

# Evolutionary Origins of Human Sexual Motivation

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## Resumé:

*Utváření lidské sexuální motivace je chápáno jako systém adaptivních mechanismů, které se vyvinuly jako odpověď na různé, někdy konfliktní, reprodukční kontingence. Je diskutováno 6 lidských sexuálních systémů. 1: Hlídní partnera a soutěž spermatu je motivací pouze pro muže, 2: V páru je pokračující sexuální receptivita ženy signálem pro kooperaci s mužem zajišťujícím jeho otcovství, čímž se zajišťuje otcovská kooperace muže. 3: Mnohočetná reprodukce je pro muže výhodná a může zvýšit jeho reprodukční úspěch. Obě pohlaví jsou vybavena motivačními mechanismy pro mimopárovou reprodukci. 4: Skrytá, nebo přinejmenším nemanifestovaná, ovulace člověka podporuje stálou přítomnost a častou kopulaci, napomáhá tomu i rozložení cyklů ženy v průběhu celého roku. 5: Za vhodných podmínek může kopulace spustit neurochemické odpovědi, které posilují vazbu u obou pohlaví. Zdá se tedy, že sexuální motivace je spajena se systémem vazby, která je však dostatečně volná, aby umožňovala i mimopárovou alternativu. 6: Ženské tělo je zvláště dobře vybaveno, aby monitorovalo životní situace v souvislosti s reprodukčními možnostmi a také podle toho regulovalo fertilitu. Protože sexuální motivace je regulována stejnými hormonálními mechanismy, je propojena s ženským sledováním prostředí.*

## Introduction

There are many situations, which recur throughout the typical human life span: choosing a mate, falling in love, caring for children, responding to sexual infidelity. Repeated encounters with such situations shaped the genetic base of the emotional mechanisms that guided the typical response of our ancestors and the resulting brain circuitry is still present in recent humans. Emotions and motives might be consciously experienced, but they can also work their way without conscious awareness – they can be part of the adaptive unconscious, a large

province of our mind that is inaccessible to conscious self-observation and control. It consists of automatic mental processes, like those, which alert us to danger, help us to steer a car and provide quick categorizing of persons and situations. Many observations in social psychology (Wilson 2002) and in neurology (Damasio 1999) only make sense with the assumption of emotions that are not processed consciously. The adaptive unconscious is also home of the mechanisms influencing sexual behaviour. The neuropsychological circuitry, which evolved in our evolutionary past, enables sexual motivation to be experienced and become modified by these experiences (Ledoux 2002). True, sexual motivation is heavily shaped by culture, but nevertheless, in the words of Jaron Lanier (1999, p. 67): *Sexual culture flies and flutters like a jojo. There is no contradiction between the elaborateness and flexibility of sexual culture and the central position of its genetic foundation.*

### The sex drive

The Freudian sex drive is basically a pleasure seeking device which receives its power from its ability to generate a state of pleasure or to reduce displeasure. But why do we have a system that enables us to experience pleasure at all? Even though Freud did not understand Darwin's ideas to the full his answer is darwinian: the sex drive has been established by nature because it was necessary for the procreation of the species. Explanations with reference to the good of the species were well accepted at the times of Freud and were present in evolutionary biology until the sixties. Clearly the good of the species is a teleological principle and therefore cannot produce a causal effect but this idea still staggers on, especially in the social sciences. The sexual reward system must have originated in evolution due to other reasons; it must have provided reproductive benefits for the individual organism, quite similar to the often cited example of the taste for sweetness (Johnston 2003). Those of our ancestors, who were equipped with a particularly sensitive detector of sweetness and a corresponding motivation to seek out sweet food, succeeded in foraging and consequently furthered the spread of this motivational disposition in the gene pool. This will be the guiding idea for the following analysis of sexual motivation. In his inquiry into the evolutionary history of sexual reproduction, John Maynard Smith (1978; Maynard Smith & Szathmari 1999) contrasted sexual reproduction with asexual reproduction and asked why such a complicated and costly system emerged when reproduction could be more efficiently achieved by asexual cloning. In analogy the question will be asked, why sexual behaviour and sexual motivation is so much more complicated than the task of achieving fertilization would warrant. As precursors of human sexual

motivation have been present long before the first hominid started bipedal walking (see Baker & Bellis 1995 for an overview), infrahuman sexual motivation must also be considered.

### **Mate guarding and Sperm competition**

A good strategy to understand a phenomenon is to find out the conditions of its variation. As sexual motivation cannot be observed directly, frequency of copulation will be used as a proxy. Frequency of copulation varies greatly between species (Birkhead 2000, pp. 150–155). A queen fire ant will mate once in her lifetime, while a single female soay sheep has been observed copulating 163 times with seven males in a 5 hour period. A lioness even may copulate more than 1000 times in order to achieve one pregnancy and in a female chimpanzee this number amounts to 500–1000 copulations. For humans the respective figure is 64 copulations for women of 20 years and it rises steeply with age. In contrast a female gorilla normally achieves fertilization with just two or three copulations.

A large part of the variation in copulation frequency is tied up with the likelihood of sperm competition. This is most obvious in birds where this variation coincides with the male's opportunity to perform mate guarding. When the male can keep close proximity to his mate and fend away rivals, not much copulation is needed to fertilize a clutch of eggs, conversely, when mate guarding is difficult as in birds of prey who have to leave their mate in order to forage individually, copulation frequency is much higher. This seems to explain why goshawks copulate about 500 times for each clutch, but skylarks only about two times.

Sperm competition can occur whenever different ejaculates meet in the female reproductive tract. When two males copulate with the same female in succession, their chances of fathering an offspring depend on the interaction between order of copulation, the interval between two copulations, and the time of the ovulation (Birkhead 2000). If a male cannot prevent other males from coming close to his female partner, he can still increase the probability of fathering her offspring by inseminating her frequently enough to be the first when ovulation occurs or to establish a barrier against rival sperm. Thus, copulation as a regular routine can act as an equivalent for mate guarding.

The widespread occurrence of sperm competition in the animal kingdom and its behavioural repercussions has been recognised by biological research only in the last three decades and only against much resistance (Birkhead 2000). Then, in a surge of enthusiasm and sensationalism, some exaggerated claims have been made about the mechanisms of sperm competition in humans (Baker & Bellis

1995), which were not supported by later research (Moore et al. 1999). In humans, indicators like testes size, sperm number and sperm length point towards a relatively modest level of sperm competition, compared with other primates, and this indicates that our female ancestors must have been relatively monandrous (Birkhead 2000, p. 81–83; Gomendio et al. 1998; Smith 1984) – but only relatively. The mentioned reviews indicate some measure of human sperm competition and point towards an evolved disposition in the human male to cope with this threat to paternity. The morphology of the human penis may have been shaped by sperm competition (Gallup et al. 2003). An experiment with genital models demonstrated that the human penis effectively acts as a semen displacement device. Shackelford et al. (2002) showed that after separation, males in committed relationships rate their partners as more attractive, show greater interest in copulating with them, and think that their partners are more sexually interested in them. Psychological adaptation to sperm competition may also explain, why men get aroused by pornographic displays of sexual acts involving one female and multiple males (Pound 2002). Although men should generally find mate sharing to be aversive, should this situation arise it would nevertheless be advantageous to be sexually aroused in order to make the best out of a bad job.

### **Monogamy and extra-pair copulation**

Safeguarding for sperm competition is solely a male concern – a female can always be sure of her paternity. If females of monogamous species were faithful to their mates there would be no need for sperm competition, at least for these species. In some birds like the magpie this seems to be the case, but these are exceptions; normally females are not only engaging in extra-pair copulation but even seek them out and often try to keep them clandestine.

Male extra-pair activity is highly visible because the male role is mostly active and its adaptive advantage has often been paraded as an example of how evolved motives might have shaped male sexual psychology in humans. It is obvious how a male can gain when he impregnates a female and leaves her afterwards without parental investment. Even when, as in monogamous species, the basic strategy for a male is to expend nearly the same paternal investment as the female, the side strategy, to have extra-pair copulations with minimal investment, will normally pay. But there must be females who respond to male sexual advances, and this can only occur when it also pays for the female (in terms of reproductive success) to be inseminated by more than one male. Female polyandry is adaptive for a wide range of reasons, which are less obvious than in the case of males.

Even as observations of female animals seeking copulation with many males can easily be made, and in fact have been made for centuries, the phenomenon was fully comprehended only recently. In Darwin's days the predominant view was like that: Since fertilization can only be achieved once per pregnancy, it would be pointless for a female to copulate more than a few times. Darwin himself was led to a different view by some of his observations, especially by his study of barnacles, but did not work it out, perhaps because his idea of sexual selection had already been met with such resistance, and female promiscuity would have estranged his Victorian contemporaries even more (Birkhead 2000).

### **Why should a female copulate with more than one male when she can be impregnated only once?**

There is no obvious reason, why a greater number of copulation partners should increase female reproductive success. And this was exactly what Angus Bateman found in 1948: In *Drosophila* male reproductive success increased rapidly with the number of mating partners, but female reproductive success did not (Bateman 1948). This result didn't surprise anyone. However decades later a closer look at Bateman's data revealed a different picture (Birkhead 2000, pp. 196–197). Some of Bateman's experiments did in fact show that females after copulating with several males had more surviving offspring than females who were kept from copulating multiply, but these results were not considered trustworthy at their time. In general female fruit flies copulate again only when their supply of sperms starts to dwindle. In the experimental set that was taken as decisive, nutrition was so good, that male fruit flies could inseminate a large amount of sperm and thus relatively few females needed to copulate again in order to maintain fertility. Had the nutrition been less lavish or had the experiment gone on for longer, Bateman would not have missed the female's need for copulation in order to stay fertile. In this case the benefit of multiple mating was to refill the dwindling sperm stores, in other species different reasons account for females seeking copulations with different males.

The view of the female as generally being coy and the male as being fickle (Wilson 1978) dominated until only some decades ago. Only gradually did the ubiquity of female polyandry become apparent. So why should females copulate more than a few times? Fertilization cannot be a big problem, since a biological mechanism to ensure fertilization with a few copulations did evolve in many species. Are females simply succumbing to male pressure? In most species females are well able to discourage amorous males simply by turning away; only

in a few species, such as mallard ducks, can successful male harassment and rape be observed. In addition, copulation imposes opportunity costs and often also the risk of predation and sexually transmitted disease. The advantages of a female motivation to copulate more than a few times must counterbalance these costs. The search for sexual pleasure cannot be part of the explanation because it should be part of the motivational mechanism that has to be explained in the first place. So what are good reasons for females not to be coy? In fact there are many, but not all of them are well established by research results, and they may be different for different species. In many species, females have more viable offspring when inseminated by more than one male. The reasons are not fully understood; potential explanations include the avoidance of incest depression, the benefits of selecting a male with good genes and especially of new genetic combinations conferring disease resistance (Jennions & Petrie 2000; Johnsen et al. 2000). In addition, females in some species are capable of what is called cryptic female choice, the post-hoc selection of sperm after copulation has occurred, sometimes even of stored sperm from past copulations with different males. In some species safeguarding against infanticide by blurring the issue of fatherhood makes multiple mating beneficial to females, in others it is the attainment of tangible benefits such as gifts and protection. Yet another benefit that is theoretically possible but has not yet been proven, may be sexual selection for competitive sperm: the female lets the sperm of different males fight it out within her reproductive tract and the male whose sperm outcompetes those of his rivals will father sons with a better prospect of succeeding in future such competitions. This in turn will also help to promote their mother's genes.

Female choice is guided by signals of genetic quality, which might be assessed by the appearance of ornaments like colourful plumage, antlers, songs and dances. What is advertised with such ornaments and, as Geoffrey Miller (2000) has hypothesised, even with displays of intelligence? There must be something that has made it worthwhile for females to be attracted to these signs. Many signs are indicators of developmental stability, the resilience of the genomic developmental path against perturbations from the environment starting with embryonic development (Moller & Swaddle 1997) and they are correlated with body symmetry. Animals whose bodily features are highly symmetric are also larger healthier and better endowed with sexual ornaments and more successful in status competition compared with less symmetric animals. This has also been investigated in humans: Females assess males with highly symmetric faces as having more attractive looks, even when symmetry is not recognized directly (Grammer &

Thornhill 1994; Townsend 1999). The body odour of symmetric men is rated as particularly attractive (Rikowski & Grammer 1999), they have a larger number of lifetime sexual partners and their female partners report a higher number of orgasms during copulation (Shackelford et al. 1999).

When there is a variation in genetic quality of potential male partners, the best female strategy would be to choose the best male. In monogamous species with male parental care, the best male can be taken only once by one female. As not every female has access to number one, not even to number two or number three, most have to do with a less happy choice. But then there is still the possibility to get the best of two worlds and seek extra pair copulations with high quality males. In humans the proportion of children who are not fathered by those who think they had is estimated from a 1 to 10 percent depending on ethnic group and social status (Baker & Bellis 1995). Human females seem to be particularly motivated to seek sexual adventure, when the probability of conception is highest – close to ovulation. According to a study of Gangstead et al. (2002) at the time of highest conception probability women's sexual fantasy tend to drift towards scenarios with other men. Simultaneously their regular partners, without knowing the time of ovulation seem to intensify their mate guarding.

The evolutionary trade off between keeping to a single mate (long term mating) and changing mates (short term mating) has been addressed by the developing theory of sexual strategies (Buss 1987; Buss 2004; Gangestad & Simpson 2000), which describes the variation of mating styles between individuals and within individuals in the course of life history. The success of a sexually unrestricted strategy in contrast to a sexually restricted strategy (Gangestad & Simpson 1990) depends on how frequently this strategy is pursued already by other individuals- in the market of eligible partners. Thus the tension between the potentially incompatible goals of securing parental investment and increasing the number and/or quality of offspring gives rise to a complexity quite unexpected from earlier ideas about the workings of a sexual drive.

### **Female cooperation with male paternity interests**

As we have seen, there are many benefits for females seeking copulations with different males, but most of these benefits require the males to be different from each other. Why should a female copulate regularly with ever the same male in a pair bond when fertilization could be achieved with a very small number of copulations? Tim Birkhead (2000) gives a tentative answer of which he is not completely convinced: A display of female sexual receptivity signals female cooperation with male mate

guarding and in fact it amounts to be an act of cooperation. Therefore continual female receptivity in a pair bond might have been evolved as the result of a male preference for female sexual responsiveness, which was beneficial to the male because it raised the probability of his fatherhood. Male motivation to continue parental investment should also depend on the trustworthiness of female sexual responsiveness. Geoffrey Miller (2000) understands the display of female sexual excitement in humans, especially orgasm, as such a signal. This would also explain why in humans the authenticity of the female orgasm is much more subject to questioning than the authenticity of the male orgasm.

### **The concealed oestrus**

The concealed oestrus is rare in mammals but some degree of concealment is common in primates and it has been found that monogamy evolved more often in the presence of concealment than in its absence (Sillén-Tullberg & Møller 1993). This kind of sexual crypsis is not specific for homo sapiens and there are intermediate steps between signalled and concealed oestrus. In chimpanzees, oestrus is advertised heftily by an anogenital swelling. The consequences are (a) competition among males, (b) uncertain paternity, (c) when the signal disappears there is nothing to gain from subsequent copulation and males are free to turn their sexual attention to other females.

There are many theoretical speculations about the evolutionary benefits of the concealed oestrus in humanoid primates and in humans (Alexander & Noonan 1979; Baker & Bellis 1995; Miller 1996; Pawlowski 1999). In the view of Alexander and Noonan the concealed oestrus evolved from short periods of male monopolisation of a fertile female like the consorting in chimpanzees (Goodall 1990). In a consorting relationship the couple withdraws from the troop and lives separately for some days or weeks. This should improve the chances of the male to father the offspring of his female consort – whether it does in fact, seems to be an open question (Gagneux et al. 1997). If the gain in probability for fatherhood would be high enough, it would also pay for the male's reproductive success, to invest into parental care above the small contributions that are normally offered by male chimpanzees. As this would also benefit the female's reproductive success it may have constituted the selective advantage for an ever prolonging oestrus.

Boguslaw Pawlowski (1999) makes a case against any sexual selection hypothesis of the kind stated above. He argues that proceptivity (the active female encouragement of a male to copulate) clearly depends on the phases of the



menstrual cycle and thus the human oestrus cannot be termed concealed. The relative lack of advertising could be a side effect of other evolutionary attainments such as bipedal walking and a culturally induced relaxation of selection pressures. There are many observations showing the peak of sexual interest and activity to coincide with the ovulatory phase (Wallen 1995; Wilcox et al. 2004), among them observations of women seeking during ovulation the maximum number of contacts with males other than their regular partners and of lesbians initiating more sex. The body odour of ovulating women smells highly attractive to males and is significantly preferred to odours of women not in the ovulating phase.

Time of ovulation seems to be influenced by so many factors that it appears to occur at random (Baker & Bellis 1995). If quasi-random timing of ovulation would be absent in species with advertised oestrus, this would support a functional role of concealment. However a variable follicular phase is also found in baboons, chimpanzees and rhesus macaques (Rowell 1972).

Ovulation may not be completely concealed in humans, but it certainly is not advertised. No olfactory signal exerts the power to concentrate sexual motivation to a small time window as in most mammals with advertised oestrus. Thus the evolutionary origins of ovulatory cryptis and its relations to monogamy are still open to speculation. The concealed oestrus fits well into a picture of female receptivity as being instrumental for the task of keeping a caretaker, first by making it difficult to achieve fertilization and to assure fatherhood, and second by offering cooperation with both tasks.

### **Establishing the pair-bond**

Genital stimulation triggers a cascade of neuroactive substances like oxytocin and dopamine in many mammals. This process has been investigated intensively in voles, especially prairie voles, which are monogamous in contrast to the closely related mountain voles (Carter et al. 1995). In these animals pair formation is triggered by a large number of copulations within the first 48 hours. After that the pair bond is stable, and will be refreshed every once in a while by new bouts of copulation. Repeated copulation also intensifies aggression against outsiders, which can be considered a mate guarding behaviour in the male and a signal of cooperation in the female. In female voles oxytocin has been shown to be conducive to selective partner preferences. The substance vasopressin, which is chemically similar to oxytocin seems to play a larger role in male bonding behaviour (Gingrich et al. 2000; Lim et al. 2004; Young et al. 1999). It is still unclear to what extent these substances have similar effects in humans. The high frequency

of sexual intercourse in the first years of a newly formed couple-relationship (Klusmann 2002) would fit well with a function of repeated copulation: to generate heat in order to establish the bond.

### **Sexual motivation and fertility**

Continuous body contact with a male has the effect of normalizing the female cycle (Miller 1998). Women who cohabit with a man have more fertile cycles and a longer luteal phase compared with women who live alone. This effect is even more pronounced when women who have coitus on a regular basis are compared with women who live celibate. In the luteal phase the lining of the uterus is prepared for implantation to support a pregnancy. Thus, signals of the continual presence of a male seem to promote fertility.

Preeclampsia is a complication of pregnancy by hypertension, occurring in 3–4% of pregnancies. The incident of preeclampsia seems to be dependent on the presence of a regular male partner. Studies of women in Guadeloupe (Robillard & Hulsey 1994) show a decrease of preeclampsia in women who have cohabited with their regular partners for a long period of time before pregnancy compared with women who have been with their partners only for a short time. As preeclampsia can be considered an immunoreaction of the host against alien tissue, in this case seminal fluid and semen, the results can be interpreted as indicating a conditioning or desensitization of the immune system through prolonged exposure to the semen of a man (Robertson et al. 2003).

Considering the life history aspect of reproduction these findings would make evolutionary sense as instances of what Thiessen (1994) has termed “environmental tracking by females”. The female body seems to be prepared to assess life situations and regulate fertility accordingly. In this view the presence of a male caretaker would provide a signal to go ahead with reproduction. An important part of this signal is provided by copulation. Thus the evolved design of sexual motivation may have been influenced by the diagnostic requirements of the fertility regulating system.

The genetic base of human sexual motivation has been formed by many sources of selective pressure that have been present for a long time. As evolution by differential reproductive success never stops, the contingencies of modern life, especially the decoupling of mating success and reproductive success, will act upon genetic variations in human sexual motivation and mating strategy by favouring some traits upon others. Thus sexual culture may flee and flutter like a jojo, but the genetic base will also not stay unchanged.

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