8 By Way of Summary: An Evolutionario

8.1 Introduction

The time has now come to put all the separate pieces of the jigsaw puzzle together for a panoramic view of mankind, its place in nature, and its capacities for violence and warfare as well as peace.

In this, final, chapter, I shall argue that the complex of collective behaviors we call war evolved as a facultative male-coalitional reproductive (or parental investment) strategy. In order to understand this prima vista rather exuberant claim, I shall spell out in some detail how and why this strategy came to be, and why it, within the logic of selection, was overdetermined and so good as inevitable. Via a nearly similar trajectory some communities of chimpanzees evolved ‘lethal male raiding’, while the other pongids (gorilla and orang-utan), lacking some necessary preadaptations, evolved rape as an equivalent reproductive strategy at the individual level, as did a number of other vertebrates (see van der Dennen, 1992).

The war strategy was a novel pattern which tapped into a number of phylogenetically old adaptive behavioral systems (e.g., the agonistic system), but it was not simply an extension of the agonistic system. It also, and a fortiori, required the existence of recently acquired patterns, notably polyadically-coalitional cooperation, cultural badges as markers of group identity and ethnocentrism, social and operational intelligence and artifactual weapons; among others. It was not only a novel pattern, it was also ‘invented’ or stumbled upon by very few, typically brainy, species, which may explain why it arose so late on the evolutionary time scale.

Alcock (1979) reasoned that the evidence indicates that the genotypes of humans do not blindly program them to engage in warfare. Some ecological circumstances may, however, elevate the benefits of warfare to individuals to such an extent that they exceed the costs to individual inclusive fitness. Tragically, and perhaps paradoxically, warfare as organized and premeditated lethal group violence, is promoted by the cooperative abilities of the members of each warring group. Humans and chimpanzees also belong to the most unaggressive and nonviolent species within their own community. Both species, moreover, possess a rich repertoire of reconciliatory behaviors that serve to counteract disruptive violence and maintain or restore social harmony and promote cohesion among community members (Goodall, 1986, 1990; de Waal, 1989). There is no need to postulate a Beast Within to explain the
evolutionary origin of war.

In the evolutionary scenario, or evolutionario for short (Wrangham, 1987), we have to meticulously reconstruct the hominid/human evolutionary trajectory from its humble beginnings onward. In order to do that we also have to revivify the hominid-pongid common ancestor, by means of phylogenetic comparison (Tooby & DeVore, 1987; Wrangham, 1987), as a starting point of the specifically hominid/human trajectory. The best methodology to accomplish this is 'strategic modeling'; the development of principles of behavioral ecology (or socioecology) and evolutionary psychology that apply across taxonomic groups, and hence can be used to reconstruct (aspects of) hominid behavior (Tooby & DeVore, 1987).

In order to transcend the level of gratuitous just-so stories the evolutionario should meet the following three 'rules of the game' (Symons, 1979) and four criteria (Slurink, 1994; Tooby & DeVore, 1987):

1. Teleological explanations are not permitted; 2. No superorganic force is to be invoked as a *deus ex machina* to explain evolutionary change; 3. Behavior and mind are to be explained as adaptations to promote the inclusive fitness (i.e., reproductive success) of the individual, and not to promote the fitness of abstractions like society. It is also understood that what inclusive fitness optimizing is at the ultimate level, utility optimizing is at the proximate level. Furthermore, the evolutionario should be 4. phylogenetically plausible; 5. paleontologically adequate; 6. evolutionarily feasible; and finally 7. it should exhibit explanatory specificity (i.e., it should not only explain why hominids/humans and chimpanzees evolved 'lethal male raiding', but also why the other primates, and mammals in general, did not).

Hominization was, in all probability, not a single process but consisted of a number of discrete stages characterized by sharply differentiated selective forces and adaptive complexes: "Both socioecology and the increasingly complete stratified fossil record require that hominid evolution be regarded as a discrete series of branches and stages. In the first place, the discovery that hominids were fully bipedal at 4 million years (Johanson, White and Coppens, 1978), long before the appearance of the first detectable stone tools, has decoupled Darwin's compelling trinity of bipedalism, tool use, and brain expansion, at least in any simple form, and thereby made bipedalism the original trait requiring independent explanation. Second, the simultaneous and possibly sympatric existence of several hominid species in the 2 million year range is a fact which, by itself, destroys the linear model of human evolution" (Tooby & DeVore, 1987; Cf. Foley, 1987).

Furthermore, because a species’ adaptations form a coevolved and coadapted system, only some clusters of traits are mutually consistent with each other and therefore acceptable as models.

What could be appropriate analogues and models for events and processes in
early hominid evolution? Do contemporary hunter-gatherer societies provide suitable material for drawing parallels?

Contemporary populations of hunter-gatherers are virtually confined to areas that are currently marginal to agriculture, and furthermore do not live in a world of hunter-gatherers and nonhuman competitors as the early hominids did, but in a world dominated by agricultural and horticultural food producers.

The use of contemporary hunter-gatherers as a model for early, pre-sapient hominids involves crossing taxonomic boundaries. They are not only members of different species, they have also undergone their own subsequent evolutionary and historical trajectories and developments. Simplistic hunter-gatherer models have been heavily criticized for being based on outmoded notions of cultural evolution that place living hunter-gatherers in a primitive, ancestral state as 'living fossils' (Lafitau, 1724; Morgan, 1877; Lowie, 1937; Freeman, 1968; M.Harris, 1968; Testart, 1978; Schrire, 1980, 1984; Berndt, 1981; Shipman, 1983; Fedigan, 1986; Foley, 1987, 1991; Myers, 1988; Headland & Reid, 1989; Musonda, 1991, a.o.).

The alternative source of analogue models is nonhuman primatology, but many problems arise here as well. While we share a close phylogenetic relationship and evolutionary history with other primates, they too have evolved in response to their own, unique, evolutionary context. Apes and monkeys are not just hominids manqués, they are species as well adapted to their niches as the hominids were to theirs.

Analogies may be based on either phylogenetic or socioecological similarity. Historically, chimpanzees and baboons respectively have been taken as models for the two roles, but again there are problems with this approach, because evolution is the result of interaction between phylogeny and environment, and for every species this produces a unique set of circumstances (Foley, 1987).

Because of the limitations and difficulties provided by the analogue models, 'strategic modeling' has been proposed as the sane alternative.

But let us begin at the beginning of the story.

8.2 Prelude: Humble Beginnings

Taxonomically, humans belong to the Kingdom Animalia, the Phylum Chordata, the Subphylum Vertebrata, the Class Mammalia, the Subclass Eutheria or Placentalia, the Order Primates, the Suborder Anthropoidea, the Superfamily Hominoidea, the Family Hominidae, the Genus Homo, the Species sapiens, and the Subspecies sapiens. Each of these categories has uniquely contributed some morphological and/or behavioral features to what we are here and now.

Ever since a molecule for the first time started to replicate, i.e., to make copies
of itself, life existed on earth and, with it, the process of natural selection. Those self-replicating molecules (let us call them proto-organisms) which reproduced fastest or most efficiently, inevitably became the most numerous in the population of self-replicating molecules. From a Darwinian perspective the defining property of life is self-replication; any organism is a self-reproducing entity or 'machine'. It is important to understand that organic life as we know it - with its nucleotides, proteins, DNA, etcetera - is not essential in this conception: The principles and the logic of Darwinism would apply equally to self-reproducing robots. The matter of self-replicators is immaterial. The process of natural selection is an inevitable concomitant of reproduction and inheritance whatever chemical composition the reproducers are manufactured of. In any pool of self-replicators, some will replicate faster or more efficiently than others - and maybe even at the expense of others - and their replicas will eventually prevail (e.g., Dawkins, 1976 et seq.; Slurink, 1989, 1994; Tooby & Cosmides, 1992).

Natural selection also explains the existence of goal-directedness or teleonomy (not to be confused with teleology) in nature. The design of organisms will more and more reflect their 'purpose' to replicate themselves; their structure will increasingly behave as a program for optimal self-replication (Pittendrigh, 1958; Mayr, 1974 et seq.; Slurink, 1989, 1994). In other words, "Natural selection guides the incorporation of design modifications over generations according to their consequences on their own reproduction. Over the long run, down chains of descent, this cycle of chance modification and reproductive feedback leads to the systematic accretion within architectures of design features that promote or formerly promoted their own propagation" (Tooby & Cosmides, 1992). So, we can be reasonably certain that selection will act on any feature to the extent that it has a significant effect on reproduction. Differential reproduction, reproductive success is the currency in the calculus of evolution by means of natural selection, not, as was formerly thought, differential mortality.

Life on this earth undoubtedly originated in an oxygenless (or -poor) and aquatic environment, and certain of the earliest organisms, the cyanophytes or blue-green algae, played a crucial part in producing, after about a thousand million years, the oxygen-rich atmosphere as we breathe it by releasing gaseous oxygen as a by-product of the process of photosynthesis. The earliest cells had no nuclei. There were two groups of these prokaryotic cells; bacteria and cyanophytes. All other organisms (plants, fungi, protozoa, metazoa) are eukaryotic: Within each cell they have a membrane-bound nucleus containing the chromosomes and various other structures and organelles, such as mitochondria, which prokaryotes lack. The eukaryotes generally exchange genetic material by means of sexual reproduction. The evolution of the eukaryotes from prokaryotes was, together with the so-called Cambrian explosion (in which all the major radiations of multicellular architecture occurred in a relatively short period) about 530 million years ago (mya), one of
the most significant - and puzzling - events in the earth’s history (e.g., Leakey, 1979; Gould, 1994). These events should, however, not be construed as evidence of inevitable progress and complexification inherent in the evolutionary process; on the contrary, the great success story of life’s pathway were, are, and will be the bacteria.

Cell membranes, eukaryotic (about two billion years ago) and multicellular (about 600 mya) organisms - increasingly complex ‘survival machines’ for the replicators - may have evolved as a direct consequence of competition between similar replicators. Competition is a universal aspect of life because organisms are basically selfish (i.e., they are ‘programmed’ to propagate their own genes, not somebody else’s), and they have incompatible and conflicting goals, needs and demands in a world of limited resources; they are indeed, as Spencer and Darwin acknowledged, engaged in a continual struggle for existence. The more (phylogenetically) related and (specifically) similar organisms are, the more they tend to compete for the same resources - which is one of the reasons why intraspecific aggression (a behavioral strategy in the service of contest competition) is ubiquitous at least in the ‘higher’ organisms (the phyla arthropoda and chordata [e.g. Scott, 1969]).

From the time of these humble beginnings, organisms had two viable options, two different strategies of life regarding their energy supplies (ignoring for the sake of argument, that intermediate life forms can and do exist). Plants we call those organisms which are autotrophic (bind solar energy by means of photosynthesis for their growth and reproduction), and are relatively immobile. Animals we call those organisms which are heterotrophic, i.e., which parasitize on plants (herbivores) or on each other (carnivores) for their ‘fuel’. The parasitic lifestyle is incompatible with the immobility of the plants. Slurink (1994) explains this with great clarity:

"To collect enough fuel to grow and reproduce, it may be necessary to move and look around. But moving and looking around pose new energy problems, for which the most natural solution may be to steal the energy which another parasite has collected. But other parasites may have found that solution as well. So, there is an extra reason to be mobile: to prevent other parasites from using your valuable life as fuel. Animal mobility, therefore, can be interpreted as an optimal strategy that allows individual survival machines to collect fuel without being collected as fuel themselves".

Besides these problems of survival, there is one other problem: A mobile organism needs information about the outside world, about its position and orientation in relation to its immediate surroundings. Sensors and receptors sensitive to certain patterns of variability of physical properties of the environment (e.g., light contrasts, sound waves, etc.) thus evolved as part of the emergency or alarm systems of the mobile survival machines. The more sensors and receptors an organism has at its disposal, the greater the need to coordinate, synchronize, make sense of, and adequately react to, the various
information flows. Therefore central nervous systems and brains evolved as coordinating sensory information and motor control centers.

It is important to understand that brains did not evolve to think, or solve academic puzzles, but to act, or at least to make optimal decisions for the animal to act upon in the light of its survival interests. The picture of the outside world the senses and the brain reconstruct from the signals they receive has only to be ‘adequate for survival’ (überlebensadequat: Vollmer, 1983), not to provide deep insights into the objective world an sich.

This helps us to understand why all knowledge arises from evaluative perspectives, or from subjects that select world signals like sieves and transform them according to the meaning they have in the light of their interests. The animal only needs to know its own part in the universe, and this knowledge must direct its behavior. So, everything the animal encounters must be valued from the viewpoint of its survival interests. This may also explain the evolution of emotions and of consciousness. Pugh claims that emotions can be compared to the values that govern decisions in the so-called ‘value-driven decision system’ (Pugh, 1978)...

Pugh proposes that a key problem for an imaginary ‘evolutionary designer’ is that one cannot predict the situations that an animal will encounter. The program of a survival machine with only a fixed set of responses will result in a high number of wrong decisions. Thus, the evolution of a more flexible decision system in which alternatives can be weighed in relation to their contribution to evolutionary goals and subgoals becomes understandable (Slurink, 1994).

The human being likes to think of itself as the tabula rasa organism par excellence. There are sound theoretical reasons, however, why such a blank slate organism (i.e., an organism without some kind of value-driven decision system) could not possibly evolve. Consider the evolutionary fate of an organism that would not immediately and appropriately react to any contingencies in its environment - the appearance of a predator, say - but instead would sine ira et studio contemplate the potential impact of this event.

In order to contribute to survival, the emotions - the values of the value-driven decision system - must have a compulsory character: They must be able to force the organism to behave in an appropriate and adaptive fashion. Similarly, consciousness may be expected to be linked with emotions more than with pure informational or cognitive content.

Besides mobility, it paid off in terms of reproductive success to develop behavioral systems of self- and offspring defense and improved competitive abilities, in brief: Aggression (extensively discussed in former chapters).

But first let us explore why some of these organisms ‘invented’ sex (or, technically, amphimixis; see especially Ghiselin, 1974) as a reproductive strategy, and why the combination of sex and aggression is such an explosive
8.3 Why Did Sex Evolve?

In the view of modern evolutionary biology, organisms are just temporary biodegradable vehicles with only one purpose: To transmit their genes to future generations. The organism is ephemeral and mortal. The genes are, in principle, immortal and have the 'selfish' interest (due to their biochemical properties) of spreading as many copies of themselves as possible. Natural selection in fact selects for Reproductive Success (RS).

Many organisms, such as protozoans, have reproduced, and still reproduce, asexually, by means of budding, fission or parthenogenesis, and they have been doing so successfully for millions of years. Then what is so special about sexual reproduction (needing two different morphs who each contribute only one half of their genes to the offspring), the way all animals best known to us, the mammals, and we ourselves do it? This question becomes especially enigmatic when we realize the costs involved in sexual reproduction. Sex is wasteful and inefficient: It uses energy, materials and time; and the highest cost of all is the damage, wounds and even death incurred in the cut-throat competition for mates.

Crow (1987) and Stearns (1988) summarized the costs and disadvantages of sexual reproduction and recombination as follows:

1. Sexual reproduction is not very efficient qua reproduction. The time and energy required for meiosis and syngamy are substantial. As a means of multiplication, many asexual systems are more effective and less error-prone.

2. With anisogamy and separate sexes there is the cost of males. A female that could produce female progeny asexually with the same efficiency as by fertilization would have a twofold advantage.

For bacteria and single-celled organisms, the principal cost of sex is probably the time it takes to carry out recombination. This can lengthen the normal cell division time by a factor of two or more. In anisogamous species - all 'higher' plants and animals - the female provides cytoplasm to support the male genome. This results in the twofold cost of males, or cost of genome dilution. Compare a sexually reproducing female with an asexually reproducing female. Suppose that all offspring cost the same amount in both cases. The sexually reproducing female has offspring that are half male, half female. The asexually reproducing female has offspring that are all female, each of which also reproduces asexually and replicates her entire genome. Because she produces twice as many female offspring, after, for example, five generations she should have 32 times as many female descendants, each of which will also contain a complete copy of her genome. Not only does the sexually reproducing female make only half as many female offspring per generation; each of them contains
3. With sexual reproduction selection acts on the genic or additive component of the genetic variance, whereas selection among asexual individuals acts on the genotypic or total genetic variance. If the genetic variances are the same, an asexual species can respond more rapidly to selection - at least for a limited time.

4. If dominance and epistasis are present, there may be segregation and recombination loads.

5. Free recombination does not provide a way for two or more rare genes that are individually deleterious, but collectively beneficial, to spread through a population.

6. There are well-established examples of situations in which there is a clear advantage in holding certain genes together. Sexual reproduction regularly breaks up such favorable gene combinations.

It was these costs which first convinced G.C. Williams (1975) and Ghiselin (1974) that the prevalence of sexual reproduction poses a serious problem for evolutionary theory. The advantages of sex to the individual have to be very large if sex is to be maintained by natural selection in any population in which parthenogenesis can arise. What could the possible benefits be that transcend the substantial costs involved? Why did sex(ual reproduction) evolve?

The usual textbook answer to this vexing question is: "For the preservation of the species, of course". And, like so many textbook answers, it is wrong. The answer is based on the, still very en vogue, so-called 'group-selection' paradigm (see Ch. 1). The first problem with the traditional explanation in terms of group selection is, Stearns (1988) explains, that group selection - or in this case, selection of the attributes of species - does not work under most circumstances. The reasons for this are as follows:

1. Selection pressure on a trait is proportional to the amount of variation in reproductive success among individuals that can be accounted for (a) by variation in the trait in question, divided (b) by the generation time (In this case, the variation would be between sexual and asexual individuals).

   1a) Generation times of individuals are much shorter than lifetimes of species - by a factor of 10,000 to 100,000 for most eukaryotes. Thus selection pressures on individuals are correspondingly much larger than selection pressures on species.

   1b) The response to selection depends on the amount of heritable variation available among the units selected. There is much more variation available for selection among individuals within a sexually reproducing species than there is among species within a lineage. Therefore the response to selection is much faster and larger for individuals than for species.

2. Thus selfish individuals can always outcompete individuals that sacrifice their own interests to those of the species. If asexuality is an advantage to an individual, and sexuality an advantage to the species, then we should find that
most organisms are asexual, for only rarely would the advantages of sexuality be so strong that species selection would overcome individual selection.

So, once again, why did sex(ual reproduction) evolve if not for the good of the species? Although some asexual species have apparently survived for very long times, this is not the general rule. Asexually reproducing species may well have immediate evolutionary advantages, but must be less successful in the long run. The prevailing view is that asexual species are less able to keep up with environmental changes than are sexual ones.

The three arguments for the evolutionary advantages of sexual reproduction are (1) adjusting to a changing environment, (2) incorporating beneficial mutations, and (3) getting rid of deleterious mutations (Crow, 1987).

In practice, the advantage of being asexual is rarely twofold. In most animals the transition to asexuality is difficult. In small organisms the actual costs of sex are reduced by intermittent sexuality - a series of asexual generations followed by an occasional sexual generation. In large organisms, such as mammals and birds, the realized costs of sex are quite small because sexuality is fixed in these lineages. Because the asexual option is simply unavailable, mutant asexual competitors cannot invade.

The major contemporary hypotheses for the maintenance of recombination are:

1. **The Tangled Bank’ hypothesis**: The production of genetically diverse offspring is advantageous in an environment that is saturated, heterogeneous, or both. Ghiselin (1974) appears to have priority for this idea, which was further developed by G.C. Williams (1975), Maynard Smith (1978) and Bell (1982). Bell named it the Tangled Bank hypothesis, after the closing paragraph in Darwin’s *Origin*.

2. **The ’Red Queen’ hypothesis or Coevolutionary Arms Race** (so called after Lewis Carroll’s *Alice in Wonderland*, in which the Red Queen has to run very fast in order to stay in the same place): The idea that recombination is an advantage in a coevolutionary race against competitors, predators, parasites and disease organisms has been brought up repeatedly. Disease organisms and parasites have a fundamental advantage in an evolutionary arms race. They can adapt themselves quickly to a specific host genotype. This brings the host population under strong frequency-dependent selection, for it pays to have a rare genotype during an epidemic (See especially Ridley, 1993).

3. **DNA Repair Mechanism**: The advocates of this hypothesis postulate that recombination evolved as a mechanism by which damage in one chromosome could be repaired by information from the homologous chromosome. This advantage was later followed by biochemical complementation between the homologous chromosomes that exploited the redundant information available in the diploid genome.

The ’Red Queen’ hypothesis seems to be the most viable at the moment (e.g., Hamilton & Zuk, 1989; Hamilton, Axelrod & Tanese, 1990; Ridley, 1993).
8.3.1 Why Only Two Sexes?

Biologically speaking, a female is by definition that sex that specializes in the production of a few, large, nutritious, and relatively immobile gametes (ova), while the male is by definition that sex that specializes in the production of a huge quantity of small, non-nutritious, motile gametes (sperm). Imagine an initial isogamic population in which individuals differ slightly in the size of gametes they produce. Some individuals will produce large gametes with high prospects of survivorship as zygotes, others will produce many smaller gametes with poorer prospects of survival. Most individuals under the normal distribution curve produce intermediate gametes. With random fusion of gametes, such a system stabilizes over time - via a transient bimodal distribution - with mainly two genotypes (males and females) in a 1:1 ratio. As Parker (1984b) explains: "The third genotype tends not to be represented either because it arises as the rather inviable product of the fusion of two 'proto-sperm' or because it is formed by the fusion of two 'proto-ova', depending on dominance. This latter fusion is rare because most gametes fuse with small gametes because of their numerical predominance. After several generations, the population is essentially anisogamous as a result of disruptive selection". This means that the final result of this process is the existence of two discrete and non-overlapping distributions of ovum-producers (females) and sperm-producers (males). In other words, the Evolutionarily Stable Strategy (ESS) in this case is the stable coexistence of two morphs for gamete size. "Sperm producers survive by parasitizing the investment of ovum producers; the ESS solution (stable anisogamy) is essentially driven by sperm competition" (Parker, 1984b).

But what if for whatever reason a third breeding morph arose in such a population, or that there would be three sexes: X, Y and Z, with mating patterns XZ, YZ, and XY? In that case a minimal selective advantage of one sex or zygote would eventually outcompete the others (simply by being more prolific), and again the final result would be two sexes.

Why is there a fifty/fifty sex ratio; why are there approximately equal numbers of each sex? This puzzle was in principle solved only in the 1930s by R.A. Fisher, and is accordingly called 'Fisher's principle'. When one sex numerically predominates in a population, it becomes advantageous for parents to invest in the opposite sex because that maximizes their offspring’s reproductive success. With a preponderance of females, investment in males will ensure high opportunities for fertilization; and, conversely, with a preponderance of males, investment in females will produce the highest pay-off. This mechanism eventually stabilizes the sex ratio around 1:1. Fisher stated his solution in genetic terms, but the potential of parents to actually vary and manipulate the sex of their offspring may also be involved (Trivers-Willard hypothesis:...
8.3.2 Quantity versus Quality: r- versus K-selection

Every season, a female cod may release many millions of eggs in the ocean for external fertilization. At the other extreme, human, chimpanzee and elephant females gestate, lactate, and intensively care for a relatively small number of young during their life times. These extremes represent two basic evolutionary strategies concerning reproduction: Low parental investment in quantity versus high parental investment in quality of offspring. Where a species lives in an environment in which the population is well below carrying capacity, it will be selected for its ability to reproduce rapidly. Because resources are at least temporarily abundant, reproductive rate will be more important than competitive ability in resource exploitation. Such a species is described as r-selected (where \( r \) = maximum intrinsic rate of growth of the population). In an environment where populations are close to the carrying capacity (\( K \)), on the other hand, then a high reproductive rate will be less advantageous. More individuals cannot be 'fitted in', and so instead there will be selective advantage for those individuals able to compete effectively for what resources do exist. In this case, the species is described as K-selected.

Besides greater competitive ability, K-selection is generally associated with a number of other characteristics such as slower development and longer juvenile phase, larger body size, internal fertilization, delayed reproduction, lower birth rate, greater birth interval, fewer but larger progeny and more parental investment in progeny (low infant mortality), longer gestation, longevity, slower sexual maturation and later menarche, etc. etc. (e.g., E.O. Wilson, 1975; Hrdy, 1981; Foley, 1987).

Increased body size is in its turn, according to Foley (1987), associated with a decrease in relative metabolic costs, larger home range, greater mobility, greater heat retention, increased strength and speed, enlarged brain, increased longevity, longer prenatal period, kin-centered sociality, and altered predator-prey relations. All these factors tend to amplify each other in a complex evolutionary cause-effect network.
8.3.3 Sexual Selection

Sexual selection depends on the success of certain individuals over others of the same sex, in relation to propagation of the species; whilst natural selection depends on the success of both sexes at all ages, in relation to the general conditions of life. The sexual struggle is of two kinds; in the one it is between individuals of the same sex, generally the males, in order to drive away or kill their rivals... whilst in the other, the struggle is likewise between individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners (Darwin, 1871).

This is how Darwin introduced the concept of sexual selection. The first kind of the sexual struggle is now better known as male-male and female-female competition. The second kind of the sexual struggle envisaged by Darwin is now known as epigamic selection or, simply, the principle of female choice. Darwin indicated the sexually dimorphic secondary sexual characteristics of many species, including humans, as the result of sexual selection. The gorgeous and exorbitant plumage of male birds-of-paradise, for example, is the result of such a kind of runaway sexual selection, based on the attractiveness to the females of the most exuberant-looking males. When sexual selection operates among males, adult males tend to become larger, heavier, showier, more competitive and better armed, and their behavior patterns and ecological requirements tend to diverge from those of the females. This is one of the reasons why E.O. Wilson (1975) calls sex "an antisocial force in evolution"; it generates, exacerbates, and multiplies conflicts of interests.

A whole array of traits is associated with the greater sexual competitiveness of males in a wide range of species. These include not only greater size and gaudiness, but also the price males have to pay for this: Greater vulnerability and frailty in development, and shorter lifespans due to senescence, high risk-taking and mortality from fighting. Table 8.3.3 summarizes the modes of sexual selection.

Of the two aspects Darwin distinguished, male competition has received broader acceptance than female choice; many biologists question female choice (in humans, e.g., Low, 1988); or acknowledge constraints on female choice (e.g., Trivers, 1985), and especially the notion that it can engender runaway selection, i.e., rapid selection for traits females prefer for strictly aesthetic reasons (Fisher, 1930; Ghiselin, 1969; Arnold, 1983; Cf. Cronin, 1991). Trivers (1972) argues that the intensity of sexual selection is determined by the magnitude of the difference in parental investment of the two sexes in their offspring. Since greater parental investment in one offspring implies lesser parental investment for other offspring, the sex that invests more heavily in its
offspring (and given the inequity in sperm and eggs, this is usually the female) becomes a limiting resource for the other sex. To the degree that they are freed from parental investment in their offspring, members of the sex with the lesser investment can increase their reproductive success by leaving offspring with more members of the opposite sex. Hence males tend to be sexually selected for sexually dimorphic features that are an advantage in competition with other males (Parker, 1987; Borgia, 1979, 1980).

While the average reproduction of males and females is identical, Low (1992) explains, the variance is not (Fisher, 1930; Bateman, 1948). More males than females fail to reproduce, and the most successful male produces many more offspring than the most successful female. Males must expend enormous effort to get resources or status to accomplish even a single mating (and thus offspring), but subsequent offspring may impose relatively little additional cost. Hence, much male striving is mating effort rather than parental effort; there are potentially very high reproductive returns, and high risks are acceptable. Females in most species have no trouble getting matings, but each offspring imposes a unit cost, so that the female return curve for her parental effort is linear for some portion, and levels off earlier than the male curve. Eventually females reach a limit such that further resources cannot produce further successful offspring.

**Table 8.3.3: The modes of sexual selection (E.O. Wilson, 1975)**

I. Epigamic Selection
   A. Based on choices made among courting partners
      1. The choice among the different types of suitors is dependent on their relative frequencies
      2. The choice is not frequency-dependent
   B. Based on differences in breeding time: superior suitors offer to breed more at certain times than at others

II. Intrasexual Selection
   C. Precopulatory competition
      1. Differential ability in finding mates
      2. Territorial exclusion
      3. Dominance within permanent social groups
      4. Dominance during group courtship displays
   D. Postcopulatory competition
      1. Sperm displacement
      2. Induced abortion and reinsemination by the winning suitor
      3. Infanticide of loser’s offspring and reinsemination by the winning suitor
      4. Mating plugs and repellents
      5. Prolonged copulation
      6. In ‘passive phase’ of courtship, suitor remains attached to partner during a period before or after copulation
      7. Suitor guards partner but without physical contact
      8. Mated pair leaves vicinity of competing suitors
Thus, the ultimate basis of sexual selection is greater variance in mating success within one sex. In humans, for example, some powerful men may have many wives and children, while many poor, low-status men have neither kith nor kin. This differential in reproductive success underlies the formulation of Parental Investment Theory, developed by Trivers (1972).

8.3.4 Reproductive Success (RS) and Parental Investment Theory

We have evolved a nervous system that acts in the interests of our gonads, and one attuned to the demands of reproductive competition. If fools are more prolific than wise men, then to that degree folly will be favored by selection. And if ignorance aids in obtaining a mate, then men and women will tend to be ignorant (Ghiselin, 1974).

As explained in chapter 1, we may expect all organisms, including our own species, to be programmed to compete for differential reproductive success with conspecifics, and for the resources and status positions which lead to the enhancement of reproductive success. But because our next-of-kin also bear replicas or copies of our own genes, natural selection will also favor those behavioral strategies which increase the reproductive success of our next-of-kin.

The concepts of ‘differential parental investment’, ‘differential reproductive strategy’ and ‘male confidence of paternity’ provide the basis for an understanding of the ubiquitous phenomena relating to the conflict-ridden and uneasy coexistence of the sexes, known as the perpetual ‘battle’ or even ‘war’ of the sexes.

Basically, the sociobiological reasoning behind the ‘battle of the sexes’ is simple and straightforward: Men and women invest differently in their reproductive success. For mammalian species, such as we ourselves are, female reproductive success is limited only by the amount of resources (time, energy, nutrients, etc.) she has to invest in offspring. But for the male, the female herself is the limiting resource: One male can inseminate many females and male reproductive success is only limited by the number of matings a male can achieve. Even in species where males typically invest in their offspring - and human males certainly do - the temptation of enhancing reproductive success by means of securing extra-pair copulations and inseminating other females without further investment tends to select for a mixed male strategy of pair-bonding and philandering, and a female counter-strategy of carefully assessing the male’s potential and willingness to invest in her offspring. Thus there is a basic asymmetry in female and male parental investment strategies.

As Daly & Wilson (1978) eloquently explain: At conception the female role already involves greater care for the young, for it is the large ovum that
provides the nutrients for early development of the zygote. In the language of the evolutionary economic model, the female’s initial ‘parental investment’ in each offspring surpasses the male’s.

Parental investment is a concept developed mainly by Fisher (1930) and Trivers (1972). The latter defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring".

This definition stresses the trade-offs implicit in any course of action. Parents who invest in one offspring sacrifice the opportunity to invest in others. More generally, an animal’s parental investment is part of its total reproductive effort, which also includes the effort expended in finding and winning mates. With a finite amount of time, energy, and resources, that can be devoted to reproduction, each animal should strive to distribute its reproductive effort so as to maximize inclusive fitness...

The common denominator of all such investments is 'the expenditure of the animal's remaining reproductive potential', for it is reproductive success alone that appears on the scorecard of natural selection. The basic difference between the sexes is the vastly greater size of an ovum in comparison with a sperm. From its very beginning, then, sexual reproduction has entailed a disparity of parental investment: The mother provides the cytoplasm. This situation sets the stage for a number of evolutionary developments that have greatly amplified the initial difference in the parental investment of female and male...

Internal fertilization, gestation, placentation, lactation: Each of these evolutionary developments results in a more concentrated female investment and in a decreasing number of offspring...

The males are competing with one another for the opportunity to inseminate females. By apportioning a relatively large part of their reproductive effort to such competition, males of most species devote rather little to parental care. The nurture that females bestow becomes a resource for which males compete: The male who wins the right to inseminate a female also wins for his progeny a share of the female’s parental investment (Daly & Wilson, 1978).

The concept of differential parental investment provides an explanation for the fact that males are almost universally the more competitive sex. In general, females invest considerably in the nurture of each of a relatively small number of young, while male fitness depends on maximizing mating frequency. The resultant competition is not something that males can afford to take lightly. The prize is substantial, and the greater the prize (e.g., a harem of females), the greater will be the risk that the hopeful male should venture in order to secure it: "For a big enough prize it will even be worth his while to risk death" (Daly & Wilson, 1978).
Male-male reproductive competition can take several forms (Borgia, 1979; Parker, 1987): Gametic competition for copulations and inseminations (sperm competition); harem competition for control of females; resource competition for territories or commodities that attract females; and labor competition to provide services that females need for their eggs or their offspring. In other words, males compete through a variety of behaviors including territoriality, dominance, female guarding, nuptial feeding, and sperm production. Although less attention has been paid to female-female competition, several forms have been identified: Direct competition for resources necessary for producing and nurturing gametes, fetuses and offspring and competition for parental investment of high ranking males; and competition for males of high genetic quality (Hrdy, 1981; Hrdy & Williams, 1983; Parker, 1987). Male sexual competitiveness and promiscuity, aggression and rivalry, and other secondary sex differences are not inherent, intrinsic aspects of maleness, rather these are the resultants of sex differences in reproductive strategies. In those (few) cases in which males provide significant parental investment, there is intense female-female competition for males, and females are the larger and more aggressive sex (G.C. Williams, 1966, 1975; Ghiselin, 1974; Symons, 1979; E.O. Wilson, 1975; Hrdy, 1981; Trivers, 1985; Badcock, 1989 et seq.; a.o.). These behavioral sex differences do, therefore, not depend on the possession of a particular pendulous sexual organ, as Freud and other psychoanalysts were inclined to believe. To a male the costs of parental investment in somebody else’s offspring are very substantial, therefore males are expected to provide parental investment pari passu with their certainty of paternity.

8.4 Of Primates, HUCHIBOs and Hominids

Man likes to think of himself as the ultimate outcome of a long line of evolutionary progress and inevitable complexification: The crown of creation. In reality, however, progress and complexity are not even a primary thrust of the evolutionary process - the bacterial style of life is the most common and the most successful - and Man is but a tiny, late-arising, and very contingent twig on life’s enormously arborescent bush: ”Humans arose rather as a fortuitous and contingent outcome of thousands of linked events, anyone of which could have occurred differently and sent history on an alternative pathway that would not have led to consciousness” (Gould, 1994). Just consider the following ‘ifs’: 1. If our inconspicuous and fragile lineage had not been among the few survivors of the initial radiation of multicellular animal life in the Cambrian explosion 530 mya, then no vertebrates would have inhabited the earth at all. 2. If a small and unpromising group of lobe-finned fishes had not evolved fin bones, vertebrates might never have become terrestrial.
3. If a large extraterrestrial body had not struck the earth 65 mya, then dinosaurs would still be dominant and mammals insignificant.

### 8.4.1 The Primate Adaptations

Many vertebrates are land-dwelling (terrestrial) creatures. All animals that successfully adjusted to terrestrial life had to solve a number of problems: Respiration (obtaining oxygen), dehydration (necessitating protective covering), and reproduction (necessitating hard-shelled eggs). Between 225 and 200 mya, a new group of vertebrates, the reptiles, rose to dominance. They were the first completely terrestrial vertebrates. With the evolution of internal fertilization, reptiles were no longer required to return to water in order to reproduce. After fertilization, the embryo is contained in an amniotic egg, maintaining the moist environment, and surrounded by a thick leathery shell preventing dehydration. The egg also contains a food supply, as well as a number of other evolutionary novelties (Poirier, 1993).

From these reptiles the first true mammals evolved about 200 mya. An important mammalian feature is the ability to generate heat and maintain a constant body temperature, a condition called homeothermy. Warm-blooded mammals could exploit and inhabit a wider range of habitats than those available to reptiles. Mammals also have evolved different kinds of teeth specialized for different functions (heterodontism); canines and incisors for jabbing, cutting and slicing, premolars and molars for grinding. The mammalian mode of reproduction (internal fertilization, placentation and early stages of development in the mother’s womb) is significant in understanding mammalian evolutionary success. The reproductive mode of one group, the placentals, allows an extensive period of prenatal development. Mammals also have fewer births per parturition, and the mammalian mother protects, nurses and nourishes the neonates by providing milk secreted by her mammary glands. The developmental period among the young is extended by nursing, and the infant’s longer period of attachment to its mother increases the potential period of learning behaviors necessary (or at least helpful) for survival. Also play behavior is an important means of environmental exploration, and of practicing social behaviors and communication skills, as well as physical coordination. Not surprisingly, mammals are generally more intelligent than their reptilian predecessors (Poirier, 1993).

Angiosperm forests spread across the earth during the late Cretaceous (94 to 64 mya). About 55 mya, some small, insectivorous, tree shrew-like mammal climbed into the trees in search for insects. Its descendants came to rely substantially on edible plant parts from the canopy; a change that set the stage for the emergence of the primate order (Milton, 1993). Natural selection strongly favors traits that enhance foraging efficiency. Hence as plant foods assumed increasing importance over evolutionary time, selection
gradually gave rise to the suite of traits (mostly facilitating arboreal foraging) characteristic of the primates: Stereoscopic (3D) and color vision, enhanced depth perception and visual acuity; agile and prehensile hands and feet, adept at grasping and clutching, with opposable thumb; small number of, or single, offspring; prolongation of gestation and infancy; complexity of social behavior; behavioral flexibility, and the capacity to learn and remember the identity and locations of edible plant parts, correlated with larger brains than other same-sized mammals (Harris, 1975; Milton, 1993).

Milton found that the frugivorous spider monkeys (Ateles geoffroyi) have a brain twice as large as the same-sized (and also sharing a common ancestor) howler monkeys (Alouatta palliata), who consume large quantities of leaves. As the brain is an expensive organ to maintain, usurping a disproportionate amount of energy (glucose) extracted from food, Milton hypothesized that

a) Natural selection favored a larger brain in spider monkeys, in part because enhanced mental capacity helped them remember where ripe fruits could be found (Spider monkeys also range farther each day because in any patch of forest, ripe fruits are less abundant than leaves); and

b) The striking expansion of brain size in the genus Homo indicates that humans became so successful because selection amplified a tendency inherent in the primate order since its inception: That of using brain power, or behavior, to solve dietary and foraging problems.

Thus primates with relatively large brains have larger home ranges, perhaps because species with large home ranges need to remember complex information about food distribution (Harvey & Read, 1992; Milton, 1993). Aiello & Dunbar (1993) recently reported a robust correlation between neocortex size and group size among primates, possibly reflecting the increasing importance of social intelligence and communication in larger groups. In humans the increase in neocortical brain size is predominantly linked to the substrates of speech production and perception, suggesting that the human brain has been shaped by evolutionary processes that elaborated the capacities needed for language, and not just by a general demand for greater intelligence (Deacon, 1992).

The primates are generally regarded as an arboreal order. Yet, about a quarter of all primate species has returned to mother earth and become terrestrial (sensu stricto) again, especially species belonging to the most recently evolved group of the catarrhines, comprising the Old World monkeys and apes (Clutton-Brock & Harvey, 1977; Foley, 1987).

The primary constraint on an arboreal way of life is body size. Access to many food types in trees is best served by a small body size. For a primate, the price of release from the high energy costs of a small body size is terrestriality. Consequently, if there already is a trend towards increased size among primates, a trend towards increased terrestriality should also be expected. Constraints on body size alone, however, are insufficient to account for the
evolution of terrestriality. A terrestrial way of life must also be viable in its own right. Appropriate terrestrial environments must be present (Foley, 1987). The date of the divergence between the ancestors of the apes and the Old World monkeys is probably at about 23 mya. The best evidence for the earliest appearance of hominids in the fossil record is at about 5 mya from Tabarin and Lothagam in Kenya.

8.4.2 The Pongid-Hominid Common Ancestor

Wrangham (1987) used the method of phylogenetic comparison to identify possible conservative features in social organization of humans and the African apes (for which molecular biology suggested their close relatedness) in an attempt to characterize the hominid-pongid common ancestor. According to this approach, shared features of social organization among humans, chimpanzees, bonobos, and gorillas are likely to have been present in the common ancestor, and can be viewed as part of an ‘ancestral suite’ of behaviors likely to have characterized hominids (and pongids) at any point in their evolutionary history. From the correspondences in the behavioral repertoires of these species, Wrangham concluded that the last hominid-pongid common ancestor probably had closed social networks (i.e., some degree of ethnocentrism and xenophobia), hostile and male-dominated intergroup relationships with stalk-and-attack interactions (i.e., male coalitional psychology and [lethal] male raiding), female exogamy and a lack of alliance bonds between females, and males having sexual relationships with more than one female (i.e., polygyny). Wrangham considered territoriality to be too labile a trait (depending on ecological conditions) to reliably attribute it to the common ancestor.

It is problematic whether the usually non-coalitional interindividual aggression of the gorilla may legitimately be classified as intergroup aggression. Thus, if the gorilla is eliminated from the comparative list, we are left with the genetically most related human-chimpanzee-bonobo clade (or HUCHIBO clade, for short). Ghiglieri (1987) was able to show that the HUCHIBO clade is characterized by a unique cooperative defense of a common territory by closely related males (we might call these clans), who exhibit only moderate sexual dimorphism, "presumably because success in male-male competition hinges on having larger group size (of kin-related males) during conflicts rather than larger individual size" (Ghiglieri, 1987).
Between the common ancestor of gorillas and HUCHIBOs and the common ancestor of all HUCHIBOs (a period of about 2 million years) some kind of revolution had occurred: Unlike all other primate social organization which is largely structured around female kin groups with the adolescent males leaving their natal group, HUCHIBO males, on the contrary, stay in their own natal group providing the opportunity and impetus for increased cooperation and clannishness among kin-related males. This male cooperation and clannishness (resembling fraternal interest groups in human societies) thus sharply distinguishes the HUCHIBOs from the other great apes.

"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 polygynously, restrict their range 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).

Only in those few species with female-biased dispersal - chimpanzees, hamadryas baboons, red colobus, and perhaps spider monkeys - are there known or suspected to be enduring affiliative relationships among males; philopatry, consanguinity, and cooperation tend to coincide (Rodseth et al., 1991).

The most common kind of cladistic speciation is created simply by geographical isolation, and the early phases of hominid evolution may not have been fundamentally different from the early hominoid branches in this respect.
When was the pongid-hominid split taking place? Coppens (1994), following earlier intimations by Kortlandt (1972), suggested the following intriguing scenario.

### 8.4.3 East of Eden

What emerged clearly from excavations and finds in Africa during the last decades was that there was absolutely no sign of the common chimpanzee (*Pan*), or one of its direct ancestors, in eastern Africa during the time of the Australopithecines (to 8 mya). Yet, molecular biology, biochemistry and cytogenetics continued to demonstrate that humans and chimpanzees were molecularly extremely close, which meant, in evolutionary terms, that they shared a common ancestor not very far back in time, geologically speaking.

All the hominid sites that dated to three million years ago were found, without exception, on the eastern side of the Rift Valley, the huge furrow that cuts across eastern Africa from north to south. Only one solution could explain, according to Kortlandt (1972) and Coppens (1994), how, at one and the same time, Hominidae and Panidae were close in molecular terms but never side by side in the fossil record. And the solution was that Hominidae and Panidae had never been together.

Eight million years ago, a tectonic crisis arose on the African continent that entailed two distinct movements; sinking produced the Rift Valley, while rising gave birth to the line of peaks forming the western rim of the valley. The Rift Valley not only broke up the population of the common ancestor of the Hominidae and the Panidae in two divisions, it also disturbed the global circulation of air, the climate, and thus the vegetation. The west maintained a generous amount of precipitation and kept its forests and woodlands, while the east, gradually getting colder and drier, evolved into open savannah (via a mosaic forest/savannah phase).

Coppens speculates that the western descendants of these common ancestors pursued their adaptation to life in a humid, arboreal milieu; these are the Panidae. The eastern descendants of these same common ancestors, in contrast, invented a completely new repertoire in order to adapt to their new life in an increasingly open and arid environment; the Hominidae. Thus, geographic isolation and the need to adapt to a new habitat promoted further genetic divergence between the families. Man, one could say, is the result of a tectonic and climatic catastrophe. Coppens called this scenario the East Side Story. He might as well have called it East of Eden.

Later on, some 3 mya, the whole earth cooled, and adaptation to a still more arid and cooler habitat, with a concomitant decrease in plant foods, led in two directions, reflecting two different strategies: A strong robust physique and a narrow, specialized vegetarian diet for the large robust Australopithecines (also called *Paranthropus*), whose heavy dentition and facial musculature suggests a
diet of hard coarse roots and tubers, dry fruits, etc.; and a large brain and a broad-ranging, opportunistic diet - involving greater dependency on mobility and scavenging/hunting - for the gracile hominids (Foley, 1987; Coppens, 1994; Slurink, 1994). The dentition and tooth-wear patterns of early Homo habilis is compatible with an omnivorous diet (Musonda, 1991). Furthermore, the modern human digestive tract is adapted to a plant-rich and fibrous diet (Milton, 1993).

According to Johanson & White (1979), Foley (1987), and Parker (1987) the early Australopithecines (Australopithecus afarensis) were highly sexually dimorphic (more within the range of the gorilla than that of the chimpanzee) as were their descendants A. robustus and A. boisei. They probably specialized in extracting with tools a variety of energy-rich embedded foods such as nuts, roots, tubers, fungi, ants, termites, grubs, and eggs that were unavailable to non-tool using species living in the same environment. Although it is likely that both sexes engaged in extractive foraging with tools, as well as opportunistic foraging on a variety of fruits and buds, as in chimpanzees, males probably supplemented their foraging by hunting small birds and mammals. Extractive foraging with tools would have favored advanced sensorimotor and symbolic intelligence. Moreover, it would have provided a basis for deferred imitation and symbolic communication of the location and nature of hidden embedded foods (Parker & Gibson, 1979; Parker, 1987).

8.4.4 Bipedalism

Three basic systems of locomotion have evolved among terrestrial primates: Quadrupedalism, knuckle-walking and bipedalism. Bipedalism, adopted by the hominids, is the most specialized, requiring major anatomical modifications. Hominids (Australopithecus afarensis) were more or less bipedal by just about 4 mya, as attested by the morphology of the Hadar fossils (Lucy) and the Laetoli footprints (Johanson & Edey, 1981; Foley, 1987; Richards, 1987; some scholars deny this categorically, however, and some anatomical features such as curved phalanges [toe bones] indicate a still arboreal heritage). It thus occurred sufficiently early for it to be considered to be part of the original adaptive shifts of the hominids. Depending on one's view of the early hominid paleoenvironment (savannah, forest/woodland, and/or a more aquatic environment of marshes, lakes and rivers), different explanations identifying different selection pressures for the origin of human uprightness and bipedalism - freeing the hands for purposes

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1 The marked sexual dimorphism of these species, Slurink (1994) notes, seems to refute Ghiglieri's model of the common HUCHIBO ancestor: "Either the similarities between the HUCHIBOs are a product of convergent evolution, or the Hadar-hominids belong to more than one species as suggested by the heterogeneity of the Hadar materials (Schmid, 1989)."
other than locomotion - have been proposed: Carrying of food in the context of male provisioning (Hewes, 1961, 1964; Kortlandt, 1967; Lovejoy, 1981; Isaac, 1983); reaching upward for food (Jolly, 1970); feeding adaptations, e.g., a diet of grass seeds (DeBrul, 1962; Jolly, 1970); early warning system, increasing the visual horizon to better spot both prey and predators (Ravey, 1978); carrying tools and weapons (Darwin, 1871; Washburn, 1950 et seq.); improved bioenergetic efficiency (Taylor & Rowntree, 1973; Rodman & McHenry, 1980; Pickford, 1989); stalking, chasing and hunting (Merker, 1984); intimidating predators (Livingstone, 1962); thermoregulation, reducing the risk of hyperthermia (Wheeler, 1984 et seq.), and enabling mid-day foraging and avoidance of predators (Foley, 1987); wading in shallow water and floating in deep water (Morgan, 1972, 1982); a preadaptation in relation to climbing trees (Susman, 1986); or in relation to terrestriality (Foley, 1987); etc. (For reviews of these hypotheses see: McHenry, 1978, 1982; Lovejoy, 1981; Isaac, 1983; Foley, 1987; Richards, 1987; Slurink, 1994).

The proposed hypotheses fall into two separate categories; those that account for the origins of bipedality in terms of its direct locomotor advantages, and those that regard it as a byproduct of other selective factors, mainly the advantages of having a specialized, and 'freed', grasping hand (Foley, 1987). The selective advantage of an upright posture was apparently great enough to offset severe disadvantages involving the reproductive system itself (not to mention the vulnerability to lumbar and circulatory malfunctioning). In evolutionary terms this means that it must have been a very potent selective force. Darwin (and later repeated by Dart, Lorenz, Bigelow and many others) already suggested that an erect posture and bipedalism, together with the reduction of male canines, were favored originally by selection because the hands were freed for fighting with weapons (a view no longer tenable; the erect posture existed long before any evidence of tools).

Although bipedalism as a savannah adaptation is the most widely accepted view, it has been recognized that bipedalism in a savannah paleoenvironment makes little immediate sense: It is inherently unstable, and it is not more energy-efficient than quadrupedalism or more effective in carrying things than knuckle-walking (as chimps do). Also the slight initial advantages for improved vision would hardly have outweighed the drawbacks. Bipedality is useless for escape from predators (Lovejoy, 1981). The upright posture makes excellent sense, on the other hand, in a wading context. Most African hominid fossil sites are located in the vicinity of former marshes, lakes and/or rivers, and the early hominids - much like modern humans - may have preferred a mixed and variegated biotope of woodland, water and savannah. During the dry season savannah animals gather around the remaining water resources and the hominids may have exploited such an opportunity, while at the same time being relatively safe from, especially feline, predators in the water (Foley, 1987; Slurink, 1993).

As outlined by Richards (1987), Hardy's (1960, 1977) and Morgan's (1972,
1982) so-called Aquatic Ape theory argues that (a) a number of the most characteristic human behaviors, notably bipedalism and vocal communication (speech), and (b) a suite of idiosyncratic physiological features such as hairlessness, subcutaneous fat, sweating, weeping, nose-form, breast-form, ventral orientation of the vagina and highly developed sense of balance can be economically explained by an aquatic or semi-aquatic (lacustrine, riverine) phase in hominid evolution presumably having taken place after the chimpanzee-hominid split but before the Laetoli australopithecines. The orthodox savannah model leaves many of these unique features enigmatic, especially the erect posture and the, suicidal due to moisture loss, perspiration method. See Roede et al. (1991) for a critical evaluation of the Aquatic Ape theory.

Furthermore, Slurink (1994) points out that bonobos, who are much better adapted to water than chimpanzees, have been observed to catch fish while wading upright in the water: "It seems that in bonobos uprightness is sometimes used to intimidate predators, sometimes it is used to carry fruit and sometimes to catch fish (De Waal, 1989). This could imply that the carrying hypothesis (Hewes, 1961) and other hypotheses (a wading ape theory, a predator intimidation theory (references in Pickford, 1989) need not be mutually exclusive. Bipedality need not have evolved as the result of one specific selection pressure; but it could have been the best general solution for a multitude of separate problems".

Though still enigmatic in its origins, once in existence, however, bipedalism opened up new avenues and revolutionary strategies.

Parker (1987) suggested that bipedal locomotion initially arose in the earliest hominids through sexual selection as part of a male reproductive strategy of nuptial or courtship feeding of estrus females rather than as a means for provisioning mate and offspring. The nuptial feeding model for the origin of bipedalism has the advantage of providing a model for a transition from a pattern of low male parental investment and promiscuous mating to a pattern of high male parental investment and provisioning of mate and offspring in long term, if not necessarily exclusive, pairbonds. In Parker’s sexual selection thinking, male competition through nuptial feeding on scavenged brains and marrow would have favored larger body size in male hominids because of the rigor of long distance walking and carrying and defending themselves against competing scavengers and hunters. Male canine reduction too may have evolved through sexual selection.


Foley (1987) argued that the bioenergetic advantages of bipedalism seem to lie in long-distance endurance. This is consistent with a model of extreme thermoregulatory characteristics, and prolonged and long-distance foraging of the early hominids. The latter may have been the selective pressure leading to bipedalism acting on a number of necessary preadaptations and changing
paleoenvironments (See Aiello, 1981; Foley, 1978). Reduced thermal stress could be bought only at the cost of increased water dependence, with profound consequences for ranging and foraging behavior. It seems sensible to avoid the most extreme versions of both the savannah- and the aquatic theory (Pickford, 1989; Reynolds, 1991; Tobias, 1991; Slurink, 1994). The question of why our protohominid ancestors opted for bipedalism is still largely unanswered.

8.4.5 The Chimpanzee Connection

The vicissitudes of the chimpanzee evolutionary trajectory - on the western side of the Great Rift - have been explored in considerable detail in Ch. 3. Here I shall briefly recapitulate only the main arguments. Our knowledge of bonobo (Pan paniscus) social, especially intergroup, behavior is too fragmentary to be of much use, and I shall exclude this intriguing species, which appears to have evolved highly effective conflict-resolution and reconciliation procedures, from the discussion in this section. As we saw, it was the female transfer in the HUCHIBO clade which made the evolution of a 'male coalitional psychology' (Tooby & Cosmides, 1988) feasible. Ghiglieri (1987) speculated that it was this evolved propensity for cooperation and solidarity between kin-related males that could well have been the critical preadaptation for male cooperation in dangerous scavenging or hunting in the hominid ancestor. In the chimpanzee it must also have given rise within the group to opportunistic coalitional politics and the concomitant Machiavellian intelligence (vide infra), while, between the groups, the chimpanzee equivalent of pseudospeciation gave rise to the chimpanzee equivalent of militant ethnocentrism and xenophobia, strong consciousness of community territorial boundaries as well as community identity; a strong 'consciousness of belonging'. What factor(s) promoted the transition from male exogamy in other primate groups towards female exogamy in the HUCHIBO clade is unknown, though it

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2 It should, however, be remembered (See Ch. 3) that intergroup agonistic behavior among overlapping bonobo groups is minimal. Bonobos do not show the all-male patrols found among common chimpanzees, nor do they show cooperative hunting. Strong group cohesion is maintained by genito-genital rubbing in females, a lengthened period of female receptivity, high tolerance and male-female affinities, and widespread food sharing (Kuroda, 1979; Kano, 1982, 1990; Susman, 1987). Despite female transfer, the core of bonobo society consists of strongly bonded females and the males associated with them (Badrian & Badrian, 1984). This is quite the opposite of the male kinship groups found among common chimpanzees (Poirier, 1993). Bonobo males have never been observed to kill conspecifics. Shea (1983) suggested that group cohesiveness among pygmy chimpanzees, coupled with reduced sexual dimorphism (Kinsey, 1984), helps explain the lack of aggression. Susman (1987) suggested that the lack of aggression, reduced sexual dimorphism, and increased female sexual receptivity are tied to the bonobo's more stable forest habitat, with its reduced seasonality, relaxed feeding competition, and reduced predator pressure.
is tempting to speculate, as did Slurink (1994), that a temporarily reduced threat of predators in one of the chronospecies ancestral to all great apes was the ultimate cause, leading to an initial loosening of the group structure, via transition to one-male groups, to subsequent competition for harems starting an arms race in which dominant males were forced more and more to rely on their male kin.

8.4.6 Group Territoriality

In the male chimpanzees of Gombe "territoriality functions not only to repel intruders from the home range, but sometimes to injure or eliminate them; not only to defend the existing home range and its resources, but to enlarge it opportunistically at the expense of weaker neighbors; not only to protect the female resources of a community, but to actively and aggressively recruit new sexual partners from neighboring social groups" (Goodall, 1986). They deliberately and intentionally kill 'the enemy' for that purpose.

I submit that a similar scenario operated in hominid/human evolution: Opportunistic and occasional territorial aggrandizement and violent recruitment of females are also the fundamental causes of hominid/human warfare. It is as if both chimps and early humans had read Hamilton (1975): "[I]t has to be remembered that to raise mean fitness in a group either new territory or outside mates have to be obtained somehow", and both species had stumbled upon the same solution. Ultimately the fundamental causes are related to the different reproductive strategies of the sexes.

Group territoriality is the trait-d'union between, and the communal theme in, chimpanzee 'lethal male raiding', primitive war, and contemporary state-level warfare (not to mention the social carnivores and warmaking ants).

As we have seen (Ch. 3), the raiding chimps attempted to extend their territory by encroaching on the territory of neighboring males, thereby increasing the probability of access to reproductively valuable females.

In primitive war, territorial intrusion and the defense of territorial integrity rank next to revenge as the main war motives (Ch. 5).

In contemporary state-level war, territory/territoriality/territorial contiguity (border disputes) has been singled out by quite a number of researchers as the universal and persistent underlying cause (Richardson, 1960; Rummel, 1968, 1972; Luard, 1970; Alcock, 1972; Singer, 1972; Singer & Small, 1972; Dowty & Kochan, 1974; Starr & Most, 1976, 1978; Wallensteen, 1981; Small & Singer, 1982; Gochman & Maoz, 1984; Diehl, 1985; Luard, 1986; Maoz, 1989; Gochman, 1990; Holsti, 1991; Bremer, 1992; Goertz & Diehl, 1992; Vasquez, 1993).

Concerns over territory3 have been the underlying and fundamental source of

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3 Rather than the struggle for power as advocated by the (neo)realists. The father of political realism, Morgenthau (1948) related the ubiquitous struggle for power to "drives to live, to
conflicts ending in war during at least the last 3 or 4 centuries (Vasquez, 1993): "[I]t seems to be connected with genetic proclivities associated with territoriality, which in turn may be related to the connection between territory and biological sustenance [i.e., resources]" This 'territorial propensity', he holds (thereby reiterating and epitomizing many other scholars), is deeply ingrained and is part of humanity’s collective inheritance.

It may be argued that there must be a profound relationship between territoriality and ethnocentrism; ethnocentrism expressed spatially is territoriality; territoriality expressed psychologically as strong group identity with clear demarcation of in- and out-group is ethnocentrism. If revenge raiding in human primitive warfare is, inter alia, also a defense of the group identity and an instrument of distributive justice (reciprocal exchange), then it makes sense that the preponderant majority of accounts of warfare in primitive peoples concerns petty feuding, and ranks with territoriality as the prime motives. As Daly & Wilson (1987) observed: "Effective deterrence is the ultimate function behind the human passion for measured retributive justice - it is the reason why that passion evolved. But our passion for evening the score has thus become an entity in its own right, an evolved aspect of the human mind. Our desire for justice fundamentally entails a desire for revenge".

The acquisition of heads or other trophies, by serving the accretion of soul power, also increases the power of the entire community and intensifies group identity.

All this does not, in my opinion, imply any 'Territorial Imperative' mystique à la Ardrey, but it is rather easy to imagine that the proximate motive system underlying these behaviors may acquire some kind of Eigenappetenz, and that all other acquisitive motives reported in the literature may be spin-offs of this 'territorial propensity' (which always operates in interaction with the actual economic defendability of the resources available; see Ch. 1).
The preadaptations required to permit the emergence of warfare in both chimps and early human 'dawn warriors' (as Bigelow called them) were, according to Goodall (1986), probably cooperative group living, group territoriality, cooperative hunting skills, tool/weapon use, an inherent fear of, or aversion to, strangers, and the intellectual ability to make cooperative plans. This intellectual ability for tactical maneuvering in intergroup competition requires what has been called social and Machiavellian intelligence in the context of intragroup competition.

What is Machiavellian intelligence? In contrast to technical (or causal or instrumental) intelligence, Machiavellian intelligence works in the context of social interaction. The fundamental hypothesis (the Chance-Mead-Jolly-Kummer-Humphrey hypothesis) here is that the social world contrasts with the physical world in that it is more challenging. This leads to the hypotheses that (a) intellectual capacities adapted to social life may have special and even particularly sophisticated attributes; and (b) that very social species should be intellectually different from, or in some ways even superior to, less socially elaborate ones (Whiten & Byrne, 1988). Thus it is suggested that it is the evolution of social intelligence which explains human brain power. The social environment is special because it is reactive, and dealing with it thus requires a constant monitoring of its state and an appropriately timed regulation of even such behavior as approaching, which in the case of physical object would be straightforward.

The life of social animals is highly complicated and problematic. What is special about the social context is that the data on which the individual’s predictions are to be based are (a) highly changeable, and (b) contingent on one’s own actions too. The metaphor of social interaction as a game in which the winner is the one who outwits the other is strong in Humphrey’s (1976) analysis of what is special about social intellect: "the game of social plot and counter-plot cannot be played merely on the basis of accumulated knowledge, any more than can a game of chess" - unlike interactions with the physical environment, such as foraging. In particular, it may be necessary to change tactics as such a game evolves. In this way, he is pointing to primate intelligence being not just 'social', but Machiavellian in its origins (Whiten & Byrne, 1988).

Humphrey also discussed the possibility that, without further change in extra-social selection pressures, any increase in Machiavellian skill by one 'player in the game' will select for enhanced skill in the other, both in competitive and cooperative interaction, thus resulting in an evolutionary 'arms race' of Machiavellian cleverness.

What would be the functional advantage of being a 'natural psychologist', i.e., an animal sufficiently social intelligent to read the mind of another individual?
If we start with Craik’s (1943) suggestion that what brains do is build a ‘small-scale model’ of external reality, then a more intelligent brain can be recognized by the accuracy and completeness of its cognitive model. Now, in the case of social intellect, this modelling will have to be extended to that part of the world constituted by other individuals. If we think of social interaction as a game between competitors, in which success depends not on brute strength but on social skill, then, like in a game of chess, out-maneuvering one’s opponent will depend on how many of the possible future moves one can anticipate, and thus in turn on the adequacy of one’s internal model of the operations of the other’s mind. This will involve not only a capacity to represent a certain number of orders of intentionality, but to represent the rapidly branching alternatives which are raised with each anticipatory step back and forth between self and opponent. So yet again we have a potential selection pressure working on social intellect which is a geometric function, rather than an additive one, of increases in social complexity.

As Humphrey noted, the evolution of more sophisticated Machiavellian intelligence in succeeding generations should create a spiralling pressure for greater and greater powers of gamemanship (Whiten & Byrne, 1988) and, inevitably, deception.

'Tactical deception’ will be confined to any interaction in which Sender deliberately conceals or falsifies information in order to manipulate Receiver’s behavior (LaFrenière, 1988). The importance of deception in human affairs has long been recognized. For example, deception has been considered central to intergroup conflict from the biblical accounts of the siege of Ai and the Greek legend of the Trojan horse, to the modern example of Pearl Harbor in 1941. This fact is so much in evidence that one is inclined to agree with Sun Tzu, that "all warfare is based on deception" or with Sir Winston Churchill, who is reported to have said that "in time of war, the truth is so precious it must be attended by a bodyguard of lies". While warfare is certainly one of the most dramatic illustrations of the human capacity for deceit, the intricacies of political intrigue from Machiavelli’s (1513) classic work (Il Principe) in the early renaissance to the unfolding of Watergate in our own times, provide further examples of the extent of duplicity in public life.

In everyday life, social psychologists such as Mead (1934) and Goffman (1959) view all social interaction as involving an element of deception, in the sense that participants are engaged in a dramatic performance to control the impressions of themselves that are presented to others. Perhaps the most extreme view of human deception is everyday life was articulated by Alexander (1977) who views human society as "network of lies and deception, persisting only because systems of conventions about permissible kinds of lying have arisen". This rather one-sided view of human sociality ignores the vital function of reliable communication in human intercourse. The possibility, however, of deceptive, well calculated communications and the necessity of detecting such machinations and manipulations must have provided a major
impetus for the evolution of primate and human intelligence (LaFrenière, 1988; see also van den Berghe, 1981).

There is a profound sex difference in Machiavellian intelligence related to coalitional behavior in the evolution of chimpanzees and humans. Machiavellian intelligence (MI) is a) social (as opposed to technical); b) self-interested; c) short-term rational; d) manipulative, involving (some degree of) deceit and self-deceit.

In humans and chimpanzees (and perhaps bonobos), male coalitional behavior is more opportunistic and Machiavellian than female coalitional behavior, is more dominance/power/violence (including lethal male raiding) oriented (e.g., Harcourt & de Waal, 1992), and is ultimately related to the different reproductive strategies of the sexes; males generally compete and may fight over females, either individually or in coalitions, while females generally do not fight, either individually or in coalitions, over males, but over resources to invest in offspring.

I therefore postulate a relationship between Machiavellian intelligence (MI), (proto)ethnocentrism (PE) (codetermined by the clannishness of the HUCHI-BO clade, coalitional psychology, and xenophobia) and (lethal) intergroup competition (IC) in chimpanzees and early hominids/humans.

Low (1992) argued that men and women, pursuing as they do typically mating and parental effort, will tend to form different sorts of dyadic or polyadic coalitions, at different risk levels. Men, like other male mammals, will be more often involved in fluid, risky coalitions with non-relatives, while women will, like other female mammals, be more often involved in information-sharing and foraging coalitions with female relatives and co-wives. The two sexes will differentially be involved in community and wider levels of politics.

Tooby & Cosmides (1988) explain the striking asymmetry that exists between males and females in coalitional aggression as follows: Females are rarely limited by access to males, so that the net reproduction of a coalition of females would drop in direct proportion to the number of females killed. In a curious fashion, males may be so ready to engage in coalitional aggression because it is reproductively 'safer' for them to do so. Females have more to lose, and less to gain, and such differences in consequences should be reflected in psychological sex differences in attitudes towards coalition formation and coalition-based aggression.

Goodall (1986) pointed out that cruelty presupposes some level of cognitive sophistication as well as the ability to empathize with the victim, which probably only chimps and humans have reached. Chimps, like humans, also scavenge/hunt cooperatively in some regions (a.o. Hasegawa et al., 1983; Goodall, 1986; Boesch & Boesch, 1989; Boesch, 1994), and the amount of meat (high-quality proteins) in their diet is probably surpassed only by humans.
8.4.8 Brains and the Cognitive Niche

The core of our zoological distinctiveness, according to Tooby & DeVore (1987), is our entry into the cognitive niche, which has made available a plethora of new prey species both plant and animal, as well as allowing us to adopt flexible solutions to a wide array of other adaptive problems. At the core of this lies another type of intelligence: Causal or instrumental intelligence which is more or less clearly distinguishable from social and Machiavellian intelligence. It implies the ability to create and maintain cause-effect models of the world as guides for prejudging which courses of action will lead to which results. Behavioral flexibility is not an adequate characterization of this innovative adaptive pattern: The human cognitive system is knowledge or information driven. Many other zoologically anomalous features of hominids/humans may be considered to be aspects of the cognitive niche: Tool use, skill acquisition, and language. Language drastically reduces the costs of information transfer to other individuals. This social dimension of the cognitive niche constitutes the basis for culture - the transmission between individuals and generations of the information necessary to pursue fitness in a particular social and ecological habitat. Entering the cognitive niche was also responsible for the radiation of humans into all terrestrial habitats (Tooby & DeVore, 1987).

But why did only humans enter into the cognitive niche, why did the great apes not develop along hominid lines? One possible, and partial, answer is bipedalism (vide supra). Another partial answer might be that sociality reduces the cost of information seeking which may explain why the solitary primates did not more fully enter the cognitive niche. A third possible answer involves the ratio of the costs of added cognitive abilities versus the increased pay-offs: "The brain is a nutritionally and metabolically costly organ (Martin, 1983). To justify the marginal cost of increasing its size, the marginal benefit must be correspondingly high. It may be that for brain expansion to pay off, it must increase access to very nutritionally rich sources of food, such as meat. Open habitats are far more meat productive than tropical forests, and it may be that occupation of the meat-rich savannah is what differentiated hominids from the forest-bound apes. The role of meat may go beyond its production of calories: the constituents of the brain require essential fatty acids, which may prove to be the real limiting factor made available by meat" (Tooby & DeVore, 1987). Chimpanzees seem to have an outspoken preference for the brains of their prey (bushbucks, young baboons), as early humans may have had; brains may have evolved by feeding upon brains.

The part of the brain mainly responsible for the trebling in brain size during hominid/human evolution is the cauliflower-like neocortex, a neomammalian development that mushroomed late in evolution and achieved its greatest proportions in human beings. MacLean (1987) says about this cytoarchitecton-
ically complex structure: "The neocortex is oriented primarily to the external world and seems to serve as a kind of problem-solving and memorizing device to aid the two older formations of the brain [the reptilian brain and the paleomammalian brain or limbic system] in the struggle for survival. With its focus on material things, the neocortex develops somewhat like a coldly reasoning, heartless computer. It is a type of computer that has the capacity to devise the most violent ways of destroying our own kind as well as other forms of life".

Tiger (1990) asserts that it is precisely the most unusually highly evolved biological characteristics of *Homo sapiens sapiens*, our cognitive and symbolic skills, which offer the readiest facilitation to violence and aggression. That is, that the same kind of analytical skill and strong commitment to group norms which is the essence of science, is at the root of the successful construction of the social and ideological boundaries which are the effective prerequisite to 'large-scale persistent aggressive interaction' (i.e., war). Tiger offers four propositions on which he bases this claim: (1) Cortical tissue developed to facilitate action (not thinking) and the most basic action to which it had to become directed was courtship and reproduction. (2) While the most obvious outcome of effective aggressive behavior is on the outside environment - either people or things or places may be violated and coerced - it is possible that the more parsimonious process at work has to do with solidifying internal solidarity rather than conducting external adventure. That is, not until pastoralism or agriculture would it have made economic sense to conduct aggressive enterprises as a way of securing resources (with possible exception of female captives); but by then we had already developed our wonderful brain and as a result different processes than that would have led to rapid selection of cortical tissue. One such process could well have been a set of social skills supporting cooperation, even relatively bellicose cooperation, which would in turn translate into reproductive access and success. (3) The brain evolved in the context of a powerful ramified overwhelming concern with kinship, with the *reproductive* lives of members of family - this was more important even than their *productive* lives. (4) The function of the great learning system encoded in the brain is to make members of groups more the same rather than to stimulate them to cultivate differentiation. This brings us full circle to conflict and violence because these depend on the assured commitment of members of groups to their own indigenous certainties and on their willingness to commit themselves strenuously for the defence of their groups and their dignity. To this end kinship terminology is employed for the mobilization for conflict.

Bigelow (1969 et seq.) is one of the most ardent advocates of the thesis that human cooperation and intelligence were actually favored by the selective force of warfare. The 'highest' human qualities, he states, were demanded by the 'lowest' human qualities, with such enormous force and relentless constancy that the size of the brain trebled very rapidly.
Discussions of the evolution of the human brain tend to emphasize the explosive expansion of the cerebral cortex in relation to Man’s extraordinary cognitive abilities. But, as Symons (1979) pointed out, the ‘lower centers’ also have expanded tremendously. Thus, the neocortex and the limbic system expanded together. Organisms are moved by emotions, both figuratively and literally. ‘Motive’, ‘motion’ and ‘emotion’ are very close in derivation and in meaning. Emotions may be considered evaluations of stimuli, whether these stimuli originate outside the organism (sensation) or in the brain itself (memory, fantasy), and motivate the seeking of particular stimuli. Human beings probably exhibit unprecedented emotional complexity (Symons, 1979; Hebb & Thompson, 1968; Shaw & Wong, 1989).

8.4.9 Sociality

Why would basically selfish organisms bother to live socially? Why be social beyond what is required to mate and reproduce? The general opinion for long has been that group-living and cooperativeness are universally and automatically beneficial to all concerned, and hardly require special explanation. Alexander (1979) and Alcock (1979), however, have made clear that group-living carries with it automatic detriments and inevitably entails high costs to individuals, such as (1) augmented conflicts of interests and increased competition for all kinds of limited resources, including sexual partners; (2) increased risk of infection by contagious diseases and parasite transmission; (3) increased risk of exploitation of parental care by conspecifics; and (4) increased risk that conspecifics will kill one’s progeny (i.e., infanticide or cannibalism). So, what specific reproductive benefits accrue from social life?

Remember that selection operates principally on the genetic replicators of individuals. This leads to the expectation that individuals generally should avoid competitors and be nonsocial, and that (large) groups should appear only (1) when the resources of reproduction are so clumped that individuals must come into close proximity, a situation implying no cooperation, hence no special social organization, or (2) when cooperation contributes to individual reproduction in the population or species at large because of some hostile environmental force.

An exhaustive list of the selective background favoring group living in all organisms may contain no more than the following general items: (1) Reduction in predator pressure by improved detection or repulsion of enemies; Susceptibility to predation (by members of one’s own or some other species) may be lowered either because of aggressive group defense (as in musk oxen, for example), or because of the opportunity for individuals to use the group as cover, or to cause other individuals to be more available to predators, as with shoals of fish and herds of ungulates (‘Selfish herds’ as these have been called); (2) Improved foraging efficiency for large game or clumped ephemeral food resources: The nature of food resources may make it unprofitable for
individuals to splinter off, as, for example, with wolves and other predators
dependent on large game which cannot be caught by one lone animal; (3)
Improved care of offspring through communal feeding and protection; and (4)
Some resources, especially predator-free sleeping and breeding places, may be
extremely localized.
Alexander submits that sociality in any organism, including humans, only
appears because one or some combination of these factors renders individuals
accepting the automatic detriments of group living more fit, in terms of
reproductive success, than solitary individuals. Thus, sociality too is a
consequence of individuals pursuing their own genetic interests.
One interesting implication of this view is that those aspects of human culture
which give it a group flavor, notably its temporal inertia and its spatial
patterning, are incidental outcomes of the collective effects of generations of
individual humans pursuing their personal reproductive interests (as maximally
effective nepotists).
When humans began to live continuously in viscous social groups, first
presumably in bands of close kin and later in larger societies, within which
they could distinguish relatives of differing degree, two new selective forces
were added to their social life: Extended extrafamilial nepotism and extended
outbreeding. And, finally, social cooperativeness and eventually culture
became the chief vehicle of intergroup competition, the more violent forms of
which we call war.
Human hypersociality, the organization and maintenance of recent and large
human social groups cannot, Alexander insists, be explained by a group-
hunting hypothesis; the upper size of a group in which each individual would
gain because of the group’s ability to bring down large game would be rather
small. Instead human group sizes went right up to nations of hundreds of
millions of individuals.
8.4.10  Hunting

Sexual division of labor may be as old as the habiline hominids (*H. habilis*, ± 2.5 mya), who in all probability practiced a flexible subsistence strategy of "ecological opportunism optimized by tool use" (Slurink, 1994; Foley, 1987; Tooby & DeVore, 1987), i.e., gathering, scavenging and hunting; whatever fitted their omnivorous appetites. Despite Tooby & DeVore's (1987) criticism (Ch. 3), early hominids may have practiced scavenging, as chimpanzees sometimes do (Hasegawa, 1983), and, as only male chimpanzees do and males in contemporary hunter-gatherer societies still do, male hominids occasionally may have practiced big game hunting as a risky strategy for obtaining nutritious high-quality protein food not only for ready on-the-spot consumption but also for 'showing off' (Hawkes, 1991) and the exchange of meat for (sexual) favors, status and other privileges. With increased male parental investment (§ 8.3.13) this could develop into reciprocal food sharing between the sexes. The females of the species, often either pregnant or encumbered with dependent offspring (and somewhat impeded by the increasingly enlarged pelvic structures needed for giving birth to increasingly large-brained infants), like female chimpanzees and the females of contemporary hunter-gatherers, specialized in collecting plant foods, fruits, tubers, small animals, and other edible organic materials.

Vegetable foods are relatively abundant, sedentary, predictable and reliable, while game animals are relatively scarce, mobile, unpredictable and thus unreliable as a food source, and certainly difficult, and possibly dangerous, to catch. Hunting takes individuals also farther afield than is demanded by the gathering of food plants. So it makes good sense for females, encumbered with young infants, to forage for plant foods and leave the hunting to the males (Isaac, 1978; Symons, 1979; Leakey, 1981).

Murdock (1937) found that in all contemporary preindustrial societies he surveyed hunting was an exclusively male occupation.

Female gathering and male hunting/scavenging proved to be complementary and highly efficient survival strategies, which eventually resulted in semi-permanent home bases and male parental investment (Slurink, 1994; Tooby & DeVore, 1987). Hunting not only contributed to intelligence and the expansion of the hominid brain (Laughlin, 1968), it also led to the penetration of habitats and niches where plant foods would be scarce during winter.

Open country habitats support more game animals than forest habitats and therefore the opportunities and payoffs of increased hominid predation are highest on the savannah. "If males changed from occasional to intensive hunting, one consequence would be the extreme sexual division of labor found among humans, with females exploiting the more sessile food sources. Male parental investment through provisioning, exchange of hunted for collected food, and exchange of meat for sexual access all provide possible and mutually
compatible avenues for the extreme development of the sexual division of labor characteristic for modern humans. The evolution of this behavior requires no qualitative leaps from other primates: in chimpanzees (Teleki, 1973) and baboons (Strum, 1981; Strum & Mitchell, 1987) estrous females receive disproportionate shares of meat from hunts made by males...

For food exchange and meat provisioning to take place between independently foraging subgroups, there must be a home base. Such a meeting area to exchange food makes sense if the supply is irregular: either more (in the case of success) or less (in the case of failure) than the hunters would need for themselves" (Tooby & DeVore, 1987).

Alcock (1979) reasoned that the suite of occasional bipedalism, tool use, incidental hunting, adaptable and flexible behavior, cooperation, and prolonged infant care and family maintenance, may be a phylogenetically ancient pongid package of adaptations modified by the new selection pressures associated with the hunting-gathering niche. Hunting large and sometimes dangerous animals, repelling nonhuman predators and driving off competitive species, should favor individuals capable of cooperation in planning and executing such complex behaviors. The great likelihood that members of a band were close relatives would have further elevated the benefits of sociality and intraband cooperation.

It should be clear that accepting the greater or lesser role hunting may have played in hominid/human evolution, does not, in any way, imply some kind of 'killer ape' mystique as propagated by Dart and Ardrey, with hunting and killing prey animals as well as conspecifics as the primordial forces shaping human nature. Though it is probably true that mass extinction of megafauna may have coincided in some cases with the presence of H. s. sapiens ("prehistoric overkill": Martin, 1967), it is only very late in human evolution that unequivocal evidence of hunting turns up. The anatomical evidence of poor adaptation collected by Trinkaus has already been presented in § 3.10.

It might be added that nothing might be more ill-suited to the needs of a 'killer ape' than the set of twelve massive, high-crowned, flat 'grinders' possessed by both habilines and australopithecines, and anatomically modern humans. These are, as Harris (1975) notes, clearly the dental features of an animal with superherbivore rather than supercarnivore affinities. Furthermore, "for 3 million years, from the oldest tools at Rudolf and Omo to Bed II at Olduvai, there is no evidence of improvements in technology related to hunting. Hunting technology, in other words, remained rudimentary for millions of years. Hence if hunting were the primary adaptive mode of these ancestral hominids, it is inconceivable that their dentition would have evolved in a direction contrary to what would have been useful for puncturing, slicing, and chewing meat" (Harris, 1975).

Boxgrove Man (recently - 1994 - unearthed in the south of England and
tentatively classified as Homo heidelbergensis), estimated to have lived half a million years BP, was in all probability still a scavenger rather than a hunter. This observation undermines much of the machismo-flavored Carnivorous Psychology theories and the Foxian 'sin of Cain' version in which hunting equals destroying (Fox, 1989).

Together with the analysis by Trinkaus the evidence points in the direction of a relatively recent development of big-game hunting in Man. Also the argument that the Environment of Evolutionary Adaptedness (EEA) of Man was for million years a hunting environment loses much of its strength (Cf. also Zihlman & Tanner, 1978; Binford, 1985; and Kuper, 1994, who holds that "effective hunting must have become possible only in relatively recent times").

Especially Tooby & DeVore (1987) and Cosmides, Tooby & Barkow (1992) have argued that hunting-gathering was the ancestral EEA: "[O]ur ancestors spent the last two million years as Pleistocene hunter-gatherers, and, of course, several hundred million years before that as one kind of forager or another... The few thousand years since the scattered appearance of agriculture is only a small stretch in evolutionary terms, less than 1% of the two million years our ancestors spent as Pleistocene hunter-gatherers" (Cosmides, Tooby & Barkow, 1992).

But, as D.S. Wilson (1994) objects, it makes no sense to express evolutionary time as a proportion of the species history (the 1% fallacy). If the environment of a species changes, the evolutionary response will depend on the heritability of traits, the intensity of selection, and the number of generations the selection pressure continues. The number of generations that the species existed in the old environment is irrelevant, except insofar as it affects the heritability of traits.

Binford (1981, 1984) has claimed that early hominids did not hunt and had only very small components of meat in their diet. While such a view is probably incorrect, it is equally untrue to say that early hominids were full hunters in the same way as modern hunter-gatherers. Foley (1988) argued that if the term 'hunter-gatherer' is to mean more that just wild resource omnivory (in which case it would include baboons, chimpanzees and many other animals), "then early hominids were neither human nor hunter-gatherers".

Foley suggests that the foraging and reproductive strategies of Pleistocene anatomically modern humans differed markedly from those of most modern hunter-gatherers.

In contemporary hunter-gatherer societies (except in high latitudes where plants are scarce) one fifth to one third of the total caloric intake comes from meat, which means that females provide the bulk of the (vegetable) food (Lee, 1968; Zihlman & Tanner, 1978; Musonda, 1991; D.R. Harris, 1992; Poirier, 1993). Among agricultural societies, which depend mainly on domesticated

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4 Therefore, some have suggested that the term hunter-gatherer be replaced by a term more closely mirroring reality, such as gathering-hunting or collecting societies (Poirier, 1993).
crop plants, animals contribute still less to the average diet.

Despite the hunting hype, it may be said that by shortly after 2 mya some African hominids were exploiting a range of mammalian (especially ungulate) species to an extent unknown in nonhuman primates. This does not mean that these early hominids were hunter-gatherers in the organizational sense, merely that they were omnivores/diversivores in a significant manner, and reflecting the early hominids’ strategy of opportunistic foraging. Few changes in evolution are free from ‘knock-on’ effects that may themselves come to act as selective pressures inducing yet further change. Some of the evolutionary consequences of this new foraging pattern were:

1. Encephalization: Complex foraging strategies tend to select for larger brain size (e.g., Eisenberg, 1981; Harvey & Read, 1992; Milton, 1993; see § 8.3.1).
2. Social behavior: Tolerated scrounging and genuine food-sharing simply as a function of ‘package size’ of large game animals.
3. Spatial organization: Both increasing body size and terrestriality are likely to lead to an increase in home range for a species. The same holds for utilization of animal resources. In seasonal savannah environments resources are seldom highly predictable. Thus, in accordance with the economic defendability model, strict territoriality is unlikely to have evolved (Foley, 1987).

8.4.11 The Other Mammalian Social Hunters

The mammalian social carnivores are not closely related to humans but they have faced the same problems related to the capturing of large game. Through convergent evolution, humans have come to possess a suite of behavioral traits and attributes found more commonly in the social carnivores than in our primate relatives. Lions, for example, have a sexual division of labor in hunting: The females hunt while the males act as baby-sitters (Schaller, 1972). Male and female carnivores also establish reasonably permanent pair bonds. But of special significance for the understanding of the evolution of warfare among humans is the exceptionally high degree of cooperation and group integration exhibited by the social carnivores, demonstrated in (1) communal hunting of big game and food sharing within the group; (2) defense of the hunting preserve of the pride, pack, or clan to some extent against carnivores of other species but especially against conspecific intruders; and (3) the occasional killing of members of their own species in such encounters. Interestingly, the social carnivores are no more blindly programmed to be aggressive and ‘warlike’ than are human beings. Individuals are sensitive to the risks of aggression and seek to avoid conflict they are likely to lose. They kill one another when the odds are highly in their favor, as when an adult male lion finds the cubs of another male in a den (Schaller, 1972). They engage in group aggression to defend or expand group territorial borders only when game is
exceptionally abundant within certain defensible areas. Thus comparisons with social carnivores make more plausible the argument that the cooperative capacity of individuals, which promotes the efficiency of group hunting, will be extended only to members of one’s own group and may be used in ‘wars’ against the members of other bands. These comparisons, as Alcock (1979) argued, draw attention to the ecological foundations of ‘group aggression’.

In a study of territorial behavior by a clan of spotted hyenas, Henschel & Skinner (1991) suggest that larger clans can gain access to new food patches at the expense of smaller clans. Their study outlines the consequences of clans attempting and finally succeeding to expand their territories into those of neighbors. They could demonstrate some of the costs of defense for residents, but the actual costs of offense are much less clear. Furthermore, in spotted hyenas the degree of exhibiting territorial behavior (in which the adult females were the most active) is also a function of the degree of intrusion pressure:

In comparing various studies of spotted hyaenas, there indeed appears to be a relationship between the degree of intrusion pressure, the intensity of direct and indirect defence of territories and the scale of resource fluctuations. Where resident prey is relatively abundant, such as at Mavumbye and Ngorongoro (Kruuk, 1972), intruding and resident hyaenas compete for predictable, rich resource patches. This gives rise to strong territoriality. In contrast, where most prey is highly mobile and concentrated, as in Serengeti (Kruuk, 1972), hyaenas tend to follow prey migrations to some extent. With such high intrusion pressure, the potential costs of territory defence may be so high that it is little expressed. Where resident hyaenas depend on a succession of migrating prey passing through their territory, as at Mara (Frank, 1986) and Etosha (Gasaway et al., 1989), intrusions (by non-immigrants) and territorial activities were reported to be rare. Intermittently mobile prey was so widely dispersed in the Namib (Tilson & Henschel, 1986) and Kalahari (Mills, 1990) that territories were vast, the chances of detecting intruders in the periphery was slim, and only the territory centre was advertised strongly (Henschel & Skinner, 1991).

8.4.12 Tool Use and Culture

Hominids have been manufacturing stone tools for at least 2 million years (Isaac, 1984; Harris, 1986). The changing technology of the early hominids reflects partly greater manipulative skill, but also partly a change in cognitive skills (Foley, 1987).

The use of tools - promoted by the liberation of the hands due to bipedalism - became a central adaptation that enabled the (proto)hominids to forage on vegetative food resources and capture and process game more efficiently. The
importance of this culturally transmitted adaptation may be related to the increase in brain size and the explosive increase of the neocortex, but is surely reflected in the anatomy of the hand, permitting a more powerful power grip and a more precise precision grip (Alcock, 1979; Harris, 1975).

Once it was thought that bipedalism, tool use and brain size came in one neat package in hominid evolution. More recently, however, it has become clear that there is no necessary connection between erect gait and encephalization (the robust Australopithecines walked erect for more than a million years without showing any increase in brain size); between tool use and encephalization (chimpanzees may use tools for several hours a day); or between the erect posture and tool use (the robust Australopithecines were probably able to use tools - their hands are completely modern - but did not) (Slurink, 1993).

It has long been thought that it was the butchering of game animals that stimulated the development of tool making. Equally plausible arguments have been made, however, in favor of tool-making as a part of plant exploitation strategies, and, furthermore, nonhuman primates can hunt and consume prey without the use of tools (Foley, 1987). One area, according to Foley, where tools would have been of some use, and would have given hominids an advantage, is the scavenging of very large, thick-skinned mammals. These animals, which are usually immune from predation, often remain untouched for some time after death, as no animals can break the skin and gain access to the meat. Tools might well have given the hominids the ability to have early access to these carcasses, and thus a competitive advantage over other scavengers at least in the initial phases of exploitation.

Broadly speaking, ‘culture’ refers to the non-genetically transmitted aspects of the human species, incorporating such features as tool-use and tool-making, making artifacts and art, symbolic thought and language, mentifacts and accumulated knowledge, vast capacity for learning, imitation and innovation, increased behavioral flexibility and plasticity, all transmitted through learning and teaching rather than through any genetic system. Humans like to think of culture as distinctly or uniquely human, as the proper domain of the ‘Crown of Creation’. Culture in this sense is not confined to humans, however (e.g., Bonner, 1980). Furthermore, in the context of this study, the concept is not analytically useful for a number of reasons (Foley, 1987). The main reason is the following: Culture is a composite term bringing together a whole series of attributes that are important in the life of humans today. In studying the origins of these features (speech, tool-making, etc.), it may not be particularly useful to link them together, however. We do not know when any of these features first occurred within the homininid lineage. That is what we are trying to find out. Each of these features may have evolved separately, subject to independent selective forces, and so to lump these all together as ‘culture’ is to remove the possibility that hominids may, in the past, have possessed only part of their...
present behavioral repertoire, or that repertoire combined in different ways. Foley reasons that it is far more productive to adopt a reductionist approach to deal with the minimalist categories of behavior, and making the fewest assumptions. It is methodologically unacceptable to assume a different set of evolutionary rules for hominids.

But what about learning? Humans are inclined to think that there is some evolutionarily inherent advantage or superiority in learning abilities, and tend to forget how rare these actually are in nature; adaptation in most animal species depends very little on learning abilities. Indeed, why should an organism learn anything at all? It smacks of negligence, of unfinished business of evolution. Why not make the behavior built-in from the start? Learning is wasteful of time and energy; it is highly inefficient and may lead to maladaptive and even disastrous behaviors (e.g., when the correct response to sighting a predator has to be learned, or even the identity of the predator; a rabbit who had to learn that the presence of a fox signals a state of acute danger would probably not grow to reproductive age), or wrong and self-destructive ideas and superstitions, and manipulability, exploitability, deceivability and indoctrinability by conspecifics, etc.

There seem to be three general circumstances in which selection may favor learning abilities (Alcock, 1975; E.O. Wilson, 1975; Symons, 1979):
1. Learning processes may be a byproduct of selection for neural economy; 2. learning abilities may represent adaptations to make complex discriminations (e.g., in species or sex recognition); and 3. learning may be adaptive when environmental unpredictability (i.e., unpredictable by the genome) of some biological importance to an individual is reliably present in certain situations.

Furthermore, as Tooby & Cosmides (1992) noted, 'learning', like 'culture' is not an explanation for anything, but is rather a phenomenon that itself requires explanation. These authors, and other evolutionary psychologists, submit that the human capacity for adaptive flexibility and powerful problem solving is so great not because we have fewer, but exactly because we have more 'instincts' (i.e., content-specific problem-solving specializations, or Darwinian algorithms) than other animals, as William James (1892) already argued. What is so special about the human mind is not that it gave up 'instinct' in order to become flexible, but that it proliferated 'instincts'.

The single major question facing hominid social theory, as Tooby & DeVore (1987) noted, is the reconciliation of group life with high male parental investment and sexual exclusivity. To this problem we now turn.
8.4.13 The Human Mating System

Bonobos are the least known of any ape. What we do know, however, is that bonobos do have a number of unique and striking features among primates that may prove pivotal in discovering the principles governing male-female relations among hominoids, by providing yet another distinctive configuration of evolutionary variables (Tooby & DeVore, 1987; Susman, 1987). These features include female nearly-continuous sexual receptivity, the resumption of ovulation within one year after parturition, semipermanent male-female associations, male hunting and meat sharing contingent on copulation, and cohesive mixed sex groups.

"Among primates, humans are unique in simultaneously practicing (on a facultative basis): high MPI, multiple breeding males and females in the same social group, and sexual exclusivity (of at least limited duration) of individual females for males and males for females, frequently simultaneous and reciprocal. The features of this unique mating system are not directly paralleled by any other primate, and are not well captured by the term 'monogamy', especially given the statistical distribution of deviations on most of these practices" (Tooby & DeVore, 1987).

As we saw, several researchers have claimed that there is considerable sexual dimorphism in body size within *Australopithecus afarensis*, the earliest recognizable hominid. If the specimens ascribed to this taxon do indeed belong to a single species, then the earliest hominids are probably the most dimorphic of the family as a whole. Other members of the Hominidae also seem to show large to moderate sexual dimorphism.

With the evolution of anatomically modern humans there seems to have been a reduction in sexual dimorphism. This pattern suggests that the classical model of the early appearance of the pair bond, monogamy, in human evolution is incorrect, and instead that the early hominids may have possessed a social organization not dissimilar to that of other terrestrial primates; large group size and competition between males for access to females.

Harcourt et al. (1981), following work initiated by Short (1979) have shown that among primates testes size correlates with the social system (intensity of sperm competition). Martin & May (1981) have extended this analysis to include a discussion of possible mating patterns of early hominids. From this evidence it may tentatively be concluded that early hominids may have had a small-group, single-male, polygynous reproductive system (resembling modern gorilla).

Moving to a more open savannah environment, however, would have placed tremendous strain on this system as males would be unable to defend large territories, and, furthermore, there would be considerable selection pressure for larger group size as is seen among other terrestrial primates. This strain could
be resolved, according to Foley (1987), through increased kin-based male cooperation - in other words, away from simple polygyny to kin-regulated polygyny, where groups of related males remain loosely associated in larger groups with more specific polygynous family structures.

The most general reason for primate monogamy is the reproductive benefit to males if they protect their offspring from either predators or other, conspecific, infanticidal males (who may kill the infants in order to breed with the female). Infanticide has been observed in a great number of primate species. The solitary-living females benefit by having a protecting male around to reduce these risks (Dunbar, 1992; van Schaik & Dunbar, 1990).

Food-sharing occurs in all human societies, and, given its rarity among non-human primates (where it never transcends the level of 'tolerated scrounging'), it is taken to be a key human characteristic.

Assuming that it must have been primarily male hominids who did long-distance scavenging and/or hunting for large carrion and/or prey; assuming that the relatively less mobile females and their dependent offspring had something to gain from the nutrients in large game and/or carrion, and assuming that the females themselves continued to gather vegetable foods and perhaps killed small game, then the way was paved for active food sharing (as opposed to tolerated scrounging sometimes observed in chimpanzees).

A number of scholars (e.g., Morris, 1967; Washburn & Lancaster, 1968; Fox, 1972, 1980; Reynolds, 1974; Lancaster, 1975; Isaac, 1976, 1978; Zihlman & Tanner, 1976; Shepher, 1978; Zihlman, 1978; Campbell, 1979; Parker & Gibson, 1979; Symons, 1979; Endleman, 1981; Galdikas & Teleki, 1981; McGrew, 1981; Mellen, 1981; Fisher, 1982; Passingham, 1982; Daniels, 1983; Rancour-Laferrière, 1985; Parker, 1987; Foley, 1987, 1988; Slurink, 1994; a.o.) envisage that males and females at some point started to share/exchange food. These exchanges probably took place, moreover, at the 'home base' of a group, where males rejoined females and young after an expedition.

Isaac (1978) has argued on the basis of archaeological evidence that food sharing can already be documented among the early hominids of the Plio-Pleistocene. In this view, the division of labor, food-sharing, and the establishment of a home base where food is shared all occur rather early in hominid evolution (Foley, 1987).

Fox (1980) suggested that the ever increasing period of infant dependency put females at a disadvantage in the exchange, that is, left them more in need of meat than males were in need of plant food. Females began to offer themselves as part of the exchange:

"The impulse was more likely to have come from the female kin-coalitions. The need of the female coalitions for male provisioning - meat for the children - was undoubtedly the push. The females could easily trade on the male's tendency to want to monopolize (or at least think he was monopolizing) the females for mating purposes, and say, in effect, 'Okay, you get the monopoly -
or the appearance of it anyway - and we get the meat’. Insofar as the male was successful in turn, he would have had females to trade”.

Over a dozen different hypotheses have been proposed for human female concealed ovulation (e.g., Morris, 1967; Pfeiffer, 1969; Alcock, 1979; Alexander & Noonan, 1979; Benshoof & Thornhill, 1979; Burley, 1979; Hrdy, 1979, 1981; Symons, 1979; Lovejoy, 1981; Strassman, 1981; Turke, 1984; Alexander, 1990). Most theorists have suggested that concealed ovulation and continuous female receptivity facilitate monogamous pair-bonding through the mechanism of permanent sexual attractiveness.

Alexander & Noonan (1979) and Alcock (1979) proposed that concealment of ovulation evolved in humans because it enabled females to force desirable mates into consort relationships long enough to reduce their likelihood of success in seeking other matings, and simultaneously raise the male’s confidence of paternity by failing to inform other, potentially competing males of the timing of ovulation. If these events occurred in a situation in which paternal care was valuable, but not sufficiently valuable to males to offset philandering, and in which desertion was frequent when confidence of paternity was low, they could tip the balance, making increased paternal investment profitable to males. The intensity of sexual competition among males and the intensity of intergroup competition, both resulting in high mortality of young males, would have been of vital importance in this process. During the consort phase a male might share captured prey with the female because it would be likely that the progeny produced by the female would bear his genes; protein gifts to the female might, therefore, have genetic gain for the male. As usual, there is no requirement that individuals have to be aware of the genetic consequences of their acts.

According to Symons (1979), the most straightforward interpretation of the loss of estrus is suggested by the data on chimpanzee hunting. Estrous female chimpanzees are more successful than their anestrous counterparts in obtaining meat from males. When hunting became a dominant male economic activity, as it did during human evolution, perhaps the costs (in terms of fitness) to females of constant sexual activity were outweighed by the benefits of receiving meat, hence selection favored females who advertised continuously and thus were continuously attractive to males. Heterosexual exchanges of sex for food are common in the animal kingdom generally, and hominid female sexual overtures may have been motivated more by pragmatism about protein than by sexual emotion (Symons, 1979).

If hominid males regularly possessed meat surpluses before estrus was lost, a good hunter might do best reproductively by exchanging meat for copulations with estrous females. If ovulation could not be detected, however, a successful male might be better off acquiring permanent sexual rights to a female or females, resulting in a relatively high confidence in paternity, male provisioning of his mate’s offspring, and the evolution of other kinds of
paternal behaviors and dispositions. In this scenario the loss of estrus is a precipitating cause of the evolution of marriage and the family.

In Isaac’s (1978 et seq.) model home bases are an essential component of hominid foraging patterns. Potts (1984), on the other hand, argued that areas where carcasses are located would be places where hominids would minimize rather than maximize their activities on account of the threat of interactions with large carnivores. Potts envisages, as energetically most efficient, caches of stone tools distributed across the home range, and carcasses transported to the caches when discovered or hunted down. These caches would have been the antecedents of central-place-foraging, and, eventually, of shelters and home bases. Binford (1984), on the other hand, has argued that there is no indication of the development of home bases until the appearance of anatomically modern humans.

As male parental investment increased in importance in early Homo (± 2 mya), female competition for resource contributions would increase along with male efforts to increase their confidence of paternity. In Parker’s (1987) sexual selection model, he envisaged it as follows. A male subsistence strategy of bringing carcasses of scavenged prey to special sites where processing tools were stored (tool caches: Potts, 1984) would have paid off reproductively by attracting females to locations where they could be guarded at least temporarily. Hence a shift in subsistence toward butchery sites may have been the first step toward increasing control of females by hominid males. It may also have increased the incentive for aggressive competition among males and hence the value of using aimed missiles in combat.

At the same time the existence of desirable high-energy food gifts may have favored females who shifted from estrus advertizing to estrus concealment, thereby increasing their share of male courtship feeding as compared to females who relied on extended estrus and estrus advertizement. Display of permanently enlarged breasts and hips may have been favored as substitutes for epigamic genital display of chimpanzees (Short, 1980), or they may have evolved as advertizements of lactation competence (Lancaster, 1984). The advantage of storing energy for reproduction in fat deposits in the breasts and hips would have increased in proportion to the increasing energy demands inherent in the development of large brained infants (Lancaster, 1984). A larger brain implies increased infant dependency which implies increased parental investment and hence in increased period of food sharing and economic apprenticeship. This in turn would favor females who traded the increased confidence of paternity (or the appearance of it) for increased male parental investment.

Sexually selected shifts in courtship would have provided a mechanism for rapid divergence of early Homo from Australopithecus given minor habitat changes. Once early hominids evolved, continued sexual selection for increasing male control of females through provision of meat would have
fuelled the evolution of cooperative scavenging and hunting of big game. Sexual selection may also have favored shelter construction as another form of nuptial gift and parental investment especially as hominids migrated out of the tropics into temperate regions (Parker, 1987).

Increasing male control of females conflicts with female strategies. Females stand to benefit from polyandry (access to several males) in a variety of ways: "[G]ood genes, sexy son’s effects (both somatic and genetic), genetic diversity, fertility backup, material resources, and protection of self and offspring... and enhancement of social status" (R.L. Smith, 1984). Smith argued that continuous sexual receptivity in human females, cryptic or concealed ovulation, and some other female anatomical peculiarities and feminine characteristics (such as the hemispheric, pendulous breasts, and menstrual synchronization) have evolved to obscure a human female’s current reproductive value and confuse males as a countermeasure to male resource allocation and anticuckoldry strategies. These female adaptations enhance opportunities for facultative polyandry and thus promote human sperm competition. In a marital environment, females may have minimized their husbands’ abilities to monitor and to sequester them by not advertizing ovulation, and at the same time maximized their own opportunities to be fertilized by males other than their husbands (Symons, 1979; Benshoof & Thornhill, 1979; a.o.).

The conceptual modeling of this part of the hominid/human trajectory is marred with androcentric thinking (a 'Tarzanist’ scenario as Morgan [1985] called it, in which males are created with sexual needs and desires, the attainment of which is attended with sexual pleasure, and females are created to serve their needs and facilitate their pleasures and bear their young).

Furthermore, concealed ovulation may not even be an exclusively hominid/human female attribute. None of the theorists have ever systematically reviewed the patterning of sexual activity among nonhuman primates. When this is done, it might well be that the dichotomy is really an oversimplification (Hrdy & Whitten, 1987; Cf. Hrdy, 1981). Thus, rather than asking, ‘Why have human females lost estrus?’ we might better ask ‘Under what conditions do primates generally shift away from circumscribed to noncyclical or situation-dependent receptivity, and how do these changes contribute to female reproductive success?’.

Alexander (1990) argued that male confidence of paternity can be high in multi-male bands only (a) when each female restricts her matings to one male, and (b) when that male has a way of knowing it. Concealment of ovulation might have begun as concealment of copulation, or perhaps more narrowly as copulation sneaked by males otherwise subordinate, and possible because females agreed to them. A special kind of pair bonding would be tied to this
secrecy. The next step would be that the females simply conceal ovulation from the other males, and eventually start resisting them in copulation. Presumably, such a scenario would appear only when males really could help females and their offspring. One massively important way that a male might help his female and the offspring he sires is the prevention of infanticide by other males.

The honoring of the female-male pair bond may have been among the beginnings of morality. Socially imposed monogamy, Alexander asserts, seems to have spread across the world largely as the result of military advantages of the peoples promoting this particular marriage system. These and other considerations suggests to Alexander "that a strong tendency toward monogamy occurred early in human history, a unique kind of monogamy because it existed under social life in groups containing multiple males who cooperated with each other against males from other groups. It suggests that paternal care became important early in human evolution, and that extreme polygyny and domination of females within groups by subgroups of old males as occurs in some modern societies may actually be a derived feature of human social life, associated with extremes of social power developed by older males".
8.4.14 Ecological Dominance

Home bases not only complicated social life, but may also have facilitated social intelligence and increase of brain size, (proto)language as a reporting system, more permanent bonds between males and females, averting predators, intermale cooperation for intergroup conflict, more elaborate cultural traditions, etc. The Acheulian culture of *Homo erectus* (about 750,000 BP) contains hand axes and other stone implements. Also the bones of large game mammals are common at Acheulian sites. Zhoukoudian *Homo erectus* seems to have taken a cultural step even more important than carefully fashioned stone implements. Deep layers of charcoal fragments and pieces of carbonized bone indicate that the cave-inhabiting Zhoukoudian hominids were among the first to control the use of fire (M.Harris, 1975; Wu & Lin, 1983; Klein, 1989; see also Fig. 8.4). The discovery of the use of fire would have made drives and surrounds more effective; would have permitted the manufacture of fire-hardened wooden spears; would have made formerly inedible vegetable foods palatable; would have improved digestibility of starch and enabled degradation of toxins; and would have opened up new ways to prepare and store (and savor and relish) meat. Remains of hearths have been found at sites occupied by hominids between 400,000 and 300,000 years ago (D.R. Harris, 1992). Davidson & Noble (1993), on the other hand, have objected that there seems to be no good evidence that hominids regularly made and used fire, built shelters or hunted systematically, earlier than 125,000 years ago. They state that "although evidence of fire has been claimed from sites such as Chesowanja, dating back to 1.4 million years ago, and Zhoukoudian, dating back to 500,000 years ago, a recent assessment suggests that none of the claims earlier than Terra Amata is reliable - and even 230,000 years ago, it is doubtful whether hominids could regularly make fire".

The control and, later, the making of fire (e.g., Brain, 1981; Gowlett et al., 1981; Poirier, 1987; Brain & Sillen, 1988; Goudsblom, 1989; Klein, 1989; Slurink, 1993, 1994) may have enabled or facilitated the conquering of caves from inhabiting predatory animals, thereby creating safe havens from predators and climatic contingencies, effectively forming a protective shield against the dangers of the outside world, turning the hunted hominid into a hunting hominid (Brain, 1981), and crossing the 'ecological dominance' barrier (Slurink, 1993, 1994).

It is surely not a coincidence that the mastery of fire and the eviction of the big feline predators from habitable caves took place in the same time period. This is what Brain (1981) has to say on the Sterkfontein cave taphonomy:

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 this 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, 1981).

Alexander argued that when man developed his weapons, culture and population sizes to levels that erased the significance of predation by other species - and that is what 'ecologically dominant' means - he simultaneously created a new predator: Other human groups, leading to either manifest intergroup competition (i.e., war) or the maintenance of balances of power between such groups (i.e., the threat of war). Alexander did not specify, however, what made our ancestors ecologically dominant, nor did he specify when and how the entire process is supposed to have started.

Somewhere along the hominid trajectory groups of males began to compete as groups over what they perceived to be limiting resources, and what actually have been limiting resources for male organisms since time immemorial: Land and women. We do not know exactly when this happened. But it is tempting to speculate that it was the moment that home bases (be it caves, caches, or other hot spots) became relatively permanent safe havens and shelters from nonhuman predators and climatic contingencies, and thereby favorable, desirable, economically defendable, and suddenly extremely scarce sites, that territorial competition between hominid groups intensified in violence and frequency, and turned into genuine 'warfare'. It was not simply an extension of 'aggression' (as the individual motivational and behavioral system for contest competition) from the individual to the group level (otherwise numerous other mammalian species would have mastered the 'art' of warfare). On the contrary, males in the groups who were able to suspend interindividual competitive aggression for even the slightest period of time in order to cooperate to compete as groups had the competitive edge. As Bigelow (1969) stated: "Cooperation-for-conflict has probably always been the key to human survival".

Similarly, differences in groups between preadaptations for (a) group or tribal identity (ethnocentrism), together with xenophobia and slight paranoia (as the
evolved proximate psychology of intergroup competition); (b) some ability to
dehumanize the 'enemy' (turning intraspecific violence into interspecific
predation); (c) as well as numerical superiority; (d) weapon technology; (e) and
social intelligence (itself the result of intragroup competition); and (f) whatever
apotropaic ritual, anxiolytic drug, or superiority-delusional belief, doctrine or
religion which could overcome or reduce fear; would have given the
competitive edge.

8.4.15 War as a Parental Investment Strategy

During the Pleistocene male sexual access to women was in part dependent on
achieving positions of dominance or leadership. Selection probably favored
social skills and political abilities, such as judgment, oratory, and persuasion,
abilities to conceive and carry out complex plans, and skills in cooperative and
coalitional violence, including the evaluation of violent situations and the
taking of calculated risks, as well as controlling and managing aggression. In
such a milieu selection is extremely unlikely to favor simple male belligerence,
aggressive drives, or territorial imperatives. Human violence usually is a
complex group activity, and good judgment, not simple belligerence, seems to
be adaptive in a state of chronic violence (Chance & Mead, 1953; Fox, 1967;
Tiger, 1969; Bigelow, 1969, 1973; Tiger & Fox, 1971; Caspari, 1972; Symons,
1979; Chagnon, 1979 et seq.; a.o.).

In a situation of relentless intergroup competition and the continuous dangers
posed by other groups on the one hand, and complete intragroup mutual inter-
dependence for defense and protection on the other, cooperation with members
of one's own group was a matter of life and death, and the evolution of the
hominid ability to cooperate in ever larger groups can be explained without
resort to group selection (Slurink, 1994).

It seems likely as well that in a milieu of complex, cooperative violence,
selection would favor a male who was able to induce other males to take risks
for his benefit. To these skills and abilities might be added: Hunting-prowess,
and capacities as seducer and/or lover. Chagnon (1979 et seq.) notes that
among the Yanomamö Indians a major portion of the variation in male repro-
ductive success results from differential success in the political maneuverings
and machinations associated with male competition for mates. Among many
hunting-gathering peoples a man's hunting prowess is directly related to the
number of wives he can obtain.

"The evidence suggests, then, that for millions of years hominid males and
females pursued substantially different reproductive 'strategies' and typically
exhibited very different behaviors: throughout most of human evolutionary
history, hunting, fighting, and that elusive activity, 'politics', were highly
competitive, largely male domains. It is not a simple question of high female
parental investment and male competition for females: males and females
invested in different ways. Not only did males hunt while females gathered,
but, if warfare was often over land and other scarce resources from which the winning males’ offspring benefited, male fighting was in part parental investment; that is, like hunting and gathering, fighting and nurturing were part of the human division of labor by sex" (Symons, 1979).

In a similar vein, Trivers (1985) states: "We appear to have built on a chimpanzee proclivity for organized intergroup conflict and murder to produce a sexual selection extravaganza, in the form of full-scale war: the death of many or all male combatants, the capture of concubines or rape of the defeated women, the plunder of wealth, and the enslaving of peoples" (italics added).

If hominid/human warfare is evolutionarily the result of (sexually dimorphic) brains and vice versa (as argued by Bigelow and Alexander), and if brains developed in the interests of, and as an extension of, our gonads (as argued by Ghiselin), it follows that war evolved as a facultative male reproductive (or parental investment) strategy (as argued by Symons and Low).

This, then, is how a sexually reproducing, K-selected, mammalian, terrestrial, bipedal, tool-using, hypersocial, slightly ethnocentric and predatory, and, especially, brainy primate also became a group territorial and warring species.

Once in existence, (once "one band would have the capacity to consciously ponder the significance of adjacent social groups and to deal with them in an intelligent, organized fashion"), the process would be autocatalytic, and no group could, on penalty of extermination, afford to ignore this new mode of competition, as E.O. Wilson (1975; see Ch. 4) explained. "Once begun, such a mutual reinforcement could be irreversible. The only combinations of genes able to confer superior fitness in contention with genocidal aggressors would be those that produce either a more effective technique of aggression or else the capacity to preempt genocide by some form of pacific maneuvering".

It probably was not so much "consciously pondering the significance of adjacent groups" as envisaged by Wilson, as it was immediately and unreflectively recognizing competitors, and acknowledging the tactical advantage of preemptive attack, as envisaged by Alcock (1979).

From the point of view of a member of one band of hominids/humans, stranger hominids/humans are serious competitors whose presence will probably reduce the resources available to the band. Intraspecific competition for valuable resources might have favored hominids/humans that mobilized their cooperative and tool-using abilities against competing bands, giving the edge to the members of a band possessing superior technology and/or organization: "A sufficiently well-armed and well-organized group could hope to destroy the defenses of an unprepared group so quickly that the risk of personal injury to the attackers would be greatly lowered, reducing a major cost of aggression to them" (Alcock, 1979).
8.4.16 Group Size and Balances of Power

Alexander (1979 et seq.; Alexander & Borgia, 1978) agrees with Bigelow (1969 et seq.) and Darwin that violent intergroup competition was a *primus movens* in human evolution and that it selected for intragroup reciprocity, altruism, cooperation, intelligence, morality, etc. (As in all monocausal theories, the problem is *what moves the prime mover*?). War, according to Alexander & Borgia (1978), was a result of culture. Culture continually rebuilds the differences between neighboring human populations (a process called *pseudospeciation*; see Ch. 6). Culture is the great unbalancer that reinforces human tendencies to live and compete in groups and to engage in an unusual (and unusually ferocious) group-against-group competition. Culture frequently leads to imbalances that make such all-out aggression apparently profitable (Melotti, 1987).

Shaw & Wong (1989; Ch. 6) argued that larger groups would likely have enjoyed a competitive advantage over smaller groups (everything else being equal). This constituted a strong selection pressure toward larger group size: "In the evolutionary long run, larger groups would have displaced smaller groups and their members would thus have staked out a larger share of humanity’s gene pool. This implies that behavioral predispositions that facilitated group expansion would have been retained and incorporated into the more permanent repertoire of individual and group behavior".

Balance-of-power politics created a potent selection pressure toward bigger, stronger, more disciplined and sociopolitically better organized groups. Furthermore, within groups (a) a runaway selection for mental proficiency and complexity, inventiveness and cultural skills arose; and (b) because dominant males were increasingly dependent on cooperation with other males, they had to renounce their reproductive monopolies. This ‘reproductive opportunity leveling’ (or socially-imposed monogamy) enabled increasingly big groups to overcome potential sources of internal disruption (Slurink, 1993). "Balances of power are also significant within groups, continually denying to individuals and subgroups the possibility of initiating individualistic reproduction strategies or of fragmenting the larger group by secession or fission" (Alexander, 1979).

Another factor resulting from the increase in population may have been the increasing gracility seen in some hominid lineages. It might have paid to be a (smaller and lighter) member of a big group than to be a big member of a small group which would be no group at all in no time given the new rules of the game: It paid, in other words, to be big in number, not in stature.

Once humans began to use social cooperation as a principal means of competition, Alexander (1990) argued, they began to compete socially not only
as individuals but in coalitions of every imaginable size and variety. Moreover, once humans started living in groups (or continued group-living) explicitly because this enhanced their ability to compete with other neighboring groups, then the possibility of living nonsocially or solitary virtually disappeared - even if predators were removed, and food and shelter became abundant - because humans themselves would not allow it.

We usually think of cooperation as the opposite of competition. But if cooperation works, the evolutionary effect is to cause a kind of indirect competition with everyone else who did not cooperate quite as well. Regardless whether one individual ever interacts with another, the two are inevitably competing in regard to which will leave more copies of its genes. And, over the long run, those who are better at it become the ancestors of whoever remains. In this sense, cooperation is always competition as well, and competition thus is not only inevitable but, in evolutionary terms, has no alternative.

Social and Machiavellian intelligence (the brain as a social tool as envisaged by Humphrey, 1976), especially through success in competition achieved by cooperation, becomes paramount, and the race toward intellectual complexity, especially consciousness and the abilities to plan and anticipate, i.e., mental scenario-building and language, is on. Nothing, Alexander contends, "would select more potently for increased social intelligence - for better ability to look ahead and survey the alternatives accurately - than a within-species co-evolutionary race in which success depended on effectiveness in social competition".

None of the supposed causes except balances of power, Alexander holds, seems even remotely appropriate to explain the rise of the state.

Many scholars, from Spencer and Bagehot onward, regard the rise of tribal organization, chiefdoms, as well as state formation, as stimulated and perpetuated by continual power balancing or warfare with neighboring groups (Sahlins, 1968; Carneiro, 1970 et seq.; Harner, 1970; Service, 1971, 1975; Dumond, 1972; Adams, 1975; Fried, 1975; Lewellen, 1983; Cohen, 1984; Ferrill, 1985; Falger, 1994; among many others).

However, viewing conflict and warfare as though they were the only forces neglects other interacting factors (Holsti, 1913; Corning & Corning, 1972; Corning, 1973 et seq.; Braun & Plog, 1982; Cohen, 1984; Creamer & Haas, 1985; Masters, 1989; Shaw & Wong, 1989; Lee, 1990). Corning (1983), for example, in his synergistic view, states that warfare was most likely both a cause and an effect of socioeconomic and political evolution.
8.4.17 The Agricultural Revolution

Between 1.5 and 1.0 mya there is evidence of hominids in regions of sub-Saharan Africa and Southeast Asia. Between 700,000 and 300,000 years ago the more northerly temperate environments were colonized by *Homo erectus*; and between 300,000 and 40,000 years ago northerly latitudes came within the compass of hominid occupation (this phase coinciding with the evolution from *H. erectus* to *H. sapiens*); and between 40,000 and 10,000 years ago, by the end of the Pleistocene, virtually all the major habitats of the earth were colonized (Foley, 1987).

Interestingly, *Homo erectus* (possibly even as a single small group of a few dozen individuals) and a range of other species (lion, leopard, hyena and wolf) all reached temperate Eurasia at about the same time. Why?

There are some general principles governing the extent to which species may be stenotopic (confined to a specific habitat as a result of specialization and/or local adaptation) or eurytopic (able to tolerate a wide range of conditions and exploit resources from a variety of niches). Species with (a) relatively large body size; (b) carnivorous behavior; and (c) sociality, apparently had the adaptive capacity to exploit new temperate environments despite their tropical origins. Carnivores are more eurytopic than herbivores; relatively large body size is advantageous in colder climates; and group hunting apparently is a highly efficient resource extraction strategy.

The moment the ecological barrier was crossed, intergroup competition and/or balances of power forced groups to become bigger because numerical superiority is a vital advantage in (violent) intergroup competition. The steady increase in size of populations in Neolithic times once more made land/territory a limiting resource, and necessitated the transition to the agricultural mode of subsistence. The only advantage of agriculture compared to hunting-gathering is that agriculture requires less space and supports denser populations. The spread of agriculture was accomplished in about 8000 years beginning some 10,000 years BP (Cohen, 1977; Roele, 1993). This is also the time that war enters recorded history and is instrumental in building city-states, pristine states, and finally empires, beginning in the environs of Mesopotamia (The political instrumentality of war must have been independently ‘invented’ many times later on, e.g., in Meso- and South-America).

The agricultural societies would have had lesser economic product per capita, but they simply had more capita, and their militarily numerical preponderance would have left to the remaining hunter-gatherer societies only the marginal, peripheral, suboptimal habitats and low-quality refuges (Q.Wright, 1942; Roele, 1993; see Ch. 7).

Eventually, such a marginal international system stabilizes as a system of stalemate (war trap) and rampant war complexes, of balances-of-power and
endemic feuding, and occasional pockets of peace. In such circumstances there is no 'progress', but only stagnation.

Netting (1990) observed that even in autonomous communities of agriculturalists "fighting may well be episodic and fitful, directed at a variety of neighboring villages and without permanent coalitions or effective conquest". Observations such as these should dispel any notions of war as an inevitable 'Agent of Progress'.

The invention of agriculture made instrumental warfare in the Fertile Crescent increasingly profitable (for the victors, that is) simply because agricultural produce provided a more reliable, storable, or larger resource base (Alcock, 1979; Bigelow, 1969). It also had a price: The greater carbohydrate intake of early agricultural populations compared with hunter-gatherers led to nutritional imbalances and to protein- and vitamin-deficiency diseases, the effects of which are still manifest in their skeletal remains (D.R. Harris, 1992).

Another result of the population explosion after the agricultural transition would have been the necessity of morality (Alexander, 1979; Irons, 1991; Roele, 1993; Slurink, 1994). Roele (1993) explains: "If the size of societies increases, the basis for altruism erodes and the enactment of a (religiously inspired) system of morality becomes necessary. The system of morality would require individuals to help their neighbors and act in the common interest and would aim to reduce intragroup competition", especially reproductive competition, e.g., by means of socially-imposed monogamy, but possibly also by fomenting intergroup competition; such a system of morality is an ideal one for exploitation, indoctrination and disciplinization of young males in standing armies and warlike exploits.

Multi-village political aggregates and imminent chiefdoms are superior instruments of military defense and expansionist warfare. A permanent alliance of villages under unified authority provides protection, and community units may sacrifice local sovereignty and a degree of economic independence for this crucial goal. "In agricultural groups the primary cause of organizational elaboration appears to be defensive needs" (Johnson & Earle, 1987).

But, like everything else in evolution, such a benefit does not come cheap: Physical relocation, military service, and tribute payment would all decrease agricultural efficiency, especially for intensive cultivators with high-value fixed property. Thus, the economic costs of voluntary incorporation into a chiefdom would be considerable. Perhaps only the threat of warfare and destruction would justify the economic advantages foregone (Netting, 1990).

Once in a while pastoral peoples turned into pests and all but destroyed agricultural civilizations, but eventually the nomads were absorbed by the sedentary peoples or settled down after a period of wreaking havoc. The sinification of the Mongols is a prime example.
"Pastoralists tend to be particularly warlike and the histories of civilizations are punctuated by their inroads. [But] incursions of barbaric pastoralists seem to do civilizations less harm in the long run than one might expect [because] certain genes or traditions of the pastoralists revitalize the conquered people with an ingredient of progress which tends to die out in a large panmictic population... I have in mind altruism which is perhaps better described as self-sacrificial daring" (Hamilton, 1975).
The rest is history. As James Joyce is reputed to have said: "History is a nightmare from which I try in vain to wake up".

8.4.18 Epilogue

The main contention of this chapter is that warfare evolved as a high-risk/high-gain male-coalitional reproductive (or parental-investment) strategy. This, at least partially, explains why it is universally the males who are the warriors. Warring behavior is confined to typically highly-social and ‘brainy’ species, cognitively capable of establishing relatively long-term polyadic coalitions, mainly Hominidae and Panidae. This, at least partially, explains why warfare emerged so (relatively) late in evolution and why it is so conspicuously absent in mammals generally.