve so fast an intellect much too strong for simple everyday tasks like hunting and gathering? 2. Given the fact that in general rapid evolution and rapid multiplication of species tend to go together (Alexander, 1990), why are there (probably) only two lines of hominids during the Pliocene and why seems there to be only one line during the last million years?

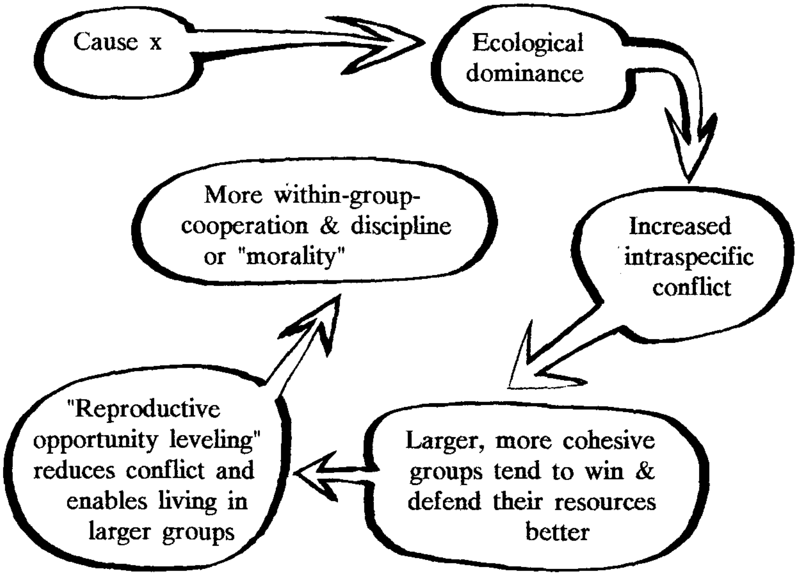

Figure 1 - In Alexander's original model an ecological dominant species tends to display more intraspecific conflict. In humans this has resulted in an arms race between groups. Larger, more disciplined groups were more successful as a result of which morality and high intellectual abilities evolved

Alexander's " balance of power hypothesis"

Figure 1 shows the main points in Richard Alexander's model. The reasoning behind it can be summarized as follows:

-At the moment that "ecological dominance" was achieved the threat from predators was replaced by intraspecific "balances of power".

-Bigger, stronger and more disciplined groups were better able to defend a territory. As a result of this group sizes increased far beyond the optimum size for hunting/gathering bands.

-To be able to live together in big groups with many non kin-related conspecifics, humans developed reciprocal altruism to a degree in which it became "generalized" reciprocity (Trivers, 1971) or "indirect" reciprocity (Alexander, 1979; 1987), meaning a form of reciprocity in which third parties record reciprocal relations to learn about the reliability and "moral profile'' of group members who are potential cooperators for themselves.

-In such a situation it becomes important to look like a very reliable and generous cooperator. This can either be achieved by really being a generous cooperator or by deception, which costs less energy but more intelligence. A runaway selection for mental proficiency and complexity arises.

-Because dominant males were increasingly dependent on cooperation with other males, they had to renounce their reproductive monopolies. "Reproductive opportunity leveling" enabled big groups to overcome potential sources of internal disruption (Alexander, 1979; 1987: 71).

-This model does not necessarily imply Wynne-Edwardsian group selection. Group selection is here not used to deny the conflicts of interest within groups (Alexander, 1987: 169) and it is not assumed that group selection is a stronger force than selection on the level of individuals. The main point is that intergroup competition has created an *environment* in which *individuals* are selected on their abilities to live in relatively big groups and to cooperate in large networks. Also intergroup competition need not necessarily result in complete genocide, but can also result in gradual replacement (called "genosorption" by Wilson, 1975: 573-574).

Reasons to change Alexander's model

There are several reasons to change Alexander's rather abstract model in a more concrete one that addresses more paleontological data. Specifically, Alexander seems not to take into account the following:

1. During the longest period of hominid evolution several hominid species coexisted, *Australopithecus* and/or *Parantropus* and *Homo*. According to one recent analysis (Wood, 1992) initially there may have existed two species of *Homo: H. habilis* and *H. rudolfensis*.
2. Neither Chimpanzees nor Australopithecines are or were ecologically dominant. Chimpanzees are sometimes predated by leopards. According to Brain's "Swartkrans leopard hypothesis" the collection of australopithecine bones in the Swartkrans cave may have been the result of the leopards' habit of taking prey into a tree in order to avoid competition with hyenas (Brain, 1983). The holes in one of the australopithecine craniums, SK 54, match exactly with the canines of a leopard. To account for the fact that in the oldest member of the Swartkrans cave more than 50% of the macrovertebrate remains are from either hominids or cercopithecoids, Brain has more recently speculated that leopards exploited the sleeping sites of the Baboons and Australopithecines. Also, it is very plausible that there existed a specialized predator of primates, a plausible candidate of which is the false sabertooth, *Dinofelis*.
3. Alexander does not make clear *what* (cause X) made our ancestors "ecologically dominant" and *when*.

4. There are other predators (bears, lions) "ecologically dominant" and some of these (lions) even exhibit signs of intergroup conflict, but nevertheless we see no signs of runaway selection on brain size in these species.

5. Intergroup conflict seems to be a characteristic of more savannah-dwelling primates (Ciani, 1992), but none of them shows "runaway selection".

A proposal to adapt Alexander's model to a collection of paleontological data

We propose to improve Alexander's model by making it more specific and testable:

1. It should become clearer what preadaptations predestinated our ancestors to be drawn into a spiral of increased intergroup competition;
2. It should become clear what ecological circumstances forced them into another evolutionary avenue than Chimps and Bonobos;
3. It should become clear what enabled them to become "ecologically dominant";
4. The model should enable us to make predictions about patterns in the paleontological record.

The rest of this paper will address these four issues.

Ad 1. What preadapations could have predestinated our ancestors to become increasingly involved in intergroup competition?

Not only the genetic data show that Humans, Chimpanzees and Bonobos (HUCHIBOs) have much in common; they also show some striking socio-behavioral similarities as a consequence of a shared tendency towards female exogamy and towards cooperation between kin-related endogamous males (Wrangham, 1986; Ghiglieri, 1987):

"*Unlike gorillas and orangutans, males of the chimpanzee-bonobo-human clade retain their male offspring predominantly, live in closed social groups containing multiple females, mate polygymously, restrict their ranging to a communal territory, are cooperatively active in territorial defense, and, apparently, when a neighboring community weakens, the males of some communities make a concerted strategic effort to stalk, attack, and kill their rivals as do men* (Ghiglieri, 1987: 346)."

This new kind of reproductive strategy could be a consequence of the opportunities offered by the shared interests of a group of kin-related males. In most primates males are exogamous and therefore more competitors than cooperators. The development of a high-risk/high pay-off strategy like organized aggression is highly unlikely to arise in females, because they are not likely to gain much reproductive advantage from it.

Ad 2. What ecological circumstances forced our ancestors into another evolutionary trajectory than Chimpanzees and Bonobos?

Bipedalism; tool use. It is very tempting to assume that somehow bipedalism is at the bottom of all subsequent differences between hominids and members of the genus *Pan*. Yet, much recent research suggests that the fully bipedal Australopithecines were not so human-like as originally assumed (see e.g. Falk, 1991 for an overview). The robust Australopithecines (sometimes separated as the genus *Paranthropus* to acknowledge their distinctiveness from the more gracile Australopithecines) walked erect for more than a million years without showing any increase in brain size.

Tool use *per se* also can not be the source of the difference: recent research in West Africa shows that some Chimpanzees use tools to crack nuts there during several hours a day (Boesch & Boesch, 1992). Also, *Paranthropus* probably was able to use tools, because his hands are completely modern (Susman, 1988).

Meat consumption? To find the origin of the uniquely human trends towards increasing brain size and probably the use of language we have to go back to 2.5 million years ago, when both the genus *Homo* and *Paranthropus* arose from some Australopithecine ancestor in a reaction to the first ice age. Both new groups had their own unique way of coping with the problems posed by the dry season, which played the role of a kind of "bottleneck". *Paranthropus* specialized in the hard and dry fruits that even in the driest circumstances would survive; *Homo* seems to have increased its level of meat consumption. During the dry season many savannah animals tend to congregate around the remaining water resources and *Homo* may have used this opportunity (Foley, 1987). Certainly, the dentition of early *Homo habilis* is compatible with an omnivorous diet of which meat was a part.

Division of labour and the home base. Already in Chimpanzees there is a trend towards a food specialism of the sexes: males cooperate more often in hunting, females gather (Boesch & Boesch, 1989). An increase in meat consumption would have led to an increase of this tendency. If males could exchange their meat for paternal certainty this could have been an attractive deal for both parties. What is needed then, however, is a meeting area to exchange food (Tooby & DeVore, 1986). In the end, the need for a home base is a logical outcome of this process. The result of all this could have been that traditional sleeping sites were more and more used as home bases. *Because home bases at favorable places probably were in limited supply, they may also have become a focal point of increased intraspecific conflict.*

Ad 3. What enabled our ancestors to become ecologically dominant?

C.K. Brain, at the end of his extensive report on his research in the Swartkrans and Sterkfontein caves, concludes that the different layers in the cave represent a fundamentally different ecological position of the successive hominids. The change is summarized in the statement that "the hunted became the hunters" (Brain, 1983)

"At Sterkfontein, the interface between the top of Member 4 and the bottom of Member 5 represents a time interval crucial in the course of human evolution. During this interval the gracile australopithecines disappeared from the Transvaal scene and the first men appeared. In this interval, too, the evolving men mastered a threat to their security that had been posed by the cave cats over countless generations. During Member 4 times the cats apparently controlled the Sterkfontein cave, dragging their australopithecine victims into its dark recesses. By Member 5 days, however, the new men not only had evicted the predators, but had taken up residence in the very chamber where their ancestors had been eaten

How the people managed his is not recorded, but it could surely have been achieved only through increasing intelligence reflected in developing technology. It is tempting to suggest that the mastery of fire had already been acquired and that this, together with the development of crude weapons, tipped the balance of power in their favor..." (Brain, 1983: 273).

Many other writers have speculated that the discovery of fire could have initiated a transition to a completely different life style (Poirier, 1987; Goudsblom, 1989). The discovery of fire may have enabled the conquering and defending of caves and with that it may have created a place of relative safety from predators and climatic uncertainties. With that, however, it may have given the impetus for new levels of intraspecific conflict, focussing on the most desirable home bases.

With that, however we have arrived at a corrected version of Richard Alexander's model in which the unknown "cause x" is replaced by an explanation of ecological dominance and in which the feedback system of causes leading to a runaway selection of moral and intellectual capacities is revealed (see Figure 2).

Ad 4. What evidence could point to a crossing of the ecological dominance barrier?

In principle, our model should be testable with the following list of signs that betray the crossing of the "ecological dominance barrier".

a. *Traces of fire and improved home bases.* Brain and Sillen (Brain & Sillen, 1988) found evidence of the use of fire in the Swartkrans cave of more than one million years ago. Traces of hearths of almost a half million years old are known from Zhoukoudian and Terra Amata, both related to *Homo erectus.* In Zhoukoudian thick layers of ash seem to indicate that the fire was kept burning for long periods (Rukang & Shenglong, 1983). This may have been partly a strategy to ensure the safety of the cave.

b. *Extinction of predators specialized in predation of hominids.* If Brain's (Brain, 1983) speculation about *Dinofelis* is right and it was a specialized primate-killer, it would be interesting to find out why it went extinct.

c. *Extinction of prey animals.* At Zhoukoudian hugh amounts of deer bones indicate that *Homo erectus* hunted these animals on a routine basis. The hunting of such large animals must have been a group activity (Rukang & Shenglong, 1983). However, only with the transition to

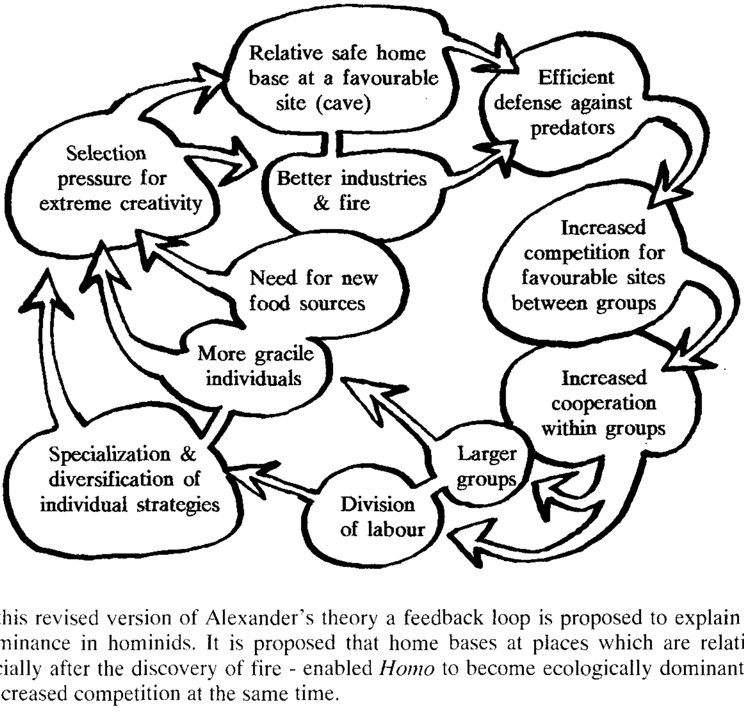

Figure 2 - In this revised version of Alexander's theory a feedback loop is proposed to explain the origin of ecological dominance in hominids. It is proposed that home bases at places which are relatively easy to defend - especially after the discovery of fire - enabled *Homo* to become ecologically dominant, but became the focus of increased competition at the same time.

Homo sapiens sapiens can we discern very clear traces of mass hunting techniques that probably have driven many prey species into extinction ("prehistoric overkill", Martin, 1967). At the same time many large species of mammals go extinct. Although some of these extinction coincides with climatic changes, it is highly plausible that moden man played a large role in them, because the patterns of extinction coincides with his presence, especially outside Africa. One example of a very fast process of extinction was the extinction of different species of American land animals that coincides with the first Americans, the Clovis people.

d. *Signs of increased intraspecific conflict: cannibalism, spear wounds, genocide.* Many presumed traces of cannibalistic practices in *Homo erectus* and *Homo sapiens* do not meet the criteria of scientific scrutiny (Roper, 1969; Binford, 1981). Yet the finds in Krapina and Hortus are difficult to explain otherwise. Research on the skull from Bodo, an archaic *Homo sapiens* of between 0.5 and 0.2 million years, show that this has been deliberately defleshed (White, 1981). As cannibalism in the contemporary peoples who practise it is associated with the hope of acquiring the strength and courage of the enemy, clear traces of cannibalism *could* indicate also higher levels of intergroup competition.

There have been also found a couple of skeletons which exhibit wounds that seem to have resulted from weapons. This claim has for example been made regarding the pelvis of a skeleton from es-Skhûl (Israel), the ribs of one of the Shanidar Neandertals and the elbow of a skeleton found in Wadi Kubbuaniya. Of course, the amount of bones of early humans is too small to justify far-reaching conclusions. Nevertheless, it is not completely impossible to make an estimate about the number of persons with wounds as a result of violent interaction that you can expect in different societies with different levels of enmity towards their neighbours.

Clear cases of prehistoric genocide are of course very rare. Klein mentions "*an extraordinary terminal Pleistocene (ca. 14,000-12,000 years-old) cemetery near Jebel Sahba in Sudanese Nubia where nearly half of the fifty-nine individuals exhumed had either unhealed antemortem skeletal injuries or had stone artifacts lodged in or near their bones*" (Klein, 1989: 387). A recent excavation in the Netherlands shows also that we should forget about the picture of prehistoric man as a peaceful hunter-gatherer (Louwe-Kooijmans, 1990). In both cases the species concerned is, however, *Homo sapiens sapiens*. This suggests that only in this species the levels of intergroup conflict increased significantly as a result of ecological dominance.

e. *Traces of arms races: new weapons, entrenchments.* The relatively slow cultural evolution in *Homo erectus* is followed by a gradual acceleration in early *Homo sapiens* and by a succession of rapid break-throughs in *Homo sapiens sapiens* (Pfeiffer, 1983). Whether we explain the spread of this last form with an out-of-Africa model or a multiregional hypothesis, the association of a very successful new breed with a fast succession of all kinds of new technology can hardly be a coincidence.

f. *Bigger groups, more gracile individuals, more hierarchical social structures, higher population densities.* There are many signs betraying deep social changes and an increase in group size during the Middle/Upper Paleolithic transition (Pfeiffer, 1983). The very fact that people were more lightly built can be interpreted as an indication that cooperation within the group became more important than the sheer force of the individual. Apparently it was more important to belong to a strong group than to be strong yourself. The appearance of body ornaments (White, 1986) and status burials indicate a compartmentalization of society that can only have resulted from a division of labour and a new sense of hierarchy. An indication of the higher population densities in Cro-Magnon man compared to the Neandertal is given by the fact that on the central Russian Plain there are only half a dozen known Neandertal sites, while there are more than 500 Cro-Magnon sites (Pfeiffer, 1983).

g. *A need for new food sources, ultimately resulting in the origin of agriculture.* After the colonization of new areas by *Homo sapiens sapiens* we often see a succession of food habits starting with big game hunting and ending with agriculture (Martin & Klein, 1985). As the life expectancy of farmers compared to hunter-gatherers actually *decreases* (Cohen, 1987: 269), there is no reason to assume that this series of changes is a result of "progress". Rather the changes are borne out of necessity. As Cohen (Cohen, 1977) shows the discovery of agriculture could have been the result of prehistoric overpopulation. This fits very well in the intergroup competition model, because it shows that modern humans were ecologically dominant and their numbers were not corrected anymore by "external forces".

Discussion

While the Sterkfontein research suggests that the relative vulnerability to predators may have been a difference between *Australopithecus* and *Homo*, real signs of ecological dominance are only scarce until the appearance of *Homo sapiens sapiens*. Intergroup competition may have been an important force during human evolution - as testified by some evidence of violence and autopredation in early humans.

At the time of *Homo sapiens sapiens*, however, we see a whole series of fundamental changes that very clearly show a crossing of the ecological dominance barrier and an increased level of intergroup tension. It is plausible, therefore, to assume that this increased level of intraspecific tensions is linked - via an increase in the need for within-group cooperation - to the sudden acceleration in the evolution of cultural and creative abilities of which Cro-Magnon man seems a sign.

Specifically, an increasingly sophisticated language may have enabled our ancestors to cope with an environment in which old habits of living in relatively small groups had to be abandoned as a consequence of an increasing hostile within-species environment. Paradoxically, a runaway selection for creative and moral capacities may have been the result of within-group arm races resulting from increased between-group arm races. An increase in group size as the result of arm races between groups may have given new reproductive opportunities to leaders that were able to manage such bigger groups. Their skills as leaders must have been based on the ability to manipulate the group with symbols and on the abilities to cooperate in networks, to plan forward and to think strategically. The idea is that selection on these abilities happened both within the group at the level of individuals and between groups, in the sense that groups that were better organized were able to gradually or suddenly replace or invade less well organized groups.

At this moment the idea that intergroup competition may have contributed to the evolution of the psychological make-up of our species is, of course, still a theoretical model. We have shown, however, that it can in principle be made more testable, using paleontological data. Of course, part of the evidence could also be provided by a close study of this strange living fossil, our own psyche. In spite of the difficulties in the interpretation of fossils, however, it could well be that in the end fossils provide less ambiguous evidence than the evidence provided by our own psychological make-up.

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