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Fertilization Systems and the Evolution of Human Capabilities.

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Synopsis.

Since the time of Darwin and Wallace, the origin of the human brain has been a controversial issue in evolutionary biology. The development of the human brain has been a dividing subject between those who attributed it to the forces of natural selection and those who emphasized the role of sexual selection. Building on Darwin's original insights, in this paper, we argue that the uniquely human cognitive capabilities are likely to have been initially spurred by sexual selection.

We consider the incentive properties of alternative fertilization systems and, following this "economic" perspective, we compare human gender relations with those of other primates. We argue that, because of its probabilistic egalitarian nature and its consequent quasi-monogamic gender relationships, the human fertilization system, is much more likely to have given selective advantages to emotional and rational intelligence and to have favoured the development of many fundamental human capabilities including language.

Even if our brain was initially spurred by sexual selection, after some time, unlike the famous case of the peacock tail, it turned out to be terribly useful also in the domain of natural selection. Thus, favourable selection complementarities had also an important role in the evolution of human capabilities.

We conclude by pointing out that human nature and human economic systems can be usefully seen in this light that emphasizes the immediate social nature of both rationality and emotions.

1. Introduction.

Ever since Darwin's and Wallace's contrasting views, the origin of human brain and of human (rational and emotional) intelligence has been a controversial issue in evolutionary theory.

Existing theories relate human intelligence to the complexity of group life (the ‘Machiavellianism’ hypothesis, see, e.g., Dunbar, 1996), to the increase in life expectancy that made possible for the initial investment in the human brain to fully repay its cost (Robson and Kaplan, 2003; see also Kaplan and Lancaster, 2003), or to the role of sexual selection in favouring the evolution of maladaptive traits that, like the celebrated peacock tail, could function as ‘fitness indicators’ (Miller, 1999).

Given the nature of the subject, all these theories seem able to claim some merits but in this paper we would like to argue for another possibility. Starting from the Darwin’s original insights that sexual selection had a fundamental role in the explanation of the development of our emotional and intellectual faculties, we try to support his thesis by comparing the human fertilization system to that of the other primates who share a common ancestor with us.

If we take an economist's point of view, different fertilization systems specify incentives to develop different kinds of gender relationships. We will argue that the unique human fertilization system set a system of rewards in the domain of sexual selection that led to the formation of quasi-monogamic relations and, as a consequence, to a first drive in the development of our emotional and intellectual faculties as opposed to the investments in body size or reproductive capabilities of our closest relatives. Given the social nature of our species, then, the relations of complementarity between sexual selection and natural selection helped to make the process self-reinforcing and irreversible by modifying the marginal costs and benefits of these alternative strategies.

The paper is structured as follows.

In the following section we consider the role that sexual selection can have in the process of speciation. We argue that, in cases where epistatic relations inhibit speciation and natural selection has a stabilizing role, sexual selection may favour the selection of populations that can better cope with the environment. In this sense, unlike the (perhaps overvalued) case of the peacock tail, sexual selection may yield positive effects also in terms of natural selection. If, because of epistatic interactions natural selection inhibits speciation, sexual selection may produce conditions analogous to those that in economics have been claimed to be useful for "infant industries" where it is claimed that some subsidy is necessary for their initial take-off.

In the third section we focus on the fertilization systems of humans, gorillas and chimpanzees and we show that each fertilization system implies a different marginal cost for males trying to get exclusive access to females. The gorilla and chimpanzees fertilization systems lie at opposite poles while the human system is characterised by incentives that may favour an egalitarian distribution of exclusive access to females.

While the third section takes a single male perspective, in the forth section we consider explicitly the interactions among males and we argue that under each fertilization system, males have different incentive to display a hawkish or dovish attitude towards their competitors in trying to acquire exclusive access to females. We argue that, while the gorilla and chimpanzees fertilization systems push again these two species towards opposite poles, concealed ovulation and other characteristics of the human fertilization system imply quasi-monogamic arrangements that are much more demanding in terms of emotional and rational intelligence.

The fifth section introduces the concept of selection complementarity and revisits the Darwin-Wallace controversy on the origin of human faculties. We argue that the selection complementarity between natural and sexual selection may lead to multiple equilibria where the marginal advantage of a trait over another in one selection domain depends on the characteristics of the selection process of the other domain. We argue that, while, in principle, the complementarity of the two domains implies that causation can flow in both directions, both Wallace's dilemma and

Darwin's insights imply that sexual selection had a decisive role in the development of human intellectual faculties.

The sixth section applies this framework to the origin of language. We review some important contributions that suggest that the changes in environmental conditions, due to climatic change were the ultimate cause of the development of human faculties. We argue that, while these factors were important, the decisive shock is likely to have arisen from the transition to the specific human fertilization system. We argue that this transition to the specific human fertilization system involves an endogenous discontinuity that can cause a high level of social stress and favour the individuals that are better endowed with the intellectual faculties necessary to deal with it.

We conclude by considering some implications of our analysis for the assumptions on human nature that are used in economic models. We argue that the social, egalitarian and reciprocating origin of human intelligence should be taken into account in all the disciplines that study human behaviour.

2. Speciation, Sexual Selection and the Redistribution of Fertility Resources.

According to the classical definition introduced by Mayr, "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr, 1988 p. 318). According to Elredge, while this definition established the primacy of reproduction as the *sine qua non* of species, it was left to Paterson to refine the conceptualisation of the nature of those reproductive communities"(Elredge, 1995 p. 466). Paterson defines a species as an inclusive community of individual biparental organisms that share a common fertilisation system. The fertilisation system includes all the components, such as courtship behaviour, genital structure, or attractiveness of the ovum to the sperm or pollen, that contribute to the ultimate function of bringing about fertilisation with another individual having the same fertilisation system.

Paterson's definition of species allows us to understand more precisely when speciation occurs. The two species become reproductively isolated when a different fertilisation system evolves. Thus, reproductive isolation does not evolve because the two species have developed two incompatible "economic relationships"[1] to the environment but it is rather a mere by-product of a change in fertilisation systems. A modification of the fertilisation system is both necessary and sufficient for speciation to occur. "In other words, a great deal of economic change can accrue within a polytypic species (whether through selection, genetic drift, or other mechanism of genetic change) without reproductive isolation necessarily following. The converse is also true as we know from numerous examples of "sibling" species, reproductive isolation can exist between two closely related species that are hardly to be distinguished on the basis of external, economic phenotypic attributes". (Elredge, 1995 pp.467-468)

Sexual selection involves such striking runaway effects such as the growth of the peacock tail that have no, or even a negative, "economic" value for the species in terms of its successful adaptation to the environment and that are rather related to a costly signalling of fitness. The selection for continued mate recognition can easily lead to a divergence of the fertilisation systems that is unrelated to successful adaptations to the environment[2].

While the literature has stressed the possible contrast between sexual and natural fitness, we would rather like to point out that sexual selection may also be useful to obtain adaptive advantages in terms of natural selection that would not occur

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[1] Here we use the terms "economic" and "reproductive" activity with meanings given by Elredge (1996). Economic activities refer to acquisition of food and other natural resources and are distinguished from the activities related to reproduction.

[2] At the same time it has been argued that "the function of courtship in sexually reproducing animals is to facilitate syngamy, and hence the male-female communication system is subject to strong stabilising selection. Unusual or fussy individuals (whether male or female) will be at a disadvantage, because they reject suitable mates or are themselves rejected." (Spencer and Masters, 1992, p. 301).

if only the latter is at work. In other words, we consider a case opposite of the "economically inefficient" runaway effect that is associated to the peacock tail. In the peacock tail case, the advantages in sexual selection are a substitute for forgone advantages in natural selection. By contrast, the focus of our paper is on the complementarity between sexual and natural selection[3].

When one considers complex organisms, fitness-improving speciation can be easily inhibited by the epistatic relations existing in their genotypes. These epistatic relations, which are, somehow, equivalent to economic complementarities, imply that complex organisms can be trapped in some of the many possible, and often inefficient, multiple "Nash equilibria". While each characteristic of the species is optimally adjusted given the other characteristics, a change of two or more complementary characteristics may, in fact, lead to the formation of a new species that is better adapted to the environment. In this situation, the pressure of natural selection may have an inefficient stabilising role for the incumbent species because it may eliminate the individuals of a population that, having changed only one characteristic, precipitate in a “fitness valley”. Such a valley, separating the present local peak from the new higher peak, may be a prohibitive obstacle when the adaptation to the environment involves the change of complementary characteristics among which these epistatic interactions occur.

Because of the characteristics that we have considered above speciation in sympatry is considered to be rather difficult. Allopatric and peripatric speciation may be then required to make the continuity of the evolution associated to the Darwinian theory consistent with the long period of stasis and the sudden changes that have characterised the evolution of many species[4]. There is however another possibilty: that the runaway effects that are associated with sexual selection bring about a major change in the situation of stasis that characterises the notion of punctuated equilibria (Eldrege and Gould, 1972). In this case a change of one characteristic would not be

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[3] We will see in section 5 how this view is very similar to that already advanced by Darwin (1879) and that it can be also expressed using a formal language similar to that of institutional complementarities.

rectified by the forces of "economic" natural selection because it increases the fitness of the individual in sexual selection. By contrast, because of "economic natural selection" other complementary characteristics may later adjust to this change made irreversible by sexual selection.

Our large brain takes time to develop, implies enormous delivery risks, absorbs many energies and makes us very dependent for many years and, in the past, an easy prey for many predators[5]. Only the development of many other complementary characteristics of our species could, at later stage, turn our large brains into our most important asset. These characteristics include women's menopause (Williams, 1957, Diamond 1998), which allows an optimal cut off time given the death delivery risk and the dependency of the existing children (both due to brain size), increased length of human life, which makes the brain initial investment paying for its huge initial cost (Robson and Kaplan, 2003), cultural selection and the accumulation of culture (Boyd and Richerson 1985) and, finally, the acquisition of technical and scientific knowledge. For this reason, it is not surprising that no other animal has developed a similar brain and it is rather a complicated puzzle to understand how we could break so many pre-existing epistatic relations.

In this paper we would like to consider the possibility that we differentiated from other species because our peculiar rules of sexual selection helped us to unfreeze our genotype breaking the many complementary characteristics that inhibited the production of a large brain. In this case, the runaway effect that often characterises sexual selection turned out at a later stage to be useful in terms of natural selection

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[4] On this point see Pagano (2001).

[5] Besides its large size, also the stages of development of the human brain constitute a considerable exception among primates. In general, Harvey, Martin and Clutton-Brock (1987, p. 193) observe that "there appears to be compensation or an "evolutionary trade-off", and thus we can define two extreme strategies for brain growth - a high rate of either prenatal or postnatal development". Humans are the only one striking exception to this pattern. "Humans' relatively large brains are achieved by producing relatively large-brained neo-nates coupled with pronounced postnatal brain growth".

increasing even further the advantages of moving in that direction[6]. In the same way in which male peacocks kept increasing their tails because it attracted more females, humans kept increasing their brain because sexual selection implied that individuals with a more developed brain could attract more partners and do better in social life with competitors[7]. However the similarity stops here. The peacock tail turned out to be only useful to attract partners but to be a disadvantage in dealing with nature and, in particular, to escape from predators. By contrast, when it was complemented by other characteristics and empowered with the cumulative accumulation of knowledge that it entails, our brain gave us an immense advantage over other species. It became possible to believe that we were God's relatives and that God created the other species for our benefit. The fact that we are a species rather obsessed with sex seems now to be a small tribute to the original sin[8] associated to the creation of our intellectual capabilities.

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[6] For a recent review of the theoretical and empirical literature on the mechanisms linking success in hunting with success in mating among hunter-gatherers, see Smith (2004).

[7] In Miller (1999), this role of sexual selection in helping the evolution of the human mind is explained in terms of ‘fitness indicators’. Sexual selection is viewed as a force favouring maladaptive or at least neutral traits with respect to natural selection, so that the analysis is confined to the most ‘creative’ feature of the human mind such as arts, music, and so on. A similar principle comes from Zahavi’s (1975)‘handicap’ theory. In section 5 we will see how Darwin (1879) had a much more positive view of sexual selection.

[8] The obsession with sex was related to the "original sin": if females could always be fertile it became evolutionary advantageous for males to find them attractive all the time (Diamond, 1991). At the same time, ovulation became effectively concealed because females were (selectively) receptive most of the time. Otherwise, their change in receptivity would have revealed their secret (however, an alternative way of keeping the secret would have been to be never receptive as it happens in the orangutan case). In this sense, Pawloski’s (1999) thesis that concealed ovulation is not a rare trait does not seem to take into account the full meaning of "concealment". The (self-)concealement of women was very effective. In spite of numerous centuries of observation women were not able to (re-)discover their own secret. This was also due to a wrong "a-priori" hypothesis: that women, like most other animals, were fertile while bleeding. The fact that this hypothesis was leading to partially successful practices made it even more difficult to discover the truth (David, 2001). David’s paper seems to disprove Roberts et al., 2004, who argues that ovulation was not actually concealed. David shows that the recent scientific knowledge on women's fertility periods did rather come as a surprise.

But why did sexual selection entail such a remarkable development of intellectual capabilities only in the case of humans?

The tentative answer of this paper is that this is due to the fact that, a certain point in time, women concealed ovulation - a rare event in natural history that involved a massive, and somehow egalitarian, redistribution of fertility resources and changed dramatically the direction of human evolution. Because of this redistribution, social skills became more important than physical strength: monitoring and understanding others, the capability of making and breaking commitments and having friends and allies became more important than winning a physical confrontations (and the large investments in body or in testis size)[9].

With advertised ovulation the males that could win the physical struggle with the other males were rewarded with a large concentrated prize of fertility resources. By contrast, with concealed ovulation the same prize was dispersed among all the females that had all the same probability of being fertile. Intensive insemination of females and/or huge investments in the acquisition of large harems did not anymore entail a high probability of reproduction. The capacity of making commitments and all the related social and communication skills became crucial to find good mating partners and to cooperate with them in exclusive relations. Thus, concealed ovulation may have started a long chain of events that changed the course of human evolution. Men had to acquire brain intensive social skills that turned out to be very useful for hunting and co-evolved with their hunting skills. For women (and in some respects even more for them), concealed ovulation implied that brain-power was a decisive element in sexual selection. With concealed ovulation receptivity signals could be sent only to the particular males that best fitted their tastes and their interests (including the parental investments that one could have expected from particular partners). While, for most species, signalling receptivity was a mechanical action, in the case of humans it became one of the many brain-intensive activities that women had to learn to perform.

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[9] Such cognitive abilities are also the necessary pre-adaptations for the Boehm’s theory of political egalitarianism in the hunter-gatherers’ moral communities (Boehm, 1999).

We can appreciate the importance of the human fertilization system for the development of our faculties only comparing it with the fertilization systems of other primates and, in particular, with those of our strict relatives: the gorilla and the chimpanzee that we will be considered in the following section. While, in making the comparison, we will often refer to concealed ovulation as some sort of abbreviation for the human fertilization system, it is important to stress that what contributed to make us humans are many characteristics of the human fertilization system and, above all, the selective and extended receptivity of females. We have argued that concealed ovulation was one of the factors that helped to develop female selective and extended receptivity, but this was far not from being an obvious outcome. Moreover, there are many ways in which female's choice may be exercised. A brief comparison with another big ape - the orangutan - may be useful to illustrate the dramatic importance of this point[10].

Female orangutans "have no external sign of ovulation but they develop pale labial swellings during pregnancy"(Rodman, Mitami 1987, p. 146). However, in this case, concealed ovulation may have produced a rather tragic result. Since non-pregnant females can always be fertile and concealed ovulation makes exclusive access very costly, males try to force mating all the time. In spite of these very promiscuous arrangements, both males and female live otherwise a solitary life and males, having no control of the transmissions of their genes, provide no form of individual or collective parental care. Females resist most attempts of mating. They are (rarely) successful only with the smallest subadult males. This may (ironically) suggest that female "may exercise choice in mating" - a doubtful hypothesis that is "currently debated" (Rodman, Mitami 1987, p. 150). The orangutan fertilization

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[10] In order to understand the specific characteristics of the human species it is very important to avoid "wrong choices of animals: Comparing humans with animals that have quite different anatomies makes little sense" (Pryor 2003, p. 98). For particular comparisons restricting the analysis to small clades including only subsets of the great apes can be very useful (Boehm 2004, p. 113).

system has encouraged a high sexual dimorphism[11] (because male size may favour reproductive success) and a limited investment in the development of emotional and rational intelligence.

The orangutans' case shows that concealed ovulation had such an important effect on the development of human faculties only because it was coupled with other traits that included a sophisticated form of female receptivity or, in other words, highly developed form of female choice[12]. This is an important caveat that we should keep in the back of our mind when we compare human concealed ovulation with other fertilization systems.

3. Exclusive Access and Fertilization Systems.

Our close relatives happen to be characterised by fertility systems that lie at opposite poles.

Gorillas are characterised by a mildly advertising of fertility occurring over a relatively short period. This favours the control of females[13], the development of harems and the investment in body size to win them. Mildly advertised ovulation

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[11] Male orangutans do not defend "clusters of females as do gorillas and some other highly sexually dimorphic primates; their sexual dimorphism in size may therefore be puzzling"(Rodman, Mitami 1987, p. 153). Here, we have advanced the hypothesis that the solution to the puzzle has to be related to their fertilization system.

[12] Indeed, from the point of view of female choice and the strength of female-female relationships, the primates that seem to be the closest to humans are the bonobos. They share with human females a prolonged period of (less selective) receptivity. Similarly to the case of chimps, the extended and prolonged period of receptivity discourages individual male parental care but their very promiscuous arrangement is otherwise very peaceful and cooperative (more so than that existing in chimpanzee societies). For a comparative analysis of chimps' and bonobos' societies see Nishida and Hiraiwa-Hasegawa (1987) and the collection of essays edited by Boesch, Hohmann and Marchant (2002) who, in the preface to the book, observe how comparative studies must cope with the difficulty posed by the possibility of cultural diversity existing among the communities of each species.

favours the monitoring of a harem because it provides quasi-private information to the dominant male who controls a given territory. The dominant male can easily know which females should be inseminated and controlled without attracting too much attention from the other males. The competition with the latter is mainly in physical strength and has implied an enormous difference in body size between males and females (typically the weight of male is about two times that of a female). A visible (and, for some humans, paradoxical) result of gorilla male dominance is the very small size of their penis and, especially, of their testis.

The fact that the chimpanzees lie at the opposite extreme is immediately testified by the remarkable investment that has gone in the male testis, that are about three times the testis of the gorilla[14], and, otherwise, by the little difference between male and female body size (that is even smaller than in humans). Here, females are engaged in a very long and evident advertising of fertility that makes the monitoring costs of a harem very high. Moreover, because of the public and stimulating nature of the female fertility signal the exclusive access to a single female becomes prohibitively costly. Chimps' Society is sexually very promiscuous. Fighting or trying to develop ties have all a very high opportunity costs in terms of the only activity that really determines the males' reproductive fitness. Investing in testis size turns out to be more advantageous than investing in body size (or in brain size).

In some respects, the human fertilization system falls in an intermediate situation. However this does not occur because human females give a fertility signal of intermediate intensity. Indeed, one may think that these intermediate signals may be unstable because they give neither an abundant supply of males nor the possibility of exclusive access and the incentives of parental care. Paradoxically, concealed ovulation implies a cost of exclusive access to females that falls in between a strong

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[13] However, females seem also to exercise choice (even if the basis on which they choose males are still poorly understood). In any case "once a female finds a suitable male, she may remain with him for many years" (Stewart, Harcourt 1987, p.163)

[14] The average size is 120 gr. against the 35 gr. of the gorilla. Observe that when they are compared to the weight of the body they are ten times bigger (0.3 % in the case of the chimpanzee and 00.3% in the case of the gorilla) See Gribbin J., Cherfas J. (2001, p. 170).

and a weak signal. Unlike a weak signal, concealed ovulation makes exclusive access very costly because it makes unclear which female is worth the male's attentions and his monitoring effort. Thus, concealed ovulation makes it difficult to have the gorilla-type harems and decreases the evolutionary fitness of the related hawkish investment in body-size. Unlike the strong public chimp fertility signal, concealed ovulation makes it possible (even if at a cost well superior to that sustained by the gorilla) the exclusive access to females. This is particularly favoured by the careful application of emotional intelligence and the creation of long terms bonds between a male and a female. Since every female (including the present partner) can in principle be fertile additional exclusive access is costly. Each male has little information about the fertility state of the new partner and of the present partner who are equally likely to be fertile. Some egalitarian redistribution of fertility resources takes place in probabilistic terms and implies that the reproductive strategies, examined in the preceding section, become convenient. Their consequences include many of the elements that make us humans: the capacity and the interest in communication, the ability of making (and breaking) deals, the willingness of sharing and the propensity towards joint parental caring.

In a single-male perspective, the fertility signals of these three primates imply different marginal cost (MC) and marginal benefits (MB) of gaining exclusive access to females and thus different optimizing choices [15]. A mating system can be considered as an equilibrium in which the 'quantity' variable is a single male exclusive access to his fellow females, and the 'currency' of its costs and benefits is 'fitness', that is their total offspring. While the marginal benefit of exclusive access can be assumed to be always positive but decreasing in the number of females (because of limited insemination capacity by the male and the trade-off between quantity and quality of children) and roughly equal for all the three species under

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[15] Note however that different fertility signals can be taken to mean different ways females choose in the first place (Hrdy, 1979). Therefore the present analysis introduces the typical ingredients of sexual selection –female choice and males competition- step by step.

consideration[16], the ‘technology’ of fertility signals determines radically different cost functions as it is shown in fig. 1 where CMC, HMC and GMC stand respectively for Chimps', Humans' and Gorilla's marginal costs of gaining exclusive access to females.

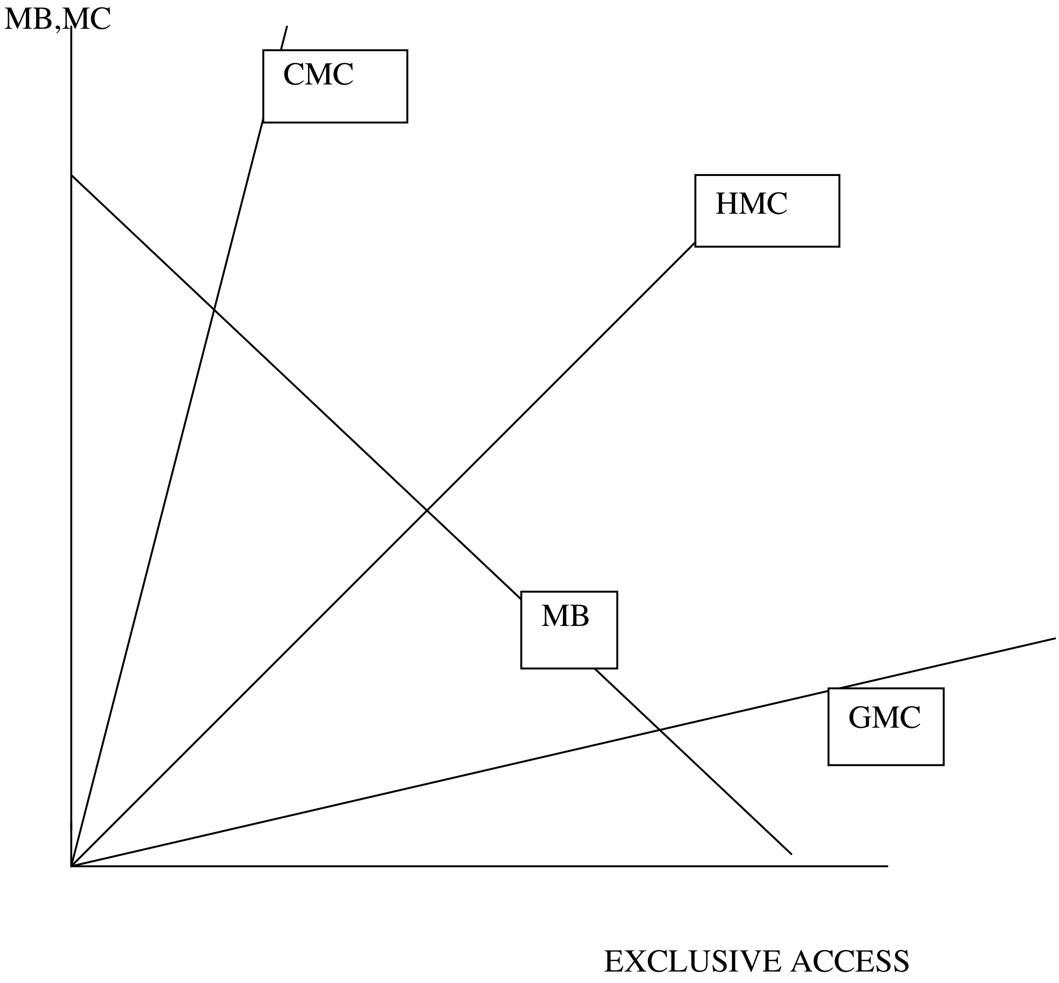

FIG 1:
MB: MARGINAL BENEFIT OF EXCLUSIVE ACCESS
CMC: CHIMP MARGINAL COST OF EXCLUSIVE ACCESS
HMC: HUMAN MARGINAL COST OF EXCLUSIVE ACCESS
GMC: GORILLA MARGINAL COST OF EXCLUSIVE ACCESS

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[16] So we are assuming that there are no differences in reproductive rates (offsprings number per birth, births intervals, and so on). Since a species-specific ‘revenue’ function would make the results more robust, the assumption is simplifying and does not imply loss of generality.

Consider in particular the opportunity cost of the ‘quantity’ variable, that is, the fitness value of the number of forgone alternative mates a male ‘pay’ in securing exclusive access to a particular female[17]. When the signal is short and weak as in the case of gorillas, the marginal cost GMC increases slowly in the number of exclusive accesses. When the signal is both time- and space-concentrated, it can be assumed that it is a private signal for the dominant male who controls a certain territory, the securing effort does not imply significant losses in terms of alternative mates, and the gorilla male ‘maximizes’ fitness by choosing a huge number of exclusive accesses (the harem solution). Indeed, in the limiting case of perfectly sequential ovulation periods, this marginal cost function actually coincides with the X-axis, obviously implying a zero marginal opportunity cost of exclusive access.

At the opposite extreme lies the chimpanzee solution. A chimp male should give up to a huge number of alternative mates in securing the exclusive access to a chimp female who is doing her typically strong and prolonged advertisement of actual receptivity. Note again that in the limiting case of a perfect synchronization of ovulation periods, the chimps’ marginal opportunity cost CMC schedule coincides with the Y-axis since the resources consumed in trying to secure access to only one female could have been employed to ‘produce’ offspring with all the other females of the group. So the ‘promiscuous’ solution of zero exclusive access seems equalize marginal costs and benefits in the normal case.

Independently of sequential or synchronized fertility periods, concealed ovulation in human females implies that the signal is absent, that is, time and space indefinite. Assuming that the only female characteristic relevant to the male’s interests is fertility, the 45° degree line represents his marginal opportunity cost schedule HMC that reflects the one-to-one nature of the human male choice, and quite clearly the egalitarian nature of this kind of fertility resources distribution. Should one male try to

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[17] Other specifications of the relevant costs such as the number of expected fights or the magnitude of expected contestation could have been fruitfully employed and will be considered in the next section. The opportunity cost specification, however, is the most convenient to illustrate the ‘egalitarian’ nature of the concealing of ovulation in human females.

secure exclusive access to one particular female, he would lose the opportunity to reproduce with another equally attractive (in fitness terms) female, and so on. A sequential monogamic mating system, typically attributed to the hunter-gatherer societies (Miller, 1999; Hrdy, 1999),[18] could easily be an equilibrium under this fertilization system.

Implicit in this formulation of the costs and benefits of exclusive access is a trade-off between offsprings' quantity and quality, which in turn derives from the more general trade-off between mating and parenting effort (Trivers, 1972). Thus, the derived results give an account of the proposed distributive explanation of the human-specific mating strategies (pair bonding and monitoring, parental care joining and sharing)[19]. By introducing male-on-male competition and the associated fights and contestation costs, in the next section we try to model the evolutionary stability of the different investment strategies outlined above.

4. Fertility Signalling and the Evolutionary Fitness of Hawkish Behaviour.

In this section we drop the single-male perspective and analyse the other side of the consequences of alternative distributions of fertility resources. If, from the single-male point of view, different fertility signals imply different opportunity costs and different allocations of the scarce resource, it is by no means surprising that they

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[18] In other words in fitness terms, with concealed ovulation, there is a negligible gain (or even no gain) to change partner until the male knows that he has succeeded at inseminating his partner.

[19] These results are also compatible with the established anthropological literature on the subject. When concealed ovulation is meant as absence of clear signals of a fertile state, its adaptive explanations range from increased males cooperation (Etkin, 1963), increased parental care (Alexander and Noonan, 1979), and decreased infanticide risk (Hrdy, 1979, 1981). According to Sìllen-Tullberg and Moller, 1993, concealed ovulation evolved first to reduce infanticide, and then facilitated the evolution of monogamy. However, the gorilla's and the chimpanzee's fertilization systems could also be seen as different solutions to the same adaptive problem of male violence on infants, either by completely clarifying paternity issues (the case of gorillas) or by completely confusing them (the case of chimpanzees).

imply also different types of competition and different kinds of the ‘weapons’ that are appropriate to compete.

Indeed, when the signal is mild and short as in the case of gorillas, it is to be expected that competitors are few and concentrated. So an aggressive behaviour and the associated investment in physical strength may be the best strategy. By contrast, when the signal is strong and prolonged as in the chimps’ case, competitors are so numerous and time-distributed that a non-possessive and promiscuous attitude, coupled with an eventual investment in testis size, may turn out to be the most attractive strategy.

These two kinds of behavioural responses –the ‘fight’ or ‘flight’ options[20]- have a natural representation in the very famous hawk and dove game that was originally proposed by Maynard Smith and Price (1973) to study the behaviour of a population of animals randomly paired to contest a resource of value *V*. Following the popular wisdom, hawks are hawkish and doves are peace-loving[21]. So when it comes to two hawks, each one of them has an equal chance of winning the prize, or of losing the cost of fighting, *C*. However, when a hawk meets a dove, the latter retreats and the former takes the prize for free. Finally, when two doves meet they share the prize (fig.2).

	H	D
H	**(V-C)/2**	**V**
D	**O**	**V/2**

FIG. 2

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[20] Pedersen (2004) contains a very interesting analysis of the proximate causes that may have led humans, and particularly human females, to develop an emotional control of rage and fear to choose between such options in an appropriate way.

[21] Lorenz (2002) clarified that doves are not peace-loving but have a capacity of flight that is far superior to their means of aggression. For this reason they have not developed inhibitions against aggressive instincts and they are particularly cruel when their enemy cannot escape.

As expected, the solution of the game depends on the two parameters. When $V>C$, the only evolutionary stable strategy is the Hawk strategy and the population will end up for being entirely composed of hawks. By contrast, when $V<C$ the only ESS strategy is a mixed strategy and the corresponding hawks' equilibrium fraction is V/C, of course increasing in V and decreasing in C.

Now it is easy to see the link with the previous argument. A weak and short signal corresponds to a relatively weak competitive pressure. So the harem solution of the gorilla-case can be represented by the hawk-hawk equilibrium (low C, $V>C$). On the other hand, the strong and prolonged advertisement of the chimps' females implies an extremely high cost of fighting, and the equilibrium population state will be composed of almost only doves[22] ($C \to \infty, V/C \to 0$).

Even if our picture of gorillas and chimps is somewhat pushed to two extreme idealized opposite situations, it is clear that the obvious superiority of one strategy (dove-type strategy in the case of chimps and hawks-type strategy in the case of gorillas) makes social life relatively simple. Indeed, this simplicity of social life is embodied in the physical competition in testis size (in the case of chimps) and in physical strength (in the case of gorillas). One would expect that the complexity of social life is greatly increased for fertilization systems that are characterised by the

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[22] The dovish attitude of chimps is only related to sexual relationships. In the case of chimps even sexual relations occur in three patterns. "Possessive mating" involves some hawkish behaviour: a male (typically the alpha) uses threats or aggression to prevent other male from mating. "Consortships" occur when a male (not the alpha) and a female travel together away from other members of the community and maintain an exclusive mating relationship for a few days. However, in large communities, 70 to 90 per cent of the matings are "opportunistic": a male copulates freely in the presence of other males "with no indication of male-male competition" (Nishida, Hiraiwa-Hasegawa, 1987, p.170). In any case, this dovish attitude is limited to the members of the community. Encounters between different communities carry a risk of severe aggression and they can involve killings, infanticides and subsequent cannibalism. Bonobos (which we group here as doves together with their sister species chimps) are an even better example of dovish and particularly promiscuous attitude. For a comparison of Chimps and Bonobos sexual relationships see Furuichi and Hashimoto (2002, p. 165) who observe that, female bonobos copulate less frequently than chimps during the swelling phase, they "show estrus for much longer period" and use "non-copulatory sexual behaviours to regulate tension or enhance social bonds".

fitness of both hawks and dove behaviour. We have observed that, in a regime of concealed ovulation, gaining exclusive access to the fertility resources of one female may (roughly speaking on average) involve the opportunity cost of losing (probabilistically) equal fertility resources of another female. In this extreme case, once a male has gained exclusive access to a female the marginal benefit from fighting for an extra-females is equal to zero. Thus, given an egalitarian distribution of females, (sequential monogamic relations) any benefit of hawkish behaviour disappears. In this case, society could completely eliminate wasteful male competition in body size investment (including testis size). Of course, this is a very idealized picture. A male can control and exploit efficiently the fertility resources of more than one female and, if he is sufficiently selfish, he can turn his attention to other females after that he has made pregnant the present female. Thus, concealed ovulation leads simply to a dramatic reduction of the benefits hawkish behaviour and not necessarily to its disappearance.

We have seen that intentional receptivity signals of females, their consequent bargaining power and their request of parental care and cooperation, the long term commitments of males and females as well the ability of breaking them (often hiding it to the partner) are all consequences of the human fertility that make our social life very brain-demanding. We can add in this section that this increased complexity of social life can be seen within the framework of the hawks and dove game itself.

The gorilla fertilization system implies a simple rule: behave as a hawk and demand as much exclusive access as you can.

The chimpanzee rule is also simple: behave like a dove and share females because fighting for exclusive access is useless.

The human rule is much more complicated: it is certainly worthwhile to fight like a hawk to acquire and to defend the exclusive access to one female but some dovish behaviour may be highly recommended beyond that point. Indeed, the human mating system may seem particularly apt to be represented by the well-known ‘bourgeois’ strategy, dictating of behaving like a hawk if owner, and as a dove if intruder (Maynard-Smith, 1982). Given the egalitarian rule it implies when applied to our context –one male for one female- its global stability properties can be seen as a proof of the nearly ‘evolutionary universal’ character of human (sequential) monogamy, and it does not suffer either from so-called ‘desperado’ effect, that is, by the fact that in general the costs and benefits depend upon the distribution of the strategies in the population (Grafen, 1987; see also Gintis, 2004, for a more recent and general treatment)[23]. Moreover, the "endowment effect", which cannot be explained on the basis of sunk costs (Gintis 2004), finds here a natural explanation. Under a regime of concealed ovulation the past time spent with a partner give more information in terms of the benefits of exclusive access about the future time dedicate to this partner and decrease the benefits of a future partner relatively to the fertility benefits of a new partner.

However, when it comes to the ‘weapons’ best suited to tackle the associated competition the ‘bourgeois’ strategy does not tell very much, and the same is true for the other fights-avoiding asymmetries -such as differences in age, strength, fighting ability- usually considered in animal contests (Hammerstein, 1981). The absence of fertility signals entailed by concealed ovulation in human females may be taken to mean something like a ‘selectively constant but far from obvious receptivity’. On the one hand, this means that the ‘bourgeois’ strategy is particularly vulnerable to errors due to imperfect information concerning possession (Hammerstein and Parker, 1982; Bowles and Choi 2003)[24]. On the other hand, it means that the number, the time-distribution and –most importantly- the type of competitors is somewhat indefinite, and that there are evolutionary gains to be realized in developing appropriate social and cognitive abilities. In this sense, each individual who wants to have a reasonable fitness should play hawk and dove strategies in different circumstances. In a situation

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[23] For example, when reproductive success requires possession of a territory but all are already owned, a non-owner has nothing to loose from a fight and, as a result, ownership will not be respected in general.

[24] Since in the hunter-gatherers societies the distribution of material wealth was also egalitarian and probably not yet man-dominated, ‘property rights’ on sexual relationships and their ‘products’ could not be taken as self-enforcing and, in the limit, the associated monitoring costs involved high opportunity costs not only in terms of forgone alternative mates (see the preceding section) but also in terms of forgone productive efforts.

where the intrinsic characteristics of the individuals have become blurred, assessing who is, in each circumstance, a hawk or a dove becomes itself another very brain intensive activity.

Individuals, who try in some circumstances to show that they are hawks, may flee like doves if a “true” hawk comes around and, vice versa individuals, pretending to be cooperative and sharing doves, may turn out to be hawks as soon as they can exploit a "true" dove. Assessing[25] the hawkish and dovish characteristics of the competitors in particular situations becomes crucially important for enhancing fitness. In this situation the emotional intelligence, which includes the cognitive capacity to understand the characteristics of the competitors and of the potential partners, becomes the most precious factor for successful mating. Highly developed political skills, and the related ability to have "rules that deliberately constructed and malleable" (Pryor 2003 p. 127), become the typical expression of human nature. Thanks to these abilities humans can go beyond the "bourgeois" forms of property that are already implicit, at rudimentary level, in the territorial defence carried out by many species. Humans can create "a society of essential political equals" where "no independent adult has the right to take the property of others by force, and no one is allowed to boss others around" (Boehm 2004 p. 122). Because of their political skills humans cannot only build more complex systems of private property but also sophisticate forms of communal property that allow successful variance reduction practices with large game hunting. In this respect, as Boehm (2004, p. 130) points out, the development of the institutions of communal property is the most specific characteristic that distinguishes the cooperation of human hunters from that of their closest relatives.

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[25] Again centered on physical attributes, an Assessor strategy dictating of behaving like a Hawk if bigger than your opponent and like a Dove if smaller has been introduced first by Parker (1974), and further elaborated by Maynard-Smith and Parker (1976). More similarly to our perspective, Panchanathan and Boyd (2003), analyze a ‘Discriminator’ strategy which allows the players in a public game to assess whether a non cooperative action comes from a selfish or a punisher strategy. Their aim is indeed to emphasize the adaptations –such as, for example, language- which are pre-conditions for the evolution of moral systems based on the notion of indirect reciprocity (see also Alexander, 1987, and Wilson, 1999).

5. Selection Complementarity: Darwin vs. Wallace on the "Origin" of the Human Brain.

The origin of the human brain has been a controversial issue in evolutionary biology for a long time. Since the time of Darwin and Wallace, the development of the human brain has been a dividing issue between those who attributed it to the forces of natural selection (like Wallace) and those who (like Darwin) attributed it to the forces of sexual selection. We will go back to this debate at the end of this section. Before that, we try to argue how, for the case of the brain, the relation between the two mechanisms should be seen more in terms of selection complementarity than in terms of selection substitution and that selection complementarity can be understood in a way analogous to institutional complementarity[26].

Suppose that we have two domains (the sexual and the natural selection domains) where individuals are selected according to two different rules. The individuals subject to the mutations associated to a certain type of "investment" in one domain may sometimes coincide with the ones mutating in the other domain. What matters is that the rules by which they are selected in the one domain act as parameters in the other domain. Assume also that all the individuals acting in each domain derive equal fitness from having a certain trait.

Define by

N: natural selection domain
S: sexual selection domain

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[26] Selection complementarities are analogous to "institutional complementarities". In the case of institutional complementarities individuals choose in each domain the best institutional arrangements taking as parameters the choices of other individuals. Similarly, in the case of selection complementarities the fitness of each trait in a particular domain depends on the traits that have been selected in the other domains.
Economic treatments of institutional complementarities can be found in Pagano (1992), Pagano and Rowthorn (1994) and Aoki (2001).

and by:

In: Intelligence in natural selection
Bn: Body Size in natural selection
Is: Intelligence in sexual selection
Bs: Body Size in natural selection

Let us start by considering the natural selection N domain and assume that in this domain individuals can acquire an Intelligence Advantage (In) trait or a physical advantage trait by developing a more powerful body (Bn). Both are costly investments and both can increase their chances of success to survive in a hostile environment characterised by the hardship of nature, the difficulty of finding preys and the danger of predators. Whatever the relative advantages of the two types of investment governing natural selection, they will be (marginally) affected by what happens in the sexual selection domain. In particular the marginal advantage of investing in tool making and in hunting strategies over the advantage on investing in greater physical power is increased when, in the sexual selection domain S, investments in differential social skills and various forms of rational and emotional intelligence (Is) are being selected against investments in differential physical strength (Bs). To catch preys, tool making and the development of hunting strategies are made cheaper relatively to increased investment in physical power by the fact that increased investment in social skills are favoured over hawkish behaviour in the sexual selection domain. This investment intensity, occurring in the sexual selection domain, makes it cheaper to invest in related abilities in the natural selection domain. It implies that these investments are not burdened by the fact that individuals dealing in a clever way with nature (bigger brain - smaller body) are not deprived from the access to fertility resources. Thus, concealed ovulation by increasing the advantage of Is over Bs can indirectly help the development of humans into skilful tool-makers and hunters. Denoting by u the fitness that the individuals have in the natural selection domain N we have therefore the following relation:

$$u(In; Is) - u(Bn;Is) \geq u(In;Bs) - u(Bn;Bs)$$

Conversely, in the sexual selection domain S, denoting by v the fitness of the individuals in the sexual selection domain S the following relation holds:

$$v(Bs;Bn) - v(Is;Bn) \geq v(Bs;In) - v(Is;In)$$

In other words, in the sexual selection domain S, investing in Body Advantage (Bs) yields a greater fitness than investing in Intelligence advantage (Is) when in natural selection N domain Body advantage (Bn) is selected over Intelligence advantage (In). If, in natural selection, physical power increases fitness more than brain power, this changes the parameters under which sexual selection occurs. Investing in emotional and rational intelligence becomes very costly. It does not only imply forgone investment in insemination and/or body-size differential advantage but also giving up the superior productivity of physical power in the natural selection domain. In this case, even an individual, who, thanks to a shift of investment from physical power to brain-power, would do better in the sexual selection domain, may see this advantage so much decreased that investing more in insemination capacity or in differential body-size becomes more convenient.

The two conditions, considered above, define what Milgrom and Roberts (1990) call the supermodular (or the complementarity) conditions. The first inequality implies that, for the individuals in N, the "incremental" benefit from having mutations that are associated to In rather than to Bn increases where their environment (defined by the traits that have been selected in the domain S) is Is rather than Bs. The second inequality implies that the "incremental" benefit for the individuals in S from choosing Bs rather than Is increases as their environment in N is Bn rather than In. These conditions are concerned with the property of incremental pay-offs with respect to a change in parameter value due to changes in the selection mechanism in the other domain. They do not exclude the possibility that the level of fitness of one mutation (i.

e. increased body size) is strictly greater than the other for the agents of one domain regardless of the mutation selected in the other domain. Thus, in spite of the supermodular conditions, it is still possible that there is a unique equilibrium.

However, under the supermodularity conditions, we have the possibility of two pure Nash equilibria. One (In, Is) is characterised by sophisticated cooperation in dealing with nature and by complex fertility strategies requiring both emotional and rational intelligence. The other (Bs, Bn) is characterised by hawkish reproductive strategies based on differential body size and power and great (especially male) individual physical strength in dealing with nature (and little or no male cooperation) in dealing with nature). When these multiple equilibria exist In and Is, as well as, Bn and Bs, are "selection complements" of each other. A change occurring in one domain can then trigger a change in the other domain.

Thus, unlike the arguments that rely on "selection substitution" (such as the peacock tail where the forces of natural selection are replaced and indeed overwhelmed by the forces of sexual selection), selection complementarity implies that the traits existing in one domain may have come into existence because of their favourable fitness advantages in the other domain. Thus, the existence of the complementarities considered above leaves the issue of the origin of the human brain and of human capabilities open. One has to refer to substantive arguments to understand whether the initial process is more likely to have started in one domain or in the other.

The notion of sexual selection is, of course, not inconsistent with that of natural selection, for it is another route to the Darwinian imperative of differential reproductive success. However, sexual selection implies that traits cannot be determined only on the basis of the environment exogenous to the species. It implies that a variety of solutions, due to the internal dynamics of the sexual relations, would emerge and interact with the adaptation to the external environment.

Because of the possible indeterminacy of sexual selection, Wallace rejected the notion of sexual selection that played a fundamental role in Darwin. Stephen J. Gould (1990 p. 48) has convincingly argued that "Wallace's rigid selectionism is much closer than Darwin's pluralism to the attitude embodied in our theory today which, ironically in this context, goes by the name Neo-Darwinism".

While Wallace tried to explain everything in terms of natural selection, he maintained that natural selection failed to explain the origin of the human brain and the human faculties. Thus, his rejection of Darwin's explanation of the emergence of the human brain in terms of sexual selection had very dramatic consequences for the destiny of the theory of evolution that, in Wallace's view, required some compromise with spiritualism to explain the specific human faculties. Paradoxically, he concluded his (1889) assessment of Darwinism by using it to show the existence of God:

> *We thus find that the Darwinian theory, even when carried out to its extreme logical conclusion, not only does not oppose, but lends a decided support to, a belief in the spiritual nature of man. It shows us how man's body may have been developed from that of a lower animal form under the law of natural selection; but it also teaches us that we possess intellectual and moral faculties which could not have been so developed, but must have had another origin; and for this origin we can only find an adequate cause in the unseen universe of Spirit* (1889, p. 478).

His lucid (but failed) attempt to explain human faculties referring only to natural selection is particularly instructive and it is rooted in what Gould (1990, p.49) called the "Wallace's dilemma":

> *all "savages", from our actual ancestors to modern survivors, had brains fully capable of developing and appreciating all the finest subtleties of European art, morality and philosophy; yet, they used in the state of nature, only the tiniest fraction of that capacity in constructing their rudimentary cultures, with impoverished languages and repugnant morality.*

Wallace's solution to this dilemma involved not only the rejection of natural selection as an explanation of the development of human brain but also the acceptance of a role for spiritual elements. In this respect Wallace's rejection of Darwin's theory of sexual selection had an important role in setting stringent limits for the theory of evolution.

However, according to Darwin[27], sexual selection succeeded where, according to Wallace, natural selection had dramatically failed.

> *He who admits the principle of sexual selection will be led to the remarkable conclusion that the nervous system not only regulates most of the existing functions of the body, but has indirectly influenced the progressive development of various bodily structures and of certain mental qualities. Courage, pugnacity, perseverance, strength and size of body, weapons of all kinds, musical organs, both vocal and instrumental, bright colours and ornamental appendages, have all been indirectly gained by the one sex or the other, through the exertion of choice, the influence of love and jealousy, and the appreciation of the beautiful in sound, colour or form; and these powers of the mind manifestly depend on the development of the brain.* Darwin (1879 p. 687)

Sexual selection could easily overcome the Wallace dilemma: even if different human populations had lived under different environmental and social conditions, the development of human faculties had not developed under the pressure of natural selection. It had, rather, been autonomously developed in an early stage under the pressure of common sexual selection rules.

The complementarity between natural and sexual selection implies that, in principle, human faculties could have initially developed under the forces acting in only one of each selection domain. However, both Wallace's dilemma and Darwin's

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[27] Darwin in had already clarified the role to sexual selection in the Origin of Species. There he had clarified how it "depends, not on a struggle for existence, but on a struggle between the males for possession of the females; the results not death to the unsuccessful competitor, but few or no offspring. Sexual selection is, therefore, less rigorous than natural selection. Generally, the most vigorous males, those which are best fitted for their places in nature, will leave most progeny. But in many cases, victory will depend not on general vigour, but on having special weapons, confined to the male sex." (1859 p. 136). The refinement of the theory and its application to the emergence to human faculties is, however, contained in Darwin (1879) "The Descent of Man and Selection in Relation to Sex".

insights suggest the same conclusion: that human faculties have arisen first in the domain of sexual selection. The arguments that we have developed in the preceding sections point towards the same direction. Without complementary changes, a large brain could have not been advantageous in terms of natural selection. The change in the human fertility system created the complementary conditions favorable to the selection of large brain. While it is difficult to achieve any definitive solution, Darwin's explanation of the origin of human capabilities seems still more convincing than those that could be provided by a “neo-Darwinism a la Wallace”.

6. Concealed ovulation, Endogenous Social Stress and the Origin of Language.

In the "Descent of Man and Selection according to Sex" Darwin made particular reference to the common latent ability of humans to learn languages:

.........some early progenitor of man, probably first used his voice in producing true musical cadences, that is singing, as do some of the gibbon-apes at the present day; and we may conclude from a widely-spread analogy, that this power would have been especially exerted during the courtship of the sexes - would have expressed various emotions, such as love, jealousy, triumph - and would have served as a challenge to rivals. It is, therefore, probable that the imitation of musical cries by articulate sounds may have given rise to words expressive of various complex emotions (Darwin 1879 p. 109)[28].

Modern linguistic theory has only partially followed this insight of evolutionary

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[28] In this paper we have concentrated on chimps and gorillas because they are our closed relatives. However the case of the singing gibbon-apes mentioned by Darwin is very interesting for our general argument: the negotiation of the future long-term strictly monogamic relations that characterise gibbons involves an intensive use of the vocal instrument both before and after the "marriage" is concluded (see Robbins Leighton D. 1987).

theory. John Maynard Smith and Eors Szathmary (1995, p.290) have observed that:

The main architect of the theory of universal grammar, Chomsky, put a strong emphasis on the innateness of our language acquisition device. It would therefore seem natural to assume that an evolutionary origin of language is widely accepted by modern linguistics. Yet, this is not so. Chomsky once said that, although we do have a "language organ" to speculate about its origin is as futile as to do the same about any other organ –for example the heart. This is baffling to an evolutionary biologist, who would make a 180° turn, and argue that one should contemplate the origin of any organ, including our language device.

In the view of linguistic theories, there are few if any rule that could be eliminated for a language to be a language at all. Thus, the co-evolution of language and of the linguistic organ does not make much sense. Maynard Smith and Szathmary (1995 p. 307) observe that this difficulty arises because what they ask is the wrong question.

They ask: is there any grammatical rule that could be absent, without reducing the power of linguistic expression? The answer is probably no, but the question is irrelevant. We should ask: is there any grammatical rule that, if it were absent, would still leave a linguistic competence that was better than mere protolanguage? To this question, the answer is obviously yes.

If grammatical rules could gradually develop, one can accept, that, as Darwin (1879 p. 209) suggested, (proto)-languages and human intellect may have co-evolved under the pressure of sexual selection:

From the fundamental differences between certain languages, some philologists have inferred that when man first became widely diffused, he was not a speaking animal; but it may be suspected that languages, far less perfect than any now spoken, aided by *gestures, might have been used, and yet have left no traces on subsequent and more highly-developed tongues. Without the use of some language, however imperfect, it appears doubtful whether man's intellect could have risen to the standard implied by his dominant position at an early period.* (Darwin 1879 p. 209).

Modern research on language impairment has confirmed the insight that linguistic competence is not a mere spin-off of general intelligence. While damages to particular regions of the adult brain are associated with a specific impairment of linguistic competence[29] (Damasio & Damasio 1992, Damasio 1999), in early stages of development the language organ can occupy different areas of the brain. This "organ" can be more appropriately seen as a “language amoeba” that is “as a neural activity pattern that essentially contributes to processing of linguistic information, especially syntax” and therefore as “a dynamical manifestation of Chomsky’s language organ”(Szathmary 2001 p. 42). Thanks to the plasticity of the brain, linguistic competence and neural networks are likely to have co-evolved along Darwinian lines.

Rapoport (1999) offers two mechanisms by which primate faculties and their brain may have co-evolved.

The first mechanism is “bottom-up” in the sense that “it implies that evolution of motor and sensory systems in mammals was somehow driven by and coevolved with heritable changes in peripheral sense organs and muscle effectors”, that were advantageous adaptations to new “physically” demanding milieus” (p. 154). In this case a mammalian population, displaying “heritable” variations in brain synapses and neuroplasticity, and in the surface expression of critical sense organs, is presented with a new physically demanding milieu. The young individuals of a mammalian population, who are endowed with genotypes that best elaborate their sensory skills, will, because of these heritable differences, as adults likely be most fecund. Their genes will extend within the population in some cases leading to a new species.

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[29] One example reported by Maynard Smith and Szathmary (1995 p. 300) is particularly striking. Patients with damage in the temporal segment of the left lingual gyrus suffer from

The second mechanism is “top down” in the sense that genetically heterogeneous population, faced by "a new cognitive, social, cultural or behavioral stress" (p. 155), undergoes a process of change due to the selective advantages of intellectual activities. This mechanism relies on the fact that higher-order “thought” can directly activate and modify widespread brain regions in immature primates. This activation reduces synaptic pruning and leads to the selection of genotypes whose elaborated brain “association” networks allow them to be most cognitively competent. The genes of the successful adults spread within the population, leading in some cases to a new cognitively more competent, larger brain species. This process can be self-reinforcing if the new species creates further “cultural” stresses, as was likely during evolution of the great apes and hominids[30].

Rapoport (1999) attributes the environmental changes that promoted "top down" brain evolution stress to the periods of drought that 5 million years ago replaced after a period of 2.5 million years large areas of forests with savanna. In this situation upright posture and bipedalism provided a competitive advantage for surveying the landscape, hunting and escaping predators. Hunting provided a diet large in calories and polyunsaturated fatty acids, necessary for evolving an enlarging brain.

Also the sophisticated theory developed by Kaplan and Lancaster (2003) relies on a similar logic. High level of knowledge, skill and coordination are required to acquire the resources that the hunting-societies consume. Since the acquisition of these skills takes a long time, increased brain size must be complemented by lowered mortality rates and greater longevity. The acquisition of large food packages spurs interfamilial food sharing and the nutritional dependence of the young (during their

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“colour anomia” (they experience colour normally and they are in command of world morphology, but they are unable to pair colour with names).

[30] According to Rapoport (1999, p. 155) several lines of evidence support the “top-down” mechanism. "First, *in vivo* neuroimaging and direct brain recording demonstrate that ideation and attention, free of sensory or motor components, can activate or modify activation of wide areas of cortex in humans and nonhuman primates. Additionally, studies in a wide number of species show that the intensity and pattern of neural activity can permanently modify the structure and function of the immature brain."

long training phase) favors sequential mating with the same individual. In turn, familial and interfamilial buffers allow a prolonged juvenile period and higher investment in other mechanism to increase life span. Thus, Kaplan and Lancaster (2003) come to the conclusion that:

the long human life span, lengthening of the juvenile period, increased brain capacities for information processing and storage, intergenerational resource flows, and cooperative biparental investment in offspring coevolved in response to this dietary shift and the new production processes it entailed. (Kaplan and Lancaster 2003 p. 180).

While climatic changes and the opportunity and difficulties of the savanna conditions have certainly favored the development of human capabilities, the same environmental conditions affected many other species that also moved to a diet similar to those of humans and to forms of co-operative hunting. While general environmental stress, due to climatic change, and the changed conditions of natural selection, can be some of the factors that facilitated the development of human capabilities they cannot be the specific factor that explained this "unique major transition in evolution"[31]. After all, humans were not the only species to adapt to savanna conditions.

Indeed, according to Strum and Fedigan (2000) stressing too much the importance of the transition to savanna conditions led in the early stages of primate ecology to an excessive concentration of studies on baboons "because they were one of the few primates (besides humans) to adapt successfully to the life of savanna" (p. 44). In this respect, early field studies of baboons "moved toward a simplistic form of environmental determinism. The assumption of the early studies of baboons, for example, was that because both baboons and hominids evolved on the East African savannas, baboons would make a good model for humans." Independently of its

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[31] In Smith and Szathmary (1995) " The major transitions in evolution" the origin of language is the last major transition that they examine.

specific limitations the emphasis on the common savanna conditions could never explain the dramatic differentiation between human and baboons and, in particular, the dramatic development of human intellectual abilities[32]. Following this approach would again lead to the “Wallace's dilemma” considered in the preceding section.

We would like to argue that Darwin continues to offer the most convincing explanation for the speciation of human capabilities. In particular, the main purpose of this paper can be re-phrased by arguing that, even if the tough savanna conditions may also have played an important role, the "new cognitive, social, cultural or behavioral stress" that humans faced was mainly related to the concealing of female ovulation. We have already argued that concealed ovulation implies a more stressful and brain-demanding social environment[33]. Here, we would like to add that *the way in which the transition to a regime of concealed ovulation is likely to have happened* must have implied a dramatic discontinuity causing an endogenous social stress. This stress was specific to the human species and may better explain the development of human faculties such as language.

It is, indeed, very plausible that the concealment of ovulation was preceded by a weakening of the signal of fertility periods. Observe that this gradual fading of the evidence of female fertility is likely to have made initially the exclusive access to females easier. Thus, humans are likely to have gone through a "gorilla-type"

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[32] Savanna baboons' fertilization system fits rather nicely the analysis that we have carried out. The female "exhibits a dramatic visual indicator of sexual receptivity many days before ovulation occurs" (Hrdy, Whitten 1987). This visual sign (evident only to surrounding males) allows some access for some younger members of the group before fertility period while, during ovulation, the female is monopolised by older and higher ranks members of the group. The fertilization system allows some sharing of females and cohesion of the group. However, exclusive access is easier than in the chimps' case. As expected, while high male-female differential body-size expresses that is worth to fight for exclusive access, the high testis size is consistent with the fact that society is very promiscuous. Different species of Baboons are, however, characterized by different gender relations (Stambach 1987) that are related to male or female migration in the formation of new groups - the relation between migration and relative weakness of intra-gender relations is a general pattern of primate societies (Smuts 1987).

[33] Of course, concealed evolution is not the only cause of social stress. Dumbar (1992) argues that another cause of social stress is the size of the group that is even the best predictor

fertilization system where it was relatively cheap to have stable harems. However, while a weakening of the signal makes it more private for the dominant male, who can better control his harem, a dramatic discontinuity occurs when the signal weakens so much that it cannot be easily detected even by a nearby dominant male. Suddenly, controlling fertility resources becomes terribly difficult for the dominant male who does not know which of his females is presently endowed with them. While the initial decreases of the fertility signal decrease the cost of exclusive access, after a certain point a further decrease of signal increases dramatically its price. The new situation is likely to stimulate brain size, linguistic communication and intellectual faculties not only because (as we have already seen) the new fertility regime demands these qualities with much greater intensity but also because of the abrupt nature of the transition. Such a discontinuous transition could be better faced by individuals endowed with pronounced abilities to understand sudden changes in social conditions and in the rules of sexual selection.

The origin of language may well be due to the fact that, because of a sudden egalitarian redistribution of fertility resources, we developed a urgent need to communicate and we reacted by making fair deals with the other gender and with our potential competitors. The dynamics that produced this result did not only exhibit a striking discontinuity. They were also very delicate[34]. Perhaps, what is really surprising is not that other species did not develop human-like intellectual faculties but that our species was so lucky to develop them!

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of brain development. He argues that the main selective force for increased intelligence arises from social interactions - a result that supports the approach of our paper.

[34] In absence of some other circumstances- such as female selective receptivity- could have produced the "orangutan tragedy" that we have briefly examined at the end of the second section.

7. Conclusion.

We have tried to explain some specific characteristics of the human species on the basis of the redistribution of fertility resources that is associated with the transition to a reproductive system based on concealed ovulation. Besides the speculative nature of the subject, there are some points that still need a more careful analysis.

In the first place, we have said little about the reasons for which concealed ovulation emerged. There is, indeed, one general reason for which it is such a rare case. The first females who do not advertise should be selected against. Among the many ways by which this puzzle can be explained one would be particularly consistent with our approach. Group selection could favour a population of doves (while in each group hawks may prevail). However this is simply moving the question one step backwards[35]. Why humans are more subject to group selection? Was the ability to develop cultural diversity already at work and how did we develop this ability? Or, can we argue that the evolutionary instability of fertilization systems (considered in the second section) does not require particular (co)-evolutionary explanations and that the evolution of the human fertilization system can be roughly treated as an exogenous variable?

In the second place, if the group selection advantages of dove-like behaviour may explain the advantages of group selection, there are indeed several ways by which that could be achieved. Strong and prolonged advertising would have had this effect and would have moved us towards chimpanzee equilibrium. In this case, we would have been more peaceful (and perhaps more happy) but we would have invested more in our testis than in our brains. Synchronised advertising for shorter periods could have

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[35] As Bowles and Gintis (2003b, p 436) suggest, the existence of egalitarian sharing rules (in our case related to concealed ovulation) may have favored group cohesion and, therefore, group selection. In turn, group selection may have favored concealed ovulation because groups with more internal cohesion may prevail over the other group. Observe that, while concealed ovulation favors and is favored by group selection, it may be inhibited by individual selection within the group because the first female, who conceals ovulation, may face adverse selection.

been another possible solution. Also women seem to have some tendency towards synchronization of their fertility periods and other species (lions) do it a more prominent way. This is another way of making society more peaceful but it does not favour complicated social games and, therefore, the development of the brain. More comparative thinking about the nature of these alternative ways of redistributing fertility resources is required to understand the emergence of our specific path of development.

Finally, even if the initial shock of "egalitarian" distribution of fertility resources occurred in the sexual selection domain and had only later an effect on the natural selection domain, the nature of the subsequent feedback from natural to sexual selection has to be better understood. When our brain increased its productivity in the natural selection domain, the differential ability to get food could be used as an important advantage in the sexual selection domain. Indeed, especially after this food could be stored, it allowed a very unequal access to fertility resources and a creation of harems no gorilla could have ever dreamt of[36]. Even if our species has spent a disproportionate amount of time in the rather egalitarian hunting societies, it is an open question whether the egalitarian imprinting, which was likely to be associated to concealed ovulation, has resisted the variety of (often very hierarchical) societies in which humans have organized their life.

In spite of these (and many other) problems we believe that our paper can offer some support to the view that *homo sapiens* did directly emerge as *homo reciprocans*. He was never simply, or even mainly, a rational and selfish *homo oeconomicus*. Rather, the human fertilization system may have even favoured the evolutionary success of a minority of strong reciprocators[37]. Human sexual selection favoured individuals that were endowed with emotional intelligence and emotional intelligence requires the capacity of putting ourselves in the situation of others and of imagining their points of view. This may, in turn, favour the ability to think ethically along

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[36] Royal harems sizes in despotic regimes included thousand females (Kaplan, Lancaster 2003, p.25). However, recently, thanks to social progress, Viagra and fertility control, that we may have a real chance to become a modern and clever version of chimpanzees!

"Kantian lines". More important, emotional intelligence requires that we understand our own role in social situations or, in other words, that we apply the same social skills by which we understand others to the analysis of ourselves. This evolutionary development may lead to what is perhaps the most important characteristics of humans: their consciousness.

Antonio Damasio (1999 p. 127) has observed that:

The essence of core consciousness is the very thought of you – the very feeling of you – as an individual being involved in the process of knowing of your own existence and of existence of others.

The "very thought of us" may have co-evolved with our ability to see us as one of the members of society and, in ultimate instance, with our ability to be in love with others. Assuming standard selfish behaviour cannot help much the scientific development of Economics and of the other Behavioural Sciences.

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[37] See Bowles and Gintis (2003a and 2003b).

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