

Culture and the Evolution of the Human Mating System¹

Pouwel Slurink

To what extent is the human mating system 'affected' by culture and *vice versa*? Whereas some traditional cultural anthropologists tend to believe in a kind of 'super-ecological cultural variability' (e.g. Benedict, 1935), others, especially Marvin Harris c.s., have been looking for the ecological factors that cause specific local mating patterns and habits (Divale & Harris, 1976; Harris, 1985). From an evolutionary comparative perspective, it becomes important, however, to start identifying cross-cultural universals (e.g. Buss, 1989; 1994) - to locate the human life form or 'ethogram' in the evolutionary tree of possible life forms - and *only then* to try to explain local variations on those universal themes (e.g. Flinn & Low, 1986 and some the studies compiled in Betzig, 1997). If we place the variety of human societies within the frame-work of the variety of all animal societies, it becomes clear that all human societies share specific resemblances, despite the variations on which cultural anthropologists tend to focus. It can even be claimed that local variations in types of groupings in humans are not as dramatic as those of, for example, gorillas (Rodseth et al., 1991). In any case, it is clear that the relation between ecological factors and cultural variability is always mediated by an amount of 'phylogenetic inertia' (Wilson, 1975), that is by an 'underlying' human nature which has been formed by past selective forces.

Should culture be interpreted as something which is merely *superimposed* on this underlying human nature? Sometimes, this seems to be thought. For example, in an interesting article on the mating system of bee-eaters Stephen Emlen *et al.* (1995) justify their choice of this species by noting that it has a mating system that is 'largely unaffected by culture'. This can be read as implying that culture is merely a distorting factor which makes it ever and ever more difficult to grasp the 'original' human *ethogram*. If one sees it this way, however, one ignores the possibility that human culture is somehow more intimately linked to the human mating system. On the one hand, the 'original (pre-) human mating system' could have already been unique in particular aspects, and culture

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could be a result thereof. On the other hand, particular characteristics of human evolved sexual psychology and of the human mating systems may have only have emerged as a *result* of 'gene-culture coevolution' (Lumsden & Wilson, 1981) - they may have evolved relatively recently in an era in which a cultural 'accumulation' of non-hereditary information already formed an essential component of hominid life. To disentangle these possibilities we have to reconstruct the original mating system of our prehominid ancestors, to list the properties in which modern humans have changed, and to compare, select and integrate the different models that claim to explain the transition from the original prehominid mating system into the mating system that underlies modern human behavior.

A POSSIBLE LINK BETWEEN SEXUAL SELECTION AND NEOTENY

Recently, there has been a revival of interest in 'sexual selection'-based explanations of culture (e.g. Parker, 1987). Geoffrey Miller is currently refining a model in which the threefold brain-enlargement during human evolution is explained as a result of the bilateral sexual selection of the sexes or of sexual selection in which the selected properties of one sex happens to be inherited by offspring of the other sex as well (Ridley, 1993: 326-330; Mensel, 1995). Normally one would expect properties that evolve as a result of sexual selection to be represented especially in one sex, but as both sexes share most chromosomes it is at least possible to imagine the sexual selection of properties which are highly advantageous to one sex and neutral to the other sex. Miller proposes that the most important trait that has been selected during human evolution is simply the ability to produce impressive courtship displays in the form of music, dance, poetry, rhetoric, etc.. Male humans would create art and culture just 'to impress the girls', thus for the same reason that male peacocks display their feathers and ruffs defend their leks. Females would need at least some creativity too, to be able to bind the males and lure them into investing into their offspring. This is called the 'Scheherazade strategy' by Miller after the heroine of the *Arabian Nights* that had to tell the sultan a story every night to seduce him not to kill her after having slept with her. Miller claims that most artists have their peak at a relatively young age, just when they are most sexually active.

In his popular *The Red Queen; Sex and the Evolution of Human Nature* (1993) Matt Ridley connects the idea of sexual selected creativity with the already somewhat outmoded idea of neoteny, the idea that a lot of human characteristics can be explained simply by the persistence of youthful characteristics in adult life, caused by the workings of genes that slow the maturation process. He reasons that in a situation with a certain degree of monogamous pair-bonding and paternal assistance in child-rearing, males should be

particularly interested in females with a lot of residual reproductive capacity. If mating is just a transitory noncommittal activity for males, there is no reason to be selective about female partners, but the more time it takes to concentrate on one particular female and the more the road to polygyny is blocked, the more important it becomes to have as much children with one female as is possible. As a result it would become adaptive for females to look as young as is possible and 'neoteny genes' in women would continually be selected and even be inherited by their sons. As neoteny genes are supposed not only to cause someone to look younger, but also to influence her brain-body ratio and all-over behavioral flexibility and inclination to play and to learn, this would mean that they could cause an increase in general intelligence as well.

Neoteny is often too easily used as an explanation for human uniqueness, however. Brian Shea (1992) warns that theories which refer to neoteny are often too simple to account for uniquely human properties. Almost none of the morphological features associated with bipedal locomotion can be related to neoteny, for example, and while it is true that an adult human looks like a juvenile ape in that she has a relatively big brain and little prognathism, this resemblance is caused by completely different patterns of bone-distribution. Especially the construction of the pharynx of an adult human does not look like that of a juvenile ape and the evolution of speech can therefore not be attributed simply to neoteny. All in all, neoteny theory suffers from an overdose of explanatory monism and it is not advisable to invoke neoteny too much as an explanatory *deus ex machina*.

Above that, Ridley himself notes that there is a general problem with sexual selection-based theories of human evolution in that they are circular. As Hans van der Dennen notes, 'prime mover' theories of human evolution often are unable to reply to the question "What moved the prime mover?" (Van der Dennen, 1995). Ridley answers himself that evolution often is circular and works by bootstrapping. There needs not be a single cause and effect relation, because "effects can reinforce causes". "If a bird finds itself to be good at cracking seeds, then it specializes in cracking seeds, which puts further pressure on its seed-cracking ability to evolve" (*op. cit.*, 332).

Ridley forgets here, however, that birds do not "find themselves good at cracking seeds" on any given day of their evolutionary history and do not specialize apart from the rest of an ecosystem. If they change their food habits the most likely cause is a slight disturbance within the ecosystem because of geological or climatological factors (e.g. Grant, 1991). His argument that 'evolution is circular' fails because evolution is driven by a lot of external factors, be it the amount of solar energy, the composition of the atmosphere, geological and climatological factors. If something like bootstrapping happens in evolution there are always forces which set this bootstrapping process in motion.

Thus, we have to conclude that if something like the 'sexual selected neoteny mechanism' has worked during specific periods of human evolution, we still have to look for a series of environmental pressures that drove it in the first place. To be more specific,

we shall have to know why the unique combination of paternal investment and long term 'sex contracts' (Fisher, 1982) between males and females evolved as these are absent in chimpanzees and bonobos. At the moment that these 'sex contracts' were in place and males had to invest in particular females for a relatively long time, they also had good reasons to look especially for young (neotenous?) females with a lot of residual reproductive capacity. At the same time, females would have good reasons not only to look for 'good genes', but for 'good fathers' as well.

A POSSIBLE LINK BETWEEN PROLONGED CHILDREARING, PATERNAL INVESTMENT AND CULTURAL ABILITIES

As we have seen, the neoteny hypothesis itself, although it has famous proponents (Gould, 1977), cannot account for the evolution of all human characteristics. (Shea notes that it *can* account for the resemblance between the skull and face of a juvenile common chimpanzee and those of an adult bonobo, so even he doesn't exclude the possibility of the mechanism in some evolutionary trajectories.) It is easy, however, to think of other possible relations between characteristics of the human mating system and our cultural abilities. The most striking example is, of course, the extreme prolonged period of childhood dependence which seems a condition for the cultural inheritance of large amounts of skills, practices, rituals, words and knowledge. This prolonged childhood seems to result from a reduced rate of physical growth compared with apes and monkeys: for example, the permanent molars erupt at about the age of six, eleven (or twelve) and eighteen in humans, whereas they erupt at the age of three, six and eleven in apes and at the age of one and a half, three and six in macaques (Leaky, 1994; Holly Smith, cited in Walker & Shipman, 1996). Following the anatomist Adolf Schultz, these ages are taken to represent the end of infancy, the beginning of adolescence and the beginning of adulthood respectively (based on Walker & Shipman, 1996):

Figure 9.1
Age of Eruption of Permanent Molars

	Macaque	Chimpanzee	Modern human
`End of infancy', 1st permanent molar	1 years, 5 months	3 years, 4 months	6 years
Beginning of adolescence, 2nd permanent molar	3 years, 3 months	6 years, 5 months	11/12 years
`Beginning of adulthood', 3rd permanent molar	5 years, 10 months	11 years, 5 months	18 years

These figures represent a revolution which has occurred in the mating system of our ancestors. It is difficult to imagine that a chimpanzee mother, without the aid of a father, could give her child so long a period of carelessness with relation to subsistence that the child could go on learning for decades, as children in our culture often do. Of course, it is true that in many cultures the periods in which children are dependent and the amount of paternal investment are limited. Nevertheless it is reasonable to assume that there is a link between the unique property of our mating system - paternal investment coupled to an obsession with female fidelity (e.g. Daly & Wilson, 1988) - and the prolonged period of parental investment which might be a *sine qua non* for the acquisition of complex culture. Even in modern cultures, children in father-absent households do have significantly less time to stay at home and absorb culture (Chisholm, 1993). Children from unstable families tend to start their sexual and reproductive career at an earlier age (Kim *et al.*, 1997) and do, therefore, have less time for education. Children from small families, in which parents have relatively much time to invest, have more chance in getting jobs and becoming socially successful (Terhune, 1974, cited in Boy and Richerson, 1993). At the other end of our evolutionary spectrum, it has been shown that female chimpanzees at Gombe that receive generous shares of meat produce more offspring that survive (McGrew, 1992: 110 combining data from Goodall, 1986: 62, 310; Stanford, 1995).

But such a link between prolonged child rearing and the evolution of culture does not yet give an explanation for either of them. We still have to explain why some ancestral males started to invest in children and their mothers in exchange for a certain degree of paternal certainty (partly achieved by female fidelity, partly by male possessiveness which was at some later stage reinforced by the cultural practice of marriage). We have to assume that there was a period in hominid evolution that mothers simply couldn't do without the help of fathers, as a result of which children of which the mother was not able to obtain paternal investment were seriously at a disadvantage. If this was the case, however, what caused this increased dependence?

THE ORIGINAL HUCHIBO SOCIETY AND *AUSTRALOPITHECUS*

One possible explanation for an increase of paternal investment could be the increased dependence on meat. Foley speculated that 2.5 million years ago the genus *Australopithecus* was split into two as a result of the dry circumstances during the first ice ages: *Paranthropus* specialized on nuts, dry fruits and roots, *Homo* increased its level of meat intake to cope with the shortage of proteins (Foley, 1987). We now know that the chimpanzees at Gombe also hunt on a regular basis, especially during the dry season (Stanford, 1995). As I already indicated, females that are successful at obtaining meat are also the most successful mothers (McGrew, 1992: 110, Goodall, 1986: 62, 310). Also, an alpha male at Kasoje was reported to distribute meat mainly to females with whom he consorted, and to his mother (McGrew, 1992). So the necessary preadaptation's may have existed to push the common ancestor of man and chimpanzee on the road towards 'sex contracts' in which paternal investment and paternity, or even paternal certainty, are exchanged.

What were the preadaptation's that may have made such a shift possible? It has been recently stressed that the behavioral patterns of our ancestors are extremely diverse if we go back to the period in which New World monkeys and Old World monkeys were not separated (Small, 1995). In the New World monkeys we find a couple of characteristics that are typical for some hominids, for example female dispersal, the existence of groups within groups (spider monkeys, Small *et al.*, 1987), monogamy and paternal investment (marmosets and tamarinds, Hrdy, 1981; Kinzey 1987). Thus the behavioral potential of our ancestors was already rich from the beginning, as is also proved by the variety of hominoid life styles: from monogamy (gibbon) to polygamy (gorilla), from almost solitary (big males in the orangutan) to extremely social (bonobo). Such life styles are of course both a product of phylogenetic inertia and ecological factors, like the presence of predators, the threat of conspecifics and the dispersion and variety of food items.

To understand the origin of a mating system in which fathers invest in their offspring, it is probably most useful to start with a reconstruction of the behavioral patterns that we share with the species that are most related to us, the African apes. If this would allow us, for example, to reconstruct the type of society in which the common HUCHIBO ancestors lived, we could try to explain the divergence of humans, chimps, bonobos (hence, HUCHIBOs; Slurink, 1993) as a result of specific local selection factors. Of course, we are particularly interested in factors like social life, male versus female dominance, sexual dimorphism, the different types of mating relationships and the amount of paternal investment.

CHARACTERISTICS OF THE COMMON HUCHIBO ANCESTOR

Social Life

There has been a lot of speculation and research on the differences in group size between bonobos and chimpanzees: bonobos aggregate almost continually in relatively big parties. Bonobos are thought to experience less food competition as a result of their heavy reliance on terrestrial herbaceous vegetation (Wrangham, 1986), which is more evenly spread in the environment. Wrangham even speculates that they evolved from chimpanzees in the only corner of Africa's rainforest, upper Congo, where chimpanzees did not live together with gorillas and where they could conquer the gorilla niche (Wrangham & Peterson, 1996). As a result of the omnipresence of their food, compared to the fruits that chimpanzees need, bonobos are more rarely forced to travel in small groups (Chapman *et al.*, 1994). Chimpanzees live in 'fission-fusion' societies in which continually subgroups are formed, for example at a particular fruit tree of which the fruits are ripe at that moment. As bonobos are a relatively recent species, which probably has split apart from the chimpanzees at about the same time that *Homo* was splitting apart from *Australopithecus*, their group sizes and other characteristics in which they resemble humans, should be considered as products of independent evolution. Groups of the common ancestor are most likely to have been similar to those of chimpanzees. Perhaps Foley and Lee (1989) are right when they point out that the patchy grassland/bush land habitat in which they suppose that *A. afarensis* lived, would promote larger group sizes because of predator avoidance. At some later stage hunting or intergroup competition may have forced groups to become even bigger. Those groups must have formed subgroups continually, however, to form hunting parties or to patrol along the borders of the group territory. (If the idea of Aiello & Dunbar (1993) is right and relative brain size correlates with group size, groups may have become gradually bigger during the evolution of the genus *Homo*.)

Male versus Female Dominance

Differences in group and party size are thought to explain some of the behavioral differences between chimps and bonobos. While chimpanzee societies seem to be relatively male dominated, female bonds seem to be much stronger in bonobos (Parish, 1994). In chimpanzees coalitions of males seem to form a center of power in the midst of the group, in bonobos males are thought to be more markedly linked to particular females (de Waal, 1995). Male bonobos often need the support of their mothers to become powerful and males can only become dominant if they have the support of equally dominant females in the group (Kano, 1992).

These far-reaching social differences are thought to have arisen as a result of banal ecological reasons. Female bonobos are thought to be much more powerful as a result of the

omnipresence of terrestrial herbaceous vegetation: groups do not have to split each moment, which enables females to stay together and form relatively strong coalitions. Adolescent females can become part of the female social network of a group by starting an emotional and sexual relationships with more adult females. As a result of the power of these 'lesbian matriarchies', bonobo males have become much less aggressive and 'demonic' than chimpanzees. Whereas gorillas and chimpanzees both are very aggressive towards females and children, this strategy doesn't seem to work in bonobos (Wrangham & Peterson, 1997).

It is at least imaginable that there is a kind of continuum between more-female and more-male dominated social systems which both could explain the differences between bonobos and chimpanzees and particular oscillations during human history. The more female dominated social systems probably are promoted by a lack of predators (e.g. on Madagascar, Richard, 1987), relaxed food competition and a low dependence on meat; the more male dominated systems are promoted by a situation in which males can take advantage of the competition between females, by a dependence on meat or by an increased level of intergroup competition. On the whole humans seem to be more similar to chimpanzees than to bonobos in this respect. It would be interesting to investigate whether human societies which live under the threat of war become relatively male-dominated.

Feminists have often speculated about an original human society in which females were more powerful than males and sometimes they have referred in this context to the work of Bachofen's *Das Mutterrecht* (1861) which had considerable influence on Engels and thus on the Marxist tradition. Given the fact that in apes - in contrast to most monkeys - females disperse, that chimpanzee societies are mostly dominated by a small coalition of often related males and that there are no human societies which are really female-dominated, such an original matriarchical society is extremely unlikely. Even Hatshepsut could only become pharaoh by wearing an artificial beard. Whether we like it or not, there are good reasons to suppose that patriarchies are at least as old as gorillas and chimpanzees (Hrdy, 1997).

Sexual Dimorphism

Sexual dimorphism in all HUCHIBOS is relatively mild, compared by more distantly related hominoids like gorillas and orangutans. Sexual dimorphism may have been relatively big in the common ancestor of all anthropoids, because a candidate for this species, *Aegyptopithecus* who has been found in the Fayum Depression in Egypt and is dated approximately 27 million years old, shows considerable dimorphism (Fruyer & Wolpoff, 1985). In orangutans and gorillas it is relatively big. The measures of the sexual dimorphism of *Australopithecus* differ: if one uses the canine teeth it seems relatively big (Fruyer & Wolpoff, 1985); if one uses the length of the hind limb joints, it is somewhat above that of chimpanzees and bonobos, but below the sexual dimorphism of gorilla and orangutan (McHenry, 1991). On the basis of mandibular canines Fruyer and Wolpoff (1985) have

calculated a gradual decline of the sex differences from *Homo habilis* to *Homo erectus* and *Homo sapiens*, with a somewhat bigger difference in the European Neanderthals (Frayer & Wolpoff, 1985). Other authors, however, postulate that the sexual difference within the genus *Homo* were small from the very beginning (Stanley, 1996: 178-179).

Sex differences in size are often thought to correlate with the amount of polygyny. They also result in different food habits. In chimpanzees females spend much more time in fishing termites than males (McGrew 1992: 91) and females eat also more insects generally. On the other hand, it is the males who do most of hunting, especially on prey that is relatively difficult to get, like monkeys. Females sometimes catch ungulates, but generally they are more *gatherers* than *hunters* (McGrew, 1992: 103). McGrew notes cautiously that "it is tempting to interpret this difference as a possible 'pre-adaptation' for the evolution of a system of sexual division of labor" (McGrew, 1992: 105).

Unimale or Multimale Groups?

If sex differences in size correlate with the amount of polygyny, australopithecines may have been relatively polygynous, even compared to chimpanzees. According to some theorists, the fact that chimpanzees live in multimale groups doesn't prove anything about the common HUCHIBO ancestor: he can have been like the gorilla in this respect. Schröder (1993) gives three arguments for a more gorilla-like social system:

1. the remarkable sexual dimorphism in Australopithecus, "more likely indicating an intense competition between males to control access to females than gametic competition"
2. the fact that modern humans exhibit moderate polygyny, but not promiscuity
3. the fact that female gorillas do not show sexual swellings and that the sexual swellings of chimpanzees and bonobos could be a derived trait.

However, the idea that early hominids had a social structure somewhat more similar to gorillas than to chimpanzees remains implausible. Not only are we much more related to chimpanzees, as indicated by most molecular analyses (especially by those of Sibley and Ahlquist, see the list in Tanner, 1987), but one of our oldest recently discovered hominid ancestors, *Ardipithecus ramidus* (White *et al.*, 1994; 1995), displays many similarities to chimpanzees, as well. Given the fact that the environments in which chimpanzees have lived have shrunk and expanded several times, but never completely vanished, it is not unreasonable to assume that chimpanzees have not changed too much the last five million years (Wrangham & Peterson, 1996).

As I noted already, Foley and Lee claim that the patchy grassland/bush land habitat in which they suppose that *Australopithecus afarensis* lived, would promote larger group sizes because of predator avoidance. Larger group size implies that adult males must have associated together. Even in gorillas a dominant silverback male often tolerates one or more

silverbacks - one extraordinary group in Rwanda even includes seven silverbacks (Wrangham & Peterson, 1996: 147) - so even gorillas cannot be said to live in unimale groups.

Further, the discovery of the "First Family", a place where at least 13 individuals of *A. afarensis* were found together (A.L. 333) may give us a real hint of the group composition of that species. This group consisted of at least three large individuals who probably were males and at least two small bodied individuals who may have been females.

Finally, Schröder's suggestion that the human mating system could have evolved directly from a more gorilla-like polygynous system is implausible given the behavior of human females. It is a probably universal rule that the degree of female promiscuity correlates with the amount of sperm competition and, therefore, testes-size in males (Martin & Day, 1981; Harcourt *et al.*, 1981; Hrdy, 1997). If the human mating system was really only characterized by moderate polygyny, but not by promiscuity, the size of the human testes would be smaller. Given the fact that the human testes are halfway those of gorillas (small) and chimpanzees (big), it is much more plausible to assume that the human mating system has evolved out of a more chimpanzee-like, partly promiscuous system, as a result of a process of reproductive monopolization of females, which started as a result of some kind of ecological crisis.

Mating Relationships

All in all, although we don't know anything with certainty about the mating system of the original HUCHIBO ancestor and that of *Australopithecus*, we have good reason to use the chimpanzee as a model. In chimpanzees there exist three different types of mating relationships:

1. Possessive matings of Alpha males who may prevent other males from mating (and may occasionally use force or threats).
2. Opportunistic matings in which males copulate freely in the presence of other males.
3. Consortships in which a male and a female seclude themselves from the rest of society to have an exclusive relationships for a few days or even weeks (Nishida & Hiraiwa-Hasegawa, 1987: 169, order changed). Often these consortships are initiated by males and sometimes they use aggressive means to 'convince' her of following him (Wrangham & Peterson, 1996).

Because the tendency to monopolize females in an aggressive way is shared with the gorilla, this probably has to be seen as the oldest mating pattern. It is interesting to speculate about the circumstances that would promote a specialization in one of these mating strategies:

1. Possessiveness is probably favored in situations in which males are not mutually dependent, are able to monopolize as much females as possible and in which females are unable to form strong coalitions.

2. Promiscuity is probably favored in circumstances in which males are related or mutually dependent, in which aggressive possessiveness does not work as a result of female coalitions, or in which females may promote some competition to ensure fertilization by the strongest males.
3. Consortships are promoted by a situation in which females have an interest in having special relationships with particular males, perhaps because they need some extra support for their child rearing activities.

While the first strategy reminds one of gorillas, bonobos seem to have dropped this strategy altogether and to have evolved in the direction of promiscuity (Kano, 1992; de Waal, 1995). The human mating system can be seen as descending from the third mating strategy. If this is true, the human mating system may have been promoted by a situation in which females had an interest in having special relationships with particular males. This may have been the situation in which our ancestors became increasingly dependent on meat.

Paternal investment

In both chimpanzees and bonobos there doesn't seem to exist a special father-offspring bond, as it is unknown who has fathered a particular child. It may actually be in the interest of females to leave the question open as to who is the father, as an anti-infanticide strategy (Hrdy, 1981). Perhaps this can explain why infanticide in chimpanzees is much more seldom than it is in gorilla, in which about one out of every seven children is killed and in which "it looks as though most infants unprotected by a silverback are killed" (Wrangham & Peterson, 1996). However, even in a situation in which paternity is not certain, males may behave in accordance with an (unconscious) calculation of probabilities. In baboons there is no paternal certainty either, but males do sometimes help the children of their female 'friends', partly to please their mothers, partly because they might be the fathers themselves (Strum, 1987). As we noted before, in chimpanzees there is a positive relationship between survival of offspring and the amount of meat that their mothers get at kills. Sometimes alpha males share their meat exclusively with females with which they have consorted. This is especially revealing if we realize that consortships do often result in successful conception (Goodall, 1986: 471-477). Thus, although chimp behavior gives us no indication of the existence of a father-child bond in the common HUCHIBO ancestor, 'sex contracts' could have evolved as a result of an increased dependence on meat and paternal investment could have increased gradually parallel to an increased paternal certainty.

SOME CHARACTERISTICS OF THE HUMAN MATING SYSTEM

In order to be able to make a reconstruction of the human evolutionary trajectory, we first have to list some of the typical features of the human mating system which seem to have been object of selective forces during human evolution and which an adequate model should explain.

Altriciality: Helpless Infants, Dependent Mothers

It is currently thought that the increased encephalization during the evolution of *Homo*, together with the limits posed to a broadening of the hominid pelvis, necessitated a revolution in which babies were born relatively premature (an idea as old as Portman; defended by many, e.g. Waters, 1996). In fact, in comparison with other primates a species with the brain size and longevity of humans would need a gestation length of twenty-one months (Leaky, 1994). The early birth of the human baby has created a situation in which it lives as a kind of extra-uterine embryo for more than one year, during which it needs a lot of attention and care by the parents - which defines us as a clearly altricial species. Even in our modern, extremely egalitarian and efficient industrialized societies many women stop working temporarily after childbirth. In most cases fathers are sorely needed in the raising of children and some extra assistance by grandparents is very welcome as well. It is clear that this creates a social situation that is completely different from that which we see in bonobos and chimpanzees and that at best shows a dim resemblance to the behavior of a couple of new world primates.

Paternal Care

Probably about 80-90 percent of all children in all cultures have been fathered by their purported father. (Russel & Wells, 1986, estimate that 'p' or paternity certainty is 87 percent and compare this with the p of 91 percent in Yanamamo's, obtained via genetic research; Gangestad & Thornhill, 1997, point to figures from 1957 in which p was 93 percent and Bellis and Baker, 1990, found that 6 percent of a sample of British women with one main partner reported their last act of sexual intercourse to be outside this relationship). As 'extra-pair copulations' have simply to be considered part of monogamous breeding systems (this even goes for gibbons as shown by Reichard, 1995), this figure shows that it pays for human males to exchange paternal care for paternal certainty. In that respect Murdock could claim that the nuclear family was universal and that polygyny simply means that one man has more than one family (cited in Kinzey, 1987). Many psychological theories exist proposing effects of the presence or absence of the father at home (e.g. Chisholm, 1993) and there is reason to assume that the presence of a father of relatively high rank may have profound

influences of the future rank and possibilities of a human child.

Menopause

Parental care in humans often continues well beyond the age that children are able to reproduce themselves. Different authors have hypothesized that the menopause is an adaptive phenomenon enabling older women to invest in their grandchildren rather than in their own children (Williams, 1957; Alexander, 1979; 1990; Hill & Hurtado, 1991; Pavelka & Fedigan, 1991). This may have been especially functional at the moment that the mother is high in rank and has many grandchildren. Apparently a mother who gradually has lost the advantage of being young and attractive can better use her acquired wisdom and power to assist several children at significant moments in the raising of grandchildren than simply to continue exhausting her own body and having children of her own. The evolution of menopause can probably be best explained within the context of the need of an increased period of dependence of young individuals on their family and especially within the context of the increased helplessness of the babies (Peccei, 1995).

Sex Differences

Although the sex differences in size are only moderate in our species, there are a couple of important physical and psychological differences between the sexes. The physical differences can be explained as a result of encephalization (width of the pelvis) and of sexual selection for neotenus mothers (relatively light complexion of the skin, hair, breasts). A couple of profound psychological differences between the sexes are attributed to a long stage of hunting and gathering during human prehistory. Females are better at remembering spatial configurations and objects and are very good in incidental, non-directional, learning of such configurations. Males are better in performing mental rotations and (as a result of that) at reading maps (Silverman & Eals, 1992). Women do better on precision manual tasks, too, and on mathematical calculation tests. Men, however, are more accurate in target-directed motor skills, such as aimed throwing, and do better on tests on mathematical reasoning (Kimura, 1992). In the use of speech, studies of aphasia suggest that women use their hemispheres more equally than men do (Kimura, 1992) which is also consolidated by the fact that their *corpus callosum* is bigger (e.g. Moir & Jessel, 1991). One of the effects seems to be that women have less difficulty in 'finding the right word' to express their feelings and are generally more close to their feelings and to their body. Several other female psychological characteristics suggest that women are somewhat more inclined to stay at the home-base and embellish it. It may be argued that throughout a large part of human evolution, females were somewhat more linked to the home-base and relatively more involved in the raising of children, which would also explain their linguistic superiority (Dunbar, 1996).

Concealment of Ovulation and Sexual Privacy

It is generally agreed that the loss of estrus and the concealment of ovulation constitutes a major difference between chimps on the one hand, and humans on the other hand. Without calendars many women themselves do not even have the slightest idea when they are ovulating, let alone that their potential partners do know. Several hypotheses have been proposed to explain this difference; some of these are compared by Alexander (1990) who has given them eloquent names. The 'prostitution hypothesis' explains concealment of ovulation in human females as a result of the necessity for females to obtain meat in exchange for sex. Females could obtain more meat by increasing their period of sexual attractiveness (Symons, 1979: scenario A). The 'cuckoldry hypothesis' sees concealment of ovulation essentially as a female reaction to a more monogamous lifestyle. By not advertising the exact moment of ovulation females may have made it, in some situations, difficult for their partners and easy for their lovers to fertilize them, enabling them to get just the genes that they need most (Benshoof & Thornhill, 1979; Symons, 1979: scenario B; see also Schröder, 1993). Alexander's own favorite is the 'paternal care hypothesis' which stresses the ability of women to conceal the exact timing of ovulation in order to force a specific male partner to a more continuing investment (Alexander & Noonan, 1979).

An ingenious argument to explain both estrus and its loss is offered by Hrdy (1981). Hrdy argues that the promiscuity of many female primates is a very effective way of confusing the issue of paternity and reducing the possibility of infanticide. By mating with a whole series of males, all those males are forced to consider her children as possibly their own. In a situation in which females are monitored by harem leaders or husbands, the best way of continuing to confuse both those partners and extra-pair males about their possible paternity would be to conceal the moment of fertility. This would provide females the flexibility they need to spread illusions or at least confusions about the paternity of their children. Probably we should call this hypothesis the 'confusion hypothesis'.

Fortunately, gradually some new empirical discoveries have been done which may help us to choose among such hypotheses. The Austrian ethologist Karl Grammer discovered, for example, that the behavior of women may change around the time that they are ovulating as a result of a changed perception of androstenone: most of the time this odor repels them, but not so around the time of ovulation (Grammer, 1993). Grammer himself interprets this as proof for an explanation for concealed ovulation which stresses the female's chances of obtaining good genes outside the pair bond by mating quickly and at the right moment. Other researchers have shown that women can to some extent regulate the effectiveness of an insemination by having an orgasm or not (Baker and Bellis, 1993). Both discoveries can be cited as evidence in favor of a version of the 'cuckoldry hypothesis' in which even females themselves are ignorant about their own intentions.

There is also evidence which can be used in support of other models, however. For example, if one compares the sexual behavior of chimps and bonobos, it is striking that the

duration of the maximum swelling in estrus is much longer in bonobos (20 days compared to 9.6 days; Kano, 1992). Whereas chimpanzee males compete intensely for copulations at the time that ovulation approaches, bonobos are much more indifferent and do seldomly fight. It can be argued that female bonobos conceal their ovulation (Wrangham & Peterson, 1997) in order to be able to protect their choice of the right father, which in their society need not be the most aggressive male. The advertising of ovulation in chimpanzees could be interpreted, then, as an adaptation to a male-dominated society that both ensures confusion about paternity and fertilization by the most dominant males. In bonobos the most aggressive males are no longer the most desirable fathers and females do not need longer to stimulate aggression between males, they only need to confuse. This would strengthen the 'confusion hypothesis', especially for bonobos.

One can argue that humans have evolved in an opposite direction, however. As noted, humans differ from both bonobos and chimpanzees in that females need some assistance of the father in the raising of offspring. If they would advertise their exact moment of ovulation those males would not be interested anymore at other moments. Human females are therefore both attractive to males at each stage of the monthly cycle and cryptic about their exact moment of ovulation. Originally this system may have evolved out of the habit of male chimpanzees of sharing preferentially meat with females with which they have consorted. For *Australopithecus* the 'prostitution hypothesis' may have been right. During the period of encephalization (*Homo*) such ephemeral exchanges would have become insufficient for the sustainment of the dependent mother and the helpless baby, however. Instead of an exchange of one copulation and one piece of meat an exchange between an enlarged possibility of paternity and a lasting favoritism must have evolved, with a matching psychological motivation system (falling in love). For that period, the 'parental care hypothesis' could well be right.

Perhaps it even needs to be supplemented by both the 'cuckoldry' and 'confusion' hypothesis. At the moment that societies started increasingly to consist of pair-bonded couples, females could still feel that they needed the protection of the most dominant males which were not necessarily their own providers. The same crypsis which helped them to bind their permanent partners, may have helped them to get the support of these dominant males, too, and allowed them to swap partners at any moment that they found favorable.

We can conclude, therefore, that the different explanations for the concealment of ovulation do not exclude each other. If the original HUCHIBO ancestor exhibited a mating system similar to that of chimpanzees, an increased dependence on meat may well have made it more attractive to females to join males in consortships and to exchange sex for meat. These consortships may have changed into somewhat longer periods at the moment that more paternal investment was needed. Concealment of ovulation in such a situation may have helped females to keep their special friends or partners sexually interested, while at the same time enabling them to collect a set of superior genes occasionally.

THE HUNTING HYPOTHESIS AS AN EXPLANATION OF THE ORIGINS OF *HOMO*

All this suggest that the increased period of helplessness of human infants and, simultaneously, the increase in male investment has been the crucial factor which changed the mating system of the common HUCHIBO ancestor and *Australopithecus* into the human life-style. As I said already, this increase in paternal care could be explained by assuming a period of increasing dependence on meat. 2.5 Million years ago the ice ages started and Africa became drier and drier: to assume that one line of australopithecines became increasingly dependent on meat is by no means unreasonable. There is a lot of other evidence as well that could point to an increased dependence on hunting. In an analysis of the changes one would expect in a vegetarian species that is becoming carnivorous, Shipman and Walker (1989) enumerate:

1. An increasing in either speed or sociality (adaptations required to catch prey)
2. A change in either dentition or the appearance of a meat-processing industry
3. An increase in 'free' time
4. Changes in the digestive tract
5. Either a decrease in body size or an increase in geographic range as a result of the availability of less food per square kilometer
6. A change to a more altricial pattern

One could argue that one can find back at least *two thirds* of these changes in the transition from *Australopithecus* to *Homo*:

1. The increase in brain size could point to a social life of increasing complexity (Aiello & Dunbar, 1993). This increased brain size may only have been possible as a result of an availability of more proteins (Aiello & Wheeler, 1995).
2. The Oldowan stone technology featuring sharp edges capable of slicing meat appears at about the same time that *Homo* appears. Compared to the molars of *Australopithecus* the molars of early *Homo* are small, while the incisors were larger, which seems to point to a diet in which coarse plant foods are less important.
5. As Shipman and Walker notice already, geographical expansion is characteristic of *Homo erectus*. Since 1989, when they wrote their article, it appears that the geographical expansion of *H. erectus* happened much earlier than originally thought, which strengthens their argument that it results from changing food habits necessitated by the first ice age.

6. Shipman and Walker argue that the relative brain size of early *Homo* was only possible as a result of an increase in gestation length, which they see as the most unambiguous sign that it is a “herbivore-turned-carnivore!”

Shipman and Walker also mention other evidence of both increased sociality and carnivorism in *Homo erectus* at about 1.7 million years ago. They mention a female skeleton of *Homo erectus* from this period, KNM-ER 1808, with a large amount of ossified blood on her bones, which proves that she suffered from acute hypervitaminosis A and yet survived for several weeks prior to her death. They claim that the only way in which this would have been possible is if this unlucky female was supplied water and possibly food and protection from predators during this period. At the same time, hypervitaminosis A is best explained by the consumption of meat: one can get it by either eating something like one hundred pounds of carrots or by eating one pound of carnivore liver. It seems likely that KNM-ER 1808 happened to eat somewhat too much liver, as is also suggested by the micro wear of her teeth, which is comparable only to the micro wear patterns that show up on the teeth of meat-and-bone-eating carnivores, like hyenas (Shipman & Walker, 1989; Walker & Shipman, 1996).

Another change that may have been the ultimate result of a change to a more carnivorous life style is the increased dependence on a home base for the exchange of meat and other goods (Tooby & DeVore, 1986). The increased helplessness of the babies may have necessitated such a change, too. The amount of offspring that a female could raise could increase by no longer bearing them individually, as in chimpanzees, but simply ‘storing’ and feeding them at home base (Lovejoy, 1981). This tendency would reinforce the necessity of reliable paternal aid, which could only be obtained by giving the male an increased sense of paternal certainty. If *Homo* lived in a fission-fusion society centered at a homebase, this may also have created the desirability of a communication system of increased complexity, either to report on the environment *to* the ‘home front’ (Bickerton, 1990) or to form complex coalitions *at* the home front (Dunbar, 1996). If *Homo* was an efficient hunter there may also have been more ‘free time’, which could be used for ‘cultural’ displays. Of course, at the moment it is unclear whether we should project all these adaptation back as far as *Homo habilis* or *Homo rudolfensis*. They may have only emerged gradually, or as a result of additional crises.

In an analysis that still is close to Lovejoy (1981) Hill (1982) speculates that the transition to hunting would lead to male provisioning which would allow females a greater freedom to concentrate on parental care.

This change would probably reduce infant mortality considerably, and thus, the *average* life span would increase. More importantly, with a greater number of organisms living to older ages, the advantages that could be obtained from averting causes of death later in life (aging) would increase greatly and thus provide the selection pressure for greater longevity. Organisms with a longer

juvenile developing period might then be more able to outcompete other in adulthood (through learning, etc.), but such a longer period of development would necessitate an *increase* in the birth interval. This long period of juvenile dependency would, however, have an even more important consequence. If juvenile offspring had a very low probability of surviving their mothers' death at, for example, under ten years of age, it would be an unwise strategy for a female to continue to bear offspring when the probability of her death within the next ten-year period was quite high. Old females with a low probability of surviving another ten years should shift their reproductive strategy. The optimal strategy for a female under these conditions is to assist in the parental care of her own daughters' offspring, and to cease reproductive effort herself. (p. 539)

Thus, a whole set of human characteristics seem to be explained by applying a version of the hunting hypothesis. Above that, it is strengthened by the analysis of fossilized bones and stone artifacts from several sites along the African Rift Valley (e.g. Bunn & Kroll, 1986).

Of course, as is well known, these same bones and artifacts are sometimes used to defend the hypothesis that early man was a scavenger, but several writers have pointed to the fact that this would bring our ancestors in serious competition with a list of other scavengers (Tooby & DeVore, 1987; Walker & Shipman, 1996). Above that, scavenging and hunting are completely compatible and both chimpanzees (Hasegawa *et al.*, 1983) and Hazda hunter-gatherers in northern Tanzania (O'Connell *et al.*, 1988) use both techniques at the same time, although scavenging in the Hazda accounts for only 20% of the carcasses and scavenging in chimpanzees is only rarely observed. The same pattern is found at the middle Pleistocene site at Aridos (Spain), where undisputed proof of elephant butchery was found which differs fundamentally from marginal scavenging (Villa, 1990). It should also be noted that many predators, from buzzards to lions, occasionally indulge in scavenging.

Another question is whether meat has ever been the exclusive nourishment of our ancestors (Tanner, 1987). This is unlikely as we have a maximum sustained protein intake below about 50 percent of calories. It is even speculated that the ability of Eskimo's to live on a diet with a protein intake of about 45-50 percent is due to a unique genetic capacity not seen in other populations (Speth, 1989). To discover the difference between the diet of a hominid and a real carnivore one only has to compare one's dinner plate with the bowl of one's cat. Of course, as KNM-ER 1808 and the modern race of Hamburger-eaters demonstrate, meat is sometimes eaten more than is healthy and often is venerated as a supreme source of energy. As both chimpanzees and hunter-gatherers are predominantly vegetarian, the safest conclusion is that our ancestors have always been opportunists. Meat, however, may have enabled them to survive during periods of the ice ages in which the dry season became relatively long and exacting and, at a later stage, during the long winters on the Eurasian continent.

DOES THE HUNTING HYPOTHESIS EXPLAIN THE ORIGINS OF CULTURE?

This brings us to the question whether the hunting hypothesis can explain the origins of culture. To some degree, it can. Hunting may have afforded the extra proteins needed to grow a big brain; it may have necessitated a more complex stone industry; it may have encouraged increasing cooperation and the need to pass on skills and techniques from generation to generation; it may have encouraged the use of complex communication. Indirectly, it may have brought together individuals from three generations, thus encouraging cultural transmission. Finally, it may have eventually stimulated the occupation of home bases at which individuals from different generations could pass on their skills.

Hunting may not have been the only occupation of early *Homo*, however. Several writers have stressed that gathering may have been as important and that chimpanzees use tools predominantly in the context of nut-cracking and insect-collecting (Tanner, 1987). Living along the border of tropical forests, the first step that may have enabled *Australopithecus* to live in a relatively dry environment may have been the opening up of new food sources below the ground: roots. In fact, in Tongo, a forest in eastern Congo with almost no rivers and lakes, a small population of chimpanzees lives with a tradition of digging and eating roots as a local adaptation to water shortage (Wrangham & Peterson, 1996). It seems that the skill of root-digging is complex enough to stimulate a new dependence on the acquisition of skills through social learning - mainly between mother and offspring -, as envisioned by Parker and Gibson (1979) and King (1994). From this perspective, the fact that *Australopithecus* has a brain that is slightly larger than *Pan* can be explained. Australopithecines may have been dependent on foods which were already hard enough to get to force them to relatively intelligent behavior, which may have pre-adapted particular populations for the even more demanding task of hunting and the processing of meat and bone-marrow.

All in all, we can conclude that an increased dependence on 'difficult' food sources, necessitating 'extractive foraging' (Parker & Gibson, 1979), may have forced our ancestors to become smarter. Parker and Gibson even postulate that such a transition may have furthered their linguistic proficiency:

The prehistoric ecological transition to extractive foraging on foods that were both difficult to obtain and process would have resulted in mandatory parental provisioning of post weanling children. Abortive attempts by children to open tough nuts, dig deep tubers from the ground and engage in other complex activities would have resulted in need for parental aid. Many parents would have anticipated their children's difficulties in accomplishing these tasks and would have come to their aid as soon as interest was evidenced by the child by pointing, vocalizing, reaching, etc. The probable result would have been that certain vocal or manual gestures would have acquired specific meaning within individual mother-infant pairs. (p. 374)

A couple of questions remain, however. The first is why big brains and culture did not arise during the evolution of *Australopithecus* already. This question was given a first sketchy and speculative answer by Stanley (1996) recently: their brain-sizes may have been limited, because they were unable to care for the helpless infants that need to be born if baby's with big brains have to be born. As australopithecines probably were still partly adapted to a live in the trees - in which they had to fly for predators - they did not have their hands free to carry such infants. Only as a result of a climatic change that created an environment with less trees and with less food generally, was a small population of australopithecines forced to start specializing increasingly on meat during the dry season, while they were unable to climb back in the trees for safety. The same skills that may have allowed them to hunt in groups may have enabled them to defend themselves from predators.

The second question is why our culture is so complex if it only evolved to enable us to hunt and why we tend to live in groups that are much bigger than would be efficient for group hunting. Obviously, living in relatively big groups has many disadvantages, especially for hunters. Above that, as is shown by a variety of carnivores, one certainly needs to be clever to be able to hunt, but one does not need to be able to write poetry. Why would humans have started to live in groups of increasing size and why would their brains have become bigger and their culture much more elaborate than would be required for mere hunting?

THE INTERGROUP-COMPETITION HYPOTHESIS

Alexander, who together with Noonan, developed the 'paternal care hypothesis' to explain concealed ovulation thought the hunting hypothesis insufficient to explain the 'uniquely unique' characteristics of our species and developed the theory of intergroup competition or balances of power (e.g. Alexander, 1990; van der Dennen, this volume). The idea is that our ancestors at some time in the past became "their own hostile force of nature" and that an arm race resulted between neighboring cultures which forced them to progress in both within group cooperation and in the development of weapons, new ways of food production, the creation of cooperation-stimulating myths, etc. The model depends to some extent on the notion of 'ecological dominance' (e.g. Alexander, 1990), because it presupposes an uncorrected population pressure.

As I have shown elsewhere (Slurink, 1993, 1994), there are few signs that the necessary 'ecological dominance' was really achieved in early *Homo*. Also, one would expect a transitory stage in which an ecological dominant predator first became gradually more dangerous. Therefore, I do not see the hunting hypothesis and the intergroup competition hypothesis as incompatible, but only as referring to different phases of the evolution of the genus *Homo*. An increase in parental care and a home basis to exchange food and to protect increasingly helpless juveniles can already have been a characteristic of a

carnivorous primate like *Homo ergaster/erectus*. A situation in which there were no longer other predators powerful enough to cope with *Homo ergaster/erectus* and its protected home bases, can have given rise to increased competition for favorable sites and for the necessity to join relatively big and strong groups.

Thus home bases may have played a crucial role during human evolution. During the transition to a life-style as hunter it enabled our ancestors to find a place to exchange food; gradually it became more important as a place where children could be reared and protected, but finally, it became itself a scarce resource and the object of competition among different groups. Only this last factor can explain adequately why group sizes in our species seem to be above the optimum with relation to cooperative hunting (Alexander, 1979). Above that, only this last factor can explain a tendency to socially respected monogamy.

PAIR BONDS AND REPRODUCTIVE-OPPORTUNITY REWARDS IN A MULTIMALE SOCIETY

All in all, the pattern that suggests itself is that man started as a predator, but at some relatively late point in prehistory increasingly turned into a warrior. Probably this can help us to explain the typical paradox of a species in which males to some extent mutually respect each others' relationships to particular females. The external pressure of a threat from foreign groups created a situation in which group members became mutually dependent and were forced to extinguish sources of intragroup conflict like conflict over females. There was a need for rules that would curtail an escalation of intragroup conflicts and a tendency towards 'reproductive opportunity leveling' (Alexander, 1987) would do so.

At first sight the concept of reproductive opportunity leveling might seem an artificial *deus ex machina*. However, one can find many examples in the anthropological literature that show how it might work. For example, the Mehinaku of Brazil have very outspoken ideas about what it is to be a real man: a real man is someone who is not lazy, who regularly provides food for the people and who shares it altruistically. A real man is also a good wrestler and a strong personality. Anyone who doesn't fulfill this image is looked down upon by both men and women. The important point is that the women of these disrespected men, as a result of this lack of respect, also deceive them. To cite David Gilmore (1990, who uses studies of Thomas Gregor): "The sexual norms of the Mehinaku allow tacitly that a woman deceives a bad wrestler. Knowing this, most of these women have adulterous relationships while their husbands are sulking helplessly." The important point is, of course, that a bad wrestler also makes a bad warrior and that the norms of manhood refer to some extent to cooperativeness and potential heroism.

This is even more clear in the Yanomamö, of which Chagnon has shown

(Chagnon, 1988) that men who have made most victims in intergroup conflicts, that is the best killers, also have the most women. Of course, it would be important to show that cowardice and desertion is also punished and thus that satisfying to the norm of the society is thus the only way to be reproductively successful.

Perhaps these examples show that Alexander's concept of 'reproductive opportunity leveling' is not entirely correct. Probably it should be replaced by 'reproductive opportunity trading' or even by the idea of a 'reproductive opportunity reward system'. The point is that not anyone in a society gets reproductive opportunities, but that the coalition of dominant individuals awards those men that they find helpful or indispensable. We should not forget that the balance of power model is not a model of Wynne-Edwardsian group selection, but a model explaining why human societies are characterized by so much moralistic aggression towards non-cooperators and why such a relatively high level of cooperation can be achieved among nonrelated individuals.

The idea behind the model of Alexander is that the only way in which a multimale society in which paternity was totally uncertain could turn in a society in which paternity is certain, but in which children are nevertheless safe for other males, is by introducing an extra motivation for males to cooperate. To cite Alexander:

Prevention of infanticide, ... , would be a massively important way that a male might help his female and the offspring he sires. Suppose a female begins to restrict her copulations, excluding certain males or excluding all but a single male. In a primate resembling chimpanzees we are justified in assuming that such female would place her offspring in jeopardy of infanticide by the disenfranchised males within her own group. Because of her loyalty to the male who mated with her, it would profit him to defend her offspring against attack, at least under circumstances where this would not have been the case before, and assuming that his loyalty had some chance of being effective in preventing infanticide. If unity among males is sufficiently important, then rudimentary social reciprocity among males in connection with defense of the group or the 'exporting' of aggression (...) could cause a male's importance to the group, and the importance of overall amicability among males, to prevent males who could not copulate with a particular female from attacks on her offspring or on the male who undertakes to defend them. Obviously respecting the right of the offspring of other individuals or families to exist and go about their business is also part of the social cooperativeness - the moral system - of humans today. (Alexander, 1990: 32)

CONCLUSION

As might be expected from an evolutionary perspective, human culture seems to be the coincidental product of a series of cumulative adaptive changes. These may have started as a result of ecological instability (Potts, 1996), which forced particular groups of chimpanzee-like HUCHIBO-ancestors to open up new food sources, which required new cognitive abilities. Probably the genus *Homo* resulted from a group of australopithecines that no longer was able to retreat into the trees and that became increasingly dependent on meat at the beginning of the ice ages. The birth of helpless children stimulated the origin of more or less exclusive pair-bonds within the multimale societies of these early humans. At some later stage these pair-bonds may have been one of the most important requirements of more complex societies, because they enabled the origin of a 'reproductive opportunity rewards system' which allowed the evolution of a complex division of labor. The increased internal complexity of societies was probably driven by arms races between such societies, which resulted from the ecological dominance which was achieved by *Homo* at some point during prehistory.

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