

# Ageing, Mate Preferences and Sexuality: A Mini-Review

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## Key Words

Mate choice · Sex difference · Reproduction · Error management · Evolution · Sexuality

## Abstract

The evolutionary constraints that lead to the evolution of sexual reproduction are framed by the better repair mechanisms that repair fatal mutations, as well as the need for variable immune systems imposed on large organisms by parasites, such as viruses and bacteria. Besides the evolution of sexual reproduction, these factors also affect mate choice, especially as regards the gene complex that encodes the immune system. The need to increase both the likelihood of gametes to encounter each other as well as sufficient provision of nutrition for the offspring then leads to the evolution of two sexes: large numbers of small mobile sperms ensure that gametes meet, whereas large egg cells full of energy provide for the zygote, thus leading to a developmental advantage. The asymmetric investment in the offspring then affects not only mate choice criteria, but also cognitive strategies. Men place more importance on youthfulness and fertility than women, who regard resource holding potential as a more relevant criterion. Consequently, female jealousy is connected to endangered access to resources, whereas male jealousy is rooted in paternal uncertainty. Cognitive adaptations developed to ensure reproductive success show sex

differences, such as in error management. The most obvious function of sexual behavior is reproduction. To foster the benefits for the offspring, reproduction partners should also develop an emotional bond, which is mediated by hormones connected to sexual intercourse. With increasing age, reproduction loses importance, while pair bonding functions remain relevant. Therefore, sexuality never ceases to be part of a relationship.

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## Biological System Constraints

In 1862, Charles Darwin [1] wrote: ‘We do not even in the least know the final cause of sexuality; why new beings should be produced by the union of the two sexual elements ... The whole subject is as yet hidden in darkness.’

Charles Darwin was puzzled by the fact that the great majority of animals and plants reproduce sexually. More precisely, he did not understand why males exist. If the world consisted only of parthenogenetic females, reproduction would still be possible. But evolutionary biology has made progress to answer this question: the conventional textbook explanation states that sexual populations can react more quickly to environmental changes than parthenogenetic populations [2]. If two new muta-

tions A and B would be advantageous to cope with recent environmental changes and occur in different individuals, sexual reproduction can combine them within one generation. In a parthenogenetic population, however, A and B would have to occur sequentially in the same line. Furthermore, sexuality combats the fatal evolutionary mechanism named Muller's ratchet [3]: by recombining genes in the processes of meiosis and impregnation fatal mutations can be repaired. Thus, it works against assembling deleterious mutations in our germline, which occur with a likelihood of about one mutation per generation. Deleterious mutations can be cleaned off only by sexual reproduction, which prevents the genome degenerating over several hundred generations which could result in the population becoming extinct [3].

Sex is an inefficient way to reproduce: a sexual female throws away half of her genes (during meiosis), finds a suitable male who has done similarly (mate choice), and fills up what she has thrown away with what she gets from him. The short-term advantage of sexual reproduction should be such that the combination of the new half of genes with the half that she has retained should be more than twice as fit as if she had made just a copy of herself.

The red queen hypothesis [4, 5] assumes that long-lived multicellular organisms such as humans with long generation cycles have an evolutionary problem: parasites, i.e. viruses and bacteria, reproduce much more quickly and have less sophisticated repair mechanisms. Thus, they can evolve much more quickly. The fact that infectious diseases change so rapidly requires new combinations of genes for resistance to cope with the parasites. This is actually the reason why sexual reproduction exists at all. Furthermore, mate choice can even more enhance the genetic variability of the offspring. A sexually reproducing female should select the male possessing resistance genes that complement with her genes for generating the optimal immune response against the current infectious disease. This requires that (1) there is an enormous variation of immune genes in the population to make a choice possible, (2) knowledge about the own immune genes, and (3) legibility of immune genes of others. And indeed the immune genes, i.e. the major histocompatibility complex (MHC), contain the most polymorphic gene loci known in vertebrates [6]. More than a dozen studies have shown that mice prefer those males for mating who have MHC alleles that differ from their own alleles, and that the choice can be made on the basis of smell only [7–10]. This preference would result in offspring that are heterozygous in their immune genes, which should enable them to fight off a broader spectrum

of infectious diseases. Each MHC allele codes for a specific MHC molecule, which can detect and present a specific class of foreign peptides to T lymphocytes; T lymphocytes kill infected cells and so eventually defeat the infection.

Immune genes affect body odor and can thus be literally sniffed out by a choosy female. Evidence exists for MHC dissortative odor [11, 12] and mating preferences in humans [13]. Wedekind et al. [11] found that women prefer the odor of T-shirts worn by MHC-dissimilar men to those of men with a similar MHC genotype. The preference was reversed in women who took oral contraceptives. This preference shift makes sense in the light of the fact that a pregnant woman should prefer the company of relatives to that of strangers to raise her children, and she should not dislike the odor of her own offspring. It has been shown that pregnant mice prefer to nest with MHC-similar individuals [14]. Pregnant women change their taste for particular smells; they dislike both the smell of their partners and that of their particular perfumes [15].

All this evidence supports the idea that sexual reproduction is the adaptive answer to the selection pressure of the changing environment of parasites. But still this does not explain the existence of two sexes. Two sexes are biologically costly – one half of the population does not directly reproduce, you have to find a partner, there is the possibility of aggression and even copulation might be a difficult endeavor. Parker et al. [16] showed in a computer simulation that the evolution of two different sexes is inevitable. If the success of a zygote increases quadratically with its size, the evolutionary pressure gives way to two solutions. A larger gamete will lead to a bigger zygote, which will have a growth advantage with better nutrition for the offspring. Small gametes, on the other hand, can be produced in large amounts, thus raising the overall likelihood to encounter another gamete, which is the necessary pretext for forming a zygote. Since both small and large gametes have distinct advantages over medium-sized gametes – which can neither be produced in high quantities nor provide enough energy – this results in the development of two different strategies: one sex producing large amounts of small gametes ensuring the encounter of gametes, and the other sex producing large gametes taking care of the primary supply of the offspring. Apparently these two reproduction strategies are mutually exclusive, and different reproduction strategies will evolve on the basis of the necessary investment in the offspring. Evolutionary theory explains sex differences in sexuality and mate selection criteria in terms of different levels of

parental investment [17, 18]. For women, the minimum required parental investment is greater than it is for men. A copulation that poses the minimum male investment can lead to a 9-month investment for the woman that is substantial in terms of time, energy, resources, and foreclosed alternatives. Consequently, women will be more discriminating in their choice of a mate and will be less interested in short-term relationships than men. Women will prefer characteristics in potential mates that signal the control or acquisition ability of resources beneficial for potential offspring in the long term [19, 20].

Men, in contrast, will tend toward a different strategy. Since males' necessary investment is minimal, men can afford to be less choosy. Men will be interested in a variety of short-term partners, will be more open to low-investment sexual opportunity, and will tend to focus on cues signaling fertility and reproductive health rather than resource-acquisition skills [21]. Since female fertility is limited by health and age, male sexual attraction will primarily be attached to visual stimuli [22–25].

The consequences of asymmetric parental investment can also be seen in present-day sex motivation systems. Males have a lower threshold for sexual excitation [26], tend to perceive people and relationships in a more sexualized manner [27], and are more likely to interpret a variety of stimuli as signals of sexual intent [28, 29]. Since low-investment copulation was advantageous for males in our evolutionary past, males are predisposed to attend carefully to potential sexual cues and be on the lookout for any signals that might indicate varying degrees of sexual openness.

In westernized societies the mating system is presumably monogamous, but research shows that it is probably more accurate to describe our mating system as one of serial polygamy: a succession of marriages and mating outside of marriage and committed relationships are common [30]. Estimates based on DNA evidence suggest that 9–13% of children have putative fathers that are not their genetic fathers [31]. Adultery among married couples is estimated to range from 26 to 70% for women and from 33 to 75% for men [17].

To maximize our reproductive success, evolution has equipped both males and females with different mating strategies. For males, a dual sexual strategy is likely to have been most profitable in the evolutionary past: invest in offspring with a female that has been selected for fertility and fidelity, but take advantage of any other low-investment mating opportunities that come along. Signals of fidelity and sexual restraint will be of value in a long-term partner, as this will help to increase a male's confi-

dence of paternity. Signals of sexual openness, on the other hand, will be of value in a short-term partner.

For females, the main sexual strategy will be to carefully select a mate with whom a long-term, committed relationship can be established, and who will provide the necessary resources. Mating outside a committed relationship (extra-pair copulations or EPCs), however, could also be an adaptive mating strategy for a female: the competition of sperm from two different males will ensure increased genetic quality in the offspring, and genetic variability among a female's offspring will enhance inclusive fitness and survival prospects [17, 32–34].

Recent research has shown that mating strategies might change during the female cycle, suggesting that the pursuit of EPC strategies may be a special-purpose adaptive design for females [35]. Penton-Voak et al. [36] found that females' preferences for male facial attributes change as a function of their menstrual phase. In their most fertile phase, women prefer more masculinized faces. Penton-Voak and Perrett [37] and Johnston et al. [38] found similar results. This shift for different mate preferences at ovulation coincides with an increase in females' self-reported arousal to sexual stimuli [39], peaks in sexual receptivity [40], and an increased amount of attraction to and fantasy about men who are not their primary partners. Females' extra-pair copulation frequency [31] and mate guarding by the primary [41] also increase, indicating the importance of sperm competition.

It is adaptive for females and males to develop and use cognitive strategies in mate selection, which take into account biological constraints. Adaptive cognition could be expected to lead to optimal decision-making under a wide spectrum of socio-economic constraints. The existence of ubiquitous sex-specific differences in mate selection criteria [19] emphasizes that male and female cognition is adapted to the biological constraints of mate selection.

In the light of these selection pressures the evolution of different adaptive cognitive strategies for both sexes is a logical consequence. Since every cognitive strategy is error-prone to a certain extent, the most sensible answer for a cognitive system is to ensure that the errors made are the least costly ones. Error management theory (EMT) as proposed by Haselton and Buss [42] describes the construction of decision makers as optimizations in a cost-benefit ratio. One could compare the dilemma of our cognitive apparatus with the problem a constructor of a fire alarm faces. There are two types of mistakes that are possible for a fire alarm: type 1 error would be if the fire alarm went off when there was no fire, and type 2 error

is the opposite – the alarm does not go off, even though the house is afire. Both errors involve certain costs and benefits. In the case of type 1 the cost would be that the building was evacuated without a reason. In case of type 2 the costs would be the loss of the building, maybe even involving people dying. Consequently, the decision for the constructor is an easy one: putting up with some false alarms is much less costly than a false-negative alarm. Therefore, he will construct a fire alarm that reliably goes off each time there is a fire at the cost of a few false alarms.

In mate choice, the error management for men and women differs: for women the most costly mistake would be to overestimate the long-term interest of a man – since this could lead to loss of resources provided by the father and reduced prospects for future mating. Therefore, women should tend towards EMT type 2, i.e. underestimating the interest of men. For men, on the other hand, the most costly mistake would be to let opportunities for reproduction pass, thus they would rather employ the type 1 error, i.e. overestimate the sexual interest of women. This sex difference in error management can also be observed in situations not connected to reproduction and mate choice. Men tend to overestimate their control over unfamiliar situations and women tend to underestimate it.

Additionally, female exogamy led to sex-specific selection pressures, since men remained in their birth group throughout their lives and could rely on the support of their relatives, whereas women had to integrate into a foreign group and establish reciprocal support systems with unrelated individuals. This posed the evolutionary stage on which the female preoccupation with social matters evolved. Social knowledge and social skills were crucial to the survival and the reproductive success of our female ancestors – and led to the evolution of specific adaptations in women that can still be observed.

The importance of male status as a female mate selection criterion, on the other hand, led to the male preoccupation with status-related matters, including proneness for risk-taking and the like.

### **Biological Functions of Sex**

Bonding, devotion, passion, grief on splitting up, and jealousy are only a few of the emotions mentioned in the context of romantic love. From a scientific perspective, love is a hypothetical construction with many possible dimensions and ways of interpretation. The different

emotional states and behaviors associated with love have rarely been subject to empirical science. This can be explained by the fact that love has always been the domain of poets and the arts and that it has been assumed that it lies beyond scientific exploration.

Biological interpretations of love suggest that it has its origin in the bonding between mother and child [43]. This assumption is underlined by the fact that the same hormonal regulations determine parental love and sexual love [44] and that many behavioral structures are similar in both kinds of love [43]. These behaviors are interpreted as requests of care. But up to this day there has not been empirical research on this topic. From an evolutionary point of view the function of love could be that of a bonding mechanism, which grants long-term relationships and this way serves the individual reproductive success. It could manifest in three dimensions of human behavior: the physiological basis, the actual behavior, and the cognitive processing.

What exactly is love and how does it differ from other kinds of relationships? Huston and Burgess [45] tried to explain what characteristics differ between friendships and intimate relationships. Most close relationships are characterized by similarity (the same interests, etc.) and exchange. The feeling of unity, solidarity, or identification with a partner is therefore a decisive criterion for the definition of love.

Buss [46] assumes that, if love has evolved in order to serve reproduction, its effects should be found in bonding behavior. These effects are the preparation of resources, a relative exclusivity of a relationship, bonding behavior, sexual intimacy, reproduction, sharing of resources, and parental investment. Many or all of these behavioral elements can show sex differences. Hendrick und Hendrick [47] found that men tend to play games with women more often than the other way round, and women are more often more pragmatic than men. The more ludic, playful manner of young men should on average lead to more frequent sexual contacts and therefore increase their reproductive success. A more pragmatic orientation towards love in young women should on average increase their reproductive success, because they become choosy and can find the best partner, as they consider the genetic and economic fitness of a potential partner. It can indeed be found that single men regard love from a more romantic perspective than single women, which changes during marriage. A reason for this could be that women – above all if they want children – depend on their partners' reliability and economic status and idealize their dependency as love [48].

Consequently, women more often adopt a policy of wait-and-see, tend to judge their situation more realistically, and are more critical than men. Men fall in love faster. In a study on unmarried students, who filled out the questionnaire by Hendrick und Hendrick [47], it was found that women indeed preferred closeness and practicability more than did men. But in contrast to the hypothesis, women were more passionate than men.

This is why we assume that love has an adaptive evolutionary function and comprises sex-specific tendencies of behavior. The aforementioned model of asymmetric investment predicts different reproductive strategies for men and women. Women inevitably have to limit their attention to a relatively small number of offspring, whereas men can spread their genes by impregnating a large number of women. If falling in love is the 'glue' for a relationship, young men should fall in love more often than young women, and they do so indeed [47].

In animals, social bonding is linked to hormonal activity [44]. In a very speculative theory, Liebowitz [49] has linked the phenomenon love to neurochemical processes. He assumes that first an unspecific arousal is induced by amphetamines, which are later replaced by endorphins, when infatuation is replaced by attachment.

Today, PEA (phenylethylamine, a substance similar to adrenaline) is thought to provoke this state of arousal. According to the hypothesis of Liebowitz, our bodies are flooded with dopamine and norepinephrine as soon as we meet an attractive person. Only later on is this unspecific arousal linked to a romantic partner, forming the neurophysiological basis for a lasting relationship, in which dependency is induced by endogenous endorphins. Guinea pigs that were treated with narcotic blockers that keep the cerebral endorphins from docking onto their receptors, whine more and show more fear of separation than controls that are separated from their mothers or siblings. Newer studies find that especially the hypothalamic-hypophyseal-gonadal axis (HGA) and the hormones vasopressin and oxytocin control social bonding in animals [44, 50]. Positive social behavior reduces the activity of the HGA, whereas negative social contacts have the opposite effect [44, 51]. Breast-feeding causes similar oxytocin reactions. If oxytocin is responsible for social bonding, sexuality could directly serve pair bonding. These highly speculative assumptions were supported by three experiments on humans by Murphy et al. [52, 53] and Johnson et al. [54]. It could be shown that in humans oxytocin and vasopressin are released on sexual arousal, orgasms, and stimulation of the breasts in women.

In addition to this hormonal-physiological system, we find that behavior and information processing are closely linked. Zajonc [55] describes this his Affective Primacy hypothesis, which assumes that minimal affective stimuli (in case of love the partner and his verbal and nonverbal care) can cause affects inaccessible to conscious cognitive processing. These affective reaction patterns are – according to this theory – triggered by the perception of signals that directly project to the limbic system [56]. In order to grant bonding, love or being in love has to be communicated and told to a partner.

Ovulation in humans seems not to be accessible to conscious perception. A number of overt physiological and behavioral changes have been shown to be associated with the menstrual cycle, one among those being olfaction.

Alexander and Noonan [57] and Symons [17] have argued that hidden estrus has evolved because this enabled females to form a bond, since her partner would remain with her to ensure impregnation and paternity. This development would implicate the male fear of cuckoldry as an evolutionary pressure [18]. The outcome would be that the female's ability to secure paternal care is affected by mechanisms that increase temporal aspects of the pair bond and enhance male confidence of paternity.

In contrast with this line of argument, Bensch and Thornhill [58] and Symons [17] have proposed a second evolutionary scenario in which hidden estrus evolved to increase the chances of successful cuckoldry by females, so they 'can escape the negative consequences of being pawns in marriage games' [59, p. 350]. In both cases, male knowledge of ovulation may be selected against because it would hinder the female's mating strategies [56, 60].

Recently, the second hypothesis has received considerable support. Bellis and Baker [61] conducted a study of 2,708 females and found that 13.8% of 145 'unprotected' extra-pair copulations (EPC) occurred during the fertile period and were preceded in most cases by intra-pair copulations (IPC). EPCs were rarely followed by IPCs. According to this study, EPC and thus female infidelity peaks at ovulation.

This suggests sex-specific functions of sex – although the mechanisms are the same for both sexes. Females' primary interest should be love and the bonding function of sex – in order to ensure male long-term investment. The same should be the case for males, but out of different reasons – bonding would ensure their paternity security.

## Lifetime Sexual Strategies

When we look at the human life cycle, it is at hand that the role of reproduction and sex will change according to the theoretical outline above. Female reproductive value is high at younger age and decreases over lifetime. Indeed, it is possible to show that males' main mate selection criterion is female age, and age is thus a main factor for female attractiveness [62]. In contrast, males' reproductive potential increases during lifetime with increasing status. This means that males are able to invest in more offspring with increasing age. This gives rise to the fact that male and female lifetime strategies are as different as their mate selection criteria and the resulting cognitive differences.

Recent research underlines these ideas. Fieder et al. [63] showed that male reproductive success still depends from male status when uniform social strata are considered. Moreover, Fieder and Huber [64] describe that the reproductive success of a couple is higher when the man is 4 years older than the woman. This leads to an asymmetry in the orientation to sex and copulation. During lifetime the female interest in sex might decrease hand in hand with receding reproductive function. The bonding function, on the other hand, might prevail, maintaining some importance of sex in women as they age. On the male side, the reproductive function of sex should stay the same or even augment during lifetime, because with raising status reproductive chances also rise. This is underlined by the fact that many males have more than one reproductive cycle. At about the age of 36 years males tend to leave their partners in favor of younger women with higher reproductive potential [65]. There is no evidence for a menopause-like mechanism in males, such as an andropause.

The existence of menopause has long puzzled evolutionary biologists – what should be the adaptive value of stopping to reproduce many years prior to death, thus reducing the number of possible offspring?

Several authors suggest [66, 67] that menopause is an adaptation to ensure investment in both direct offspring

and in grandchildren. Females are thought to switch their reproductive strategy when the costs of raising own offspring would exceed the benefits, which can be gained by investing in the genetically related offspring of their children. In our view, the so-called 'grandmother hypothesis' is not necessarily an adaptation with a selective advantage – because the number of female gametes is limited and they are prone to ageing, a termination of reproduction at a certain age might be a mere by-product resulting from the limitations of female physiology. Additionally, the old ages we reach nowadays are a novelty – our ancestors most likely died at young ages around 45. In this light, menopause poses not an early end for reproductive activity, but merely grants for the own offspring to have primary care until their mother dies. Thus, the power of evolutionary theory to explain ageing effects is limited – with the help of modern medicine we outlive our own evolutionary design.

This is underlined by new findings on a large dataset from people looking for partners in a real-life environment [68]. Generally, the desire for sex decreases in women during a lifetime, as it does in men. But having a partner with a high interest in sex remains stable during lifetime in women and even increases in men. Even the wish for children increases in men, but not in women. This is in line with the hypothesis of biologically primed lifetime-dependent sexual strategies. Females have to secure investment and thus the bonding function of sex is central for them – males are biologically primed for reproduction and thus the reproductive function of sex. This is why sex is fun [69].

In this short review, we started out with the evolution of sex under the pressure of parasites and proceeded to the emergence of two sexes as different reproduction strategies. The result are asymmetries in investment and as a consequence the development of cognitive and behavioral adaptations, which culminate in lifetime differences. In fact, evolutionary theory currently is the only approach which can explain these complicated mechanisms in a parsimonious way.

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