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Evolution and Human Sexual Behaviour: Ten Books which have Contributed to our Understanding of the Relationship between Evolution and Human Reproductive Behaviour

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Abstract

We are extremely fortunate in having such a range of high-quality writers who have tackled and added to our understanding of the relationship between evolution and human sexual and reproductive behaviour. In this brief review we examine ten influential books which have helped us to understand human reproductive behaviour through an understanding of Darwin's conception of sexual selection theory. In conclusion we suggest there are well established sex differences in human sexual and reproductive behaviour which can be understood using the framework of sexual selection theory.

Keywords: Darwin; Evolutionary Psychology; Sexual Selection; Sexual Behaviour

Abbreviations: EEA: Environment of Evolutionary Adaptedness; WEIRD: Western Educated Industrialized Rich and Democratic.

Introduction

Over the last one hundred and fifty years a series of researchers have attempted to understand human sexual and reproductive behaviour through the lens of evolutionary theory. This began in 1871 when Charles Darwin [1] published his second book on evolution - The Descent of Man and Selection in Relation to Sex. In this review we examine the contribution of Darwin's' original text and nine further books which have attempted to build on and expand Darwin's conception of human reproductive behaviour. This will lead us on to suggest a number of conclusions that stem from the arguments and findings outlined in these publications. In conclusion we propose that, due to these specific publications, we are now able to make a number of

suggestions about human sexuality including the evolved nature of sex differences in human sexual/reproductive behaviour.

Our list of influential publications, in chronological order, includes:

- Charles Darwin (1871) The Descent of Man and Selection in Relation to Sex
- Desmond Morris (1967) The Naked Ape
- Donald Symons (1979) The Evolution of Human Sexuality
- Sarah Blaffer Hrdy (1981) The Woman That Never Evolved
- Jerome Barkow (1989) Darwin, Sex, and Status
- Helena Cronin (1991) The Ant and the Peacock
- David Buss (1994) The Evolution of Desire
- Geoffrey Miller (2000) The Mating Mind
- Christopher Ryan and Cacilda Jetha (2010) Sex at Dawn
- Frederick Toates (2014) How Sexual Desire Works

For a brief summary of these refer to Table 1.

Our reason for choosing these particular books is threefold. First, each reflects the current state of play at the time of publication and in its own way can be said to have made an original contribution to our understanding of the relationship between human sexuality and evolution. (Note that in some cases we suggest the conclusions of the author/s are incorrect, but their publication has led to important debates in this area). Second, each of these books can be considered as a 'cross-over text'. That is, while all have been used by academics and students, all are written in an accessible way thereby opening the field to the non-expert reader. Third and finally, all, to varying degrees, consider cross cultural evidence (some more successfully than others). Cross cultural evidence is important to evolutionists since broad similarities can be taken to suggest that features of reproductive behaviour are universal and hence likely to be related to our shared evolutionary heritage.

Charles Darwin (1871) - The Descent of Man and Selection in Relation to Sex

The Descent of Man is a curious and prophetic book. It is a more confident book than The Origin of Species. Having shocked Victorians by publishing a book that humans evolved from apes in 1859 it was another 12 years before Darwin wrote a major work on evolution again. When he did so he decided to write about sex. This book has a more confident feel to it than The Origin of Species (Origin) because, during those twelve years Darwin's reputation had grown and because this was a period when many fossils were uncovered including, as he had predicted, an intermediate form – Archaeopteryx (1863) (a beautiful intermediate between birds and reptiles). Also work on the Neanderthal fossils during the 1860s suggested they were our relatives.

Although Darwin had briefly introduced sexual selection theory in Origin it was in The Descent of Man that he developed it and applied it to our understanding of human behaviour. According to Darwin, if natural selection is about survival to reproductive age, then sexual selection is about gaining access to the opposite sex and convincing them to have sex with you. Hence, whereas natural selection is survival of the fittest, we call sexual selection 'survival of the sexiest' [2,3]. Darwin suggested sexual selection generally leads to sexy competitive males and choosey drab females. Despite the human male's lack of physical attractiveness, cross culturally males of our own species are regarded as more competitive than females and females are regarded as choosier when it comes to sex. This means that as a species we do fit broadly into the pattern that Darwin suggested. The concept of sexual selection was largely ignored by psychologists as a way of understanding sex/gender differences for most of the

twentieth century. We feel this is unfortunate since it leads to a number of testable hypotheses. Astonishingly it was not until 1967 that anybody made a serious attempt to look at human reproductive behaviour within an evolutionary framework. And when this did happen, we feel it was, in part, a false start.

Desmond Morris (1967) - The Naked Ape: A Zoologist's Study of the Human Animal

In The Naked Ape, Desmond Morris helped to focus attention on human behaviour as a species of animal and was very much concerned with sexual behaviour. In particular Morris focused on human desire and reproductive behaviour and why men and women might differ with regard to this. This controversial book helped to restimulate interest in Darwin's original writings and on the relationship between evolution and human sexuality. Despite this we feel that Morris' portrayal of human sexual desire is problematic. In The Naked Ape he considers humans as an unknown species of ape. Morris suggested that human males were naturally dominant to females and that females had evolved to be faithful to their mates. In fact, it's fair to say that women, in general, were portrayed as subordinate to men and relegated to a secondary role in evolution. Morris reasoned that, as men were regularly away hunting for lengthy periods of time 'their women folk' had evolved a pair-bonding tendency in order to ensure that men weren't cuckolded. Given the attention paid to sex (and aggression), and given Morris' engaging writing style, it is not surprising that The Naked Ape was a worldwide best-seller (selling over 10 million copies and being translated into 23 languages). We feel, however, there are four problems with the Naked Ape:

- First, he presented a male-centred view of evolution

 with females evolving features to aid males and repeatedly being discussed as having a supportive role to men.
- Second, much of his writings centred on Western society. Although his writings were by-no-means racist, they were certainly somewhat 'Eurocentric' and were not in tune with the views of social scientists well versed in cultural relativism.
- Third, characteristics were explained as having arisen for 'the good of the species', despite the fact that by the mid-1960s ethologists were shifting away from this emphasis towards a focus on what was in it for the individual (or even the individual's genes).
- Fourth and finally, his writings about evolution had a teleological element to them. That is, evolution looks ahead and puts things right for the future (for example, faithfulness in females) rather than natural selection acting on characteristics to solve current problems.

Overall, we consider The Naked Ape to be a fascinating if flawed read. It is however a book that, importantly, led other academic writers to realise that they might consider writing for a general audience. It is unlikely that if The Naked Ape had not existed, Richard Dawkins would ever have written The Selfish Gene. He also set up a continuing debate, that is, are we naturally a pair-bonding species? A decade after Morris, Donald Symons entered the scene [4].

Donald Symons (1979) - The Evolution of Human Sexuality

In The Evolution of Human Sexuality Symons combined Darwin's notion of sexual selection with Trivers' concept of asymmetrical parental investment to suggest men and women have evolved somewhat different mating strategies. Hence one reason the sexes may have evolved differing mating strategies is because females invest more in each offspring produced and because they have a shorter period of fertility than males [5]. According to Symons, in addition to differences in physical characteristics, such as stature, we can trace psychological differences back to differing reproductive challenges during the EEA (the environment of evolutionary adaptedness - a combination of the time, place and ecological pressures faced by our species during our evolution to Homo sapiens). Because they are 'obligate high investors' in offspring (due to gestation, lactation and greater levels of parental care in general), ancestral women would have looked for signals of status and commitment in order to increase the chances of male parental investment. In contrast, males should be attracted to signals of youth and fertility because females have a shorter period of fertility.

Symons also examined the cost and benefits of each sex to remaining faithful. In order to explain potential differences in the nature of sexual desire between the sexes, he suggested we need to understand the challenges to reproductive success we faced during our ancestral hominin history. Women, for example, living under the harsh conditions of the savannah, might have left more surviving offspring by mating with a male that is of higher status than the one she has a bonded relationship with. Current studies suggest that rates of cuckoldry (that is, when a man brings up a child of another man believing it to be his own) are around 2% but can be significantly higher in some populations [6]. There is also cross-cultural evidence that when human females do engage in covert infidelity this is most likely to be around the time of ovulation - suggesting they may be using an evolved strategy to gain variability in their offspring [7]. This may be taken to suggest that women vary in their level of sexual desire during their monthly cycle in ways that would have been adaptive during the ancestral past. To Symons such evidence does not mean that women are now hard wired to philander, but rather that by incorporating parental investment theory and knowledge of the EEA into our understanding of human mating strategies, we might be better able to predict the

conditions under which either sex is likely to do so today. It is often felt that men have greater opportunities for extrapair copulations and that it may pay them to take advantage of these so since they can, in theory, produce far more offspring than women. As Symons pointed out, however, such behaviour could well draw resources away from the offspring of the pair bonded partner. This might help to explain why so many men remain faithful. A main argument presented in The Evolution of Human Sexuality is that the typical differences we observe in sexual behaviours and desires are largely innate. This leads Symons to suggest that changing rearing practices would not result in identical sexualities.

Sarah Blaffer Hrdy (1981) - The Woman That Never Evolved

A couple of years after the appearance of Don Symons book, Sarah Blaffer Hrdy published The Woman That Never Evolved. In many ways this tackled similar themes to Symons, but differed in that Hrdy shifted the focus on to women. Having studied monkeys in the field, she describes how our female primate relatives were often independent, competitive and sexually confident. Such findings were used as a springboard to examine the sexual and reproductive behaviour of women. In doing so Hrdy helped to alter the prevailing view in many quarters that female primates (and women) are simply nurturing, non-competitive and sexually submissive. Hrdy also questioned the conception of females as 'coy' when it comes to initiating sexual advances showing how, in both humans and primates, it is the females who regularly make the first move [8].

The Woman That Never Evolved should, however, not be seen as one which paints females as saints, since, while they may demonstrate a sense of sisterhood when bonding together for mutual defence, females (both primates and human) can, in their own way, be as competitive for mates as their male counterparts. What differentiates Hardy's book from others in this review is the fact that she suggests knowledge of our evolutionary past (including the behavioural ecology of our primate cousins) can be used to help address issues of sexual equality. While this book had a mixed reception from feminists of various flavours, it did at least shift the emphasis away from concentrating largely on what is in it for male members of a species. It is worth noting that Hrdy considers herself to be both a feminist and an evolutionist, demonstrating how the two are in no way incompatible [9].

Jerome Barkow (1989) - Darwin, Sex, and Status: Biological Approaches to Mind and Culture

In Darwin, Sex, and Status Canadian social anthropologist Jerome Barkow revisited a number of the areas which Symons had explored, but importantly, his book was aimed at bringing in people from the social sciences. Moreover, he added the important ingredient of the impact on society of men striving for status. The strength of Barkow's book is the fact that his knowledge base is so broad. Barkow is a modern-day polymath who combines and integrates anthropology with biology, psychology, sociology and animal behaviour into this works. In fact, Barkow argued that a full understanding of the human condition requires a synthesis of these approaches. Importantly he asks both how and why men and women differ in their forms of desire and in courtship tactics [10].

Like Hrdy, Barkow integrated knowledge of primate social systems, into his view of the evolved human nature. In this case, however, he suggested that primate social dominance has been transformed into human self-esteem and symbolic prestige. He considers that natural and sexual selection have led to the capacity to transmit culture and that cultural practices are related to reproductive practices. Barkow also makes the point that, while there are commonalities between cultures such as men concentrating on youth and fertility, there are also significant differences between cultures such as, for example, how acceptable homosexual behaviour is or the degree of equality between the sexes in different populations. Darwin, Sex, and Status was also one of the first books to consider the 'mismatch hypothesis' - that is there is a mismatch between our current environment and the environmental conditions under which we evolved (the 'EEA'). This, Barkow also considers, may be the case when it comes to reproductive behaviour. Hence men may strive for status in order to increase their apparent market value to women but this striving for status can lead to huge problems given the amount of power men can attain today. So, we may have manipulative male leaders today because such behaviour patterns were successful during the EEA leading some men down this path of demonstrating their status. Note that, prophetically, this suggests men who seek status at all costs can lead nation states down the path to brinkmanship and even warfare. It is worth noting at this point that Barkow was one of the prime movers in the development of evolutionary psychology [11].

Helena Cronin (1991) - The Ant and the Peacock: Altruism and Sexual Selection from Darwin to Today

The Ant and the Peacock was an adaptation of Helena Cronin's PhD thesis. Her external examiner, John Maynard-Smith, was so impressed that he suggested she tweak her thesis just a little and turn it into a book. He even wrote the 'Forward' to the book. The Ant and the Peacock is a beautifully written and clear-headed account of two evolutionary problems. First, why do individuals engage in altruistic behaviours (the ant) and second, why are male animals sexy and females not

(the peacock)? Among other things Cronin demonstrated how the concept of female choice was abandoned or ignored for almost a century and yet female choice can be such a powerful force in the evolution of behaviour in both males and females. Interestingly, Darwin's evolutionary contemporary Alfred Russel Wallace who was both a friend and admirer of the former, did not accept the notion of female choice. Sadly, most biologists followed Wallace rather than Darwin on this. Worse still, as we have stated earlier, psychologists did not even consider the concept of sexual selection during most of the twentieth century. Cronin outlines all of this and explored in detail why male sexiness has to be based on 'honest signals' in order for sexual selection to work (selection forces would remove 'false signals' due to female choice). She also predicted that female choice would eventually come to be seen as a strong selective force and how it will be shown to have a role in controlling the evolution of male sexual desire. It is to her credit that female choice is now well accepted as a driving force in both human and non-human evolution [12].

Geoffrey Miller (2000) - The Mating Mind: How Sexual Choice Shaped the Evolution of Human Nature

In 2000 American psychologist Geoffrey Miller began to champion the notion that, once biparental care had evolved, the main driving force for increasing brain size and intelligence became sexual rather than natural selection. He called this the 'mating mind' hypothesis. Miller proposed that, with an increasingly dependent offspring being born into a challenging savannah environment, it paid both sexes to recombine their genes with caring and intelligent individuals [13]. Given that sexual selection can act more rapidly than natural selection, it can be argued that the emergence of an enduring pair-bond and biparental care was a major factor in driving both human intellectual and emotional proclivities towards the position we see today.

Language, in particular, plays an important role in Miller's hypothesis. Miller noted that people generally have a much larger vocabulary than is necessary for communication (a typical adult has a 20,000-word family, but the vast majority of communication can be accomplished with a 6,000-word family). In an attempt to explain this level of redundancy Miller suggested that humans use their vocabulary in order to demonstrate their level of intelligence and this, in turn, can be taken as a measure of 'fitness' to a potential mate. This means that, rather than developing physically sexy traits such as large antlers or coloured tail feathers, our hominin ancestors developed a 'sexy brain' in order to compete. So, males with a good vocabulary can lead to an increased desire in females. His argument incorporates both male-male competition and female choice. According to Miller, those ancestral males that were best able to impress females with their communication

abilities would have had increased mating opportunities. Note that such verbal fluency is also used to compete with other males. This raises one big question – if the mating mind hypothesis proposes males use language to impress females, then why do women also possess verbal prowess? Miller explains this as women using complex language in order to probe men and assess their quality. That is, they have to be able to use a complex vocabulary in order to determine just how intelligent a given man is.

If the mating mind is correct then it means language and sex are inextricably linked and our lengthy road to adulthood arose, in part, due to the competitive edge language gave our ancestors in the game of love. (Note that, in contrast to Desmond Morris, we do not think that physically, on an objective scale, humans are a very sexy species).

David Buss (1994; 2003; 2016) - The Evolution of Desire: Strategies of Human Mating

In The Evolution of Desire David Buss suggested "Evolutionary psychology provides a meta-theory for predicting when and where to expect gender differences and when and where to expect gender similarities." He further suggests that because men and women faced largely identical recurrent adaptive challenges during our evolutionary past, we are more similar than different (examples of similar challenges include habitat selection, avoidance of predators and parasites, gaining resources and aiding kin). But it is in areas where we faced different recurrent adaptive challenges that we can predict differences. Such differences arise largely from differences in levels of parental investment, the possibility of cuckoldry and the fact that women have a shorter period of fertility. In essence, this means that we can anticipate differences in behaviour between the sexes in courtship and mating behaviour. Most of this theoretical background had, of course, already been considered by the previous writers. Where Buss differs from them is in the sheer scale of hypothesis testing he has conducted and the degree to which it fits in with these predictions of sex differences. In fact, Buss' research suggests quite strongly that these differences exist and that they are, in many cases, universal [14].

What Buss (and co-workers such as David Schmidt) has done importantly is to test both Darwin's' original ideas and the more specific ones put forward by Symons. Here's a list of just some of Buss' findings all of which have stood up to crosscultural examination and across socioeconomic classes:

- Men are more likely than women to seek short term relationships.
- Men would like to have many times more sexual partners over a lifetime than women.
- Men are more likely than women to consent to sex with a stranger.

- Men generally relax mate preference (whereas women increase selectivity) in short-term mating contexts.
- Women (more than men) prefer cues related to a man's ability and willingness to devote resources.
- Men, more than women, appear effective at displaying status-related traits to the opposite sex.
- Women who marry higher status men tend to have more children, and to have children survive to an older age.

Importantly, over its three editions (1994; 2003; 2016) The Evolution of Desire has expanded the range of those used to test such hypotheses greatly beyond WEIRD (Western, Educated, Industrialized, Rich, and Democratic) populations. This is important if evolutionists want to establish whether their findings are applicable cross culturally. Such crosscultural findings add weight to the notion that human sexual responses are related to adaptive features of human responses.

Christopher Ryan and Cacilda Jetha (2010) - Sex at Dawn: The Prehistoric Origins of Modern Sexuality

Sex at Dawn is a curious book. Its main message is that, unlike all of the other books we have considered, humans are not naturally an enduring pair-bonding species. They suggest that unlike the standard narrative of evolutionary psychology we were far more bonobo-like than chimpanzee-like for much of our evolutionary history. Bonobos are hypersexual where having sex is ubiquitous regardless of where the female is in her ovarian cycle. Moreover, homosexual sex is common. Christopher Ryan and Cacilda Jetha claim this was the state of affairs for our ancestors and, in effect, is our natural state - only suppressed by modern societal structures which arose quite recently on an evolutionary time scale. They suggest that, contrary to general belief, this did not lead to problems of jealousy but rather this regular sexual behaviour helped to strengthen bonds within the group. Hence, they argue it is not natural for us to form enduring romantic bonds although we might do so for relatively brief periods [15].

Ryan and Jetha list similarities in sexual behaviour between humans and bonobos (and in contrast to chimpanzees) include:

- Both species copulate throughout the menstrual cycle.
- Both enjoy many different copulatory positions (in particular ventral-ventral positions – chimps stick pretty much to rear-entry).
- Both often gaze into each other's eyes when copulating.
- The vulva is located towards the front of the body in bonobos like humans making ventral-ventral sex more likely.
- Food sharing is associated with sex in both humans and bonobos (less common in chimps).
- Homosexual behaviour is relatively common in both bonobos and humans (very rare in chimps).

Because of these similarities they propose that bonobos provide a better model for human desire and sexual behaviour than chimpanzees. As you can imagine Sex at Dawn sold very well and has had a big impact on the general public. It had mixed reviews. The popular press were very positive, while most evolutionists have been quite critical. One thing it does achieve is make us question evolutionary psychology's notion of an enduring human pair bond. On the negative side, we have problems with the out-dated use of 'naive' group selectionism - that is focusing on what is in it for the group rather than the individual and their genes. Also, their version of Darwin's sexual selection theory is a cherry picked one that is at times, arguably, misleading: "Darwin saw sexual selection as a struggle between males for sexual access to passive, fertile females who would submit to the victor" (p.42) [16].

This suggests that they have not read their Darwin or that they have wilfully edited him. To Darwin and to evolutionary psychologists today females are by-no-means passive bystanders awaiting the victor. But rather they very much decide the criteria by which the best males are selected. The similarity between humans and bonobos in terms of sexual behaviour certainly makes for interesting reading. But the problem here is that chimps and bonobos split from a common ancestor long after the split between humans and the joint ancestor of chimps and bonobos. Hence, if we are in some ways more similar to bonobos than to common chimps

it is more likely to be due to convergent evolution rather than a shared common ancestor. Putting these reservations aside there is also the small matter of the fact that chimps are not actually a pair-bonding species anyway. Hence, when it comes to reproductive behaviour, no serious evolutionist makes use of the 'chimpanzee model' to help explain the origin of human sexual responses. In summary, despite its shortcomings, we have placed Sex at Dawn on our list for two reasons; first, it does make us question the notion of an enduring romantic human pair-bond, and second, it has been influential with the public at large.

Frederick Toates (2014) - How Sexual Desire Works: The Enigmatic Urge

Interestingly, with regard to evolutionary psychology, while cognitive and emotional aspects had been examined in relation to human reproductive behaviour and sexual desire, the motivational component had to wait until Fred Toates book of 2014. Over the years Toates has been very much involved in developing motivational theory. In particular he has been at the forefront of the development of the concept of incentive salience. This is "the 'magnetic power' of incentives to engage and attract attention and behaviour" [17]. We can think of this as cue-triggered 'wanting' mediated by dopamine. It is often perceived as that conscious 'oomph' when it comes to desire – but as Toates documents it does not have to involve conscious awareness.

Author	Publication	Contribution to Understanding of Human Reproductive Behaviour
Charles Darwin	The Descent of Man - 1871	Introduces the concept of sexual selection and in particular the notion of female choice as a driving force in evolution
Desmond Morris	The Naked Ape - 1967	Suggests men have evolved to be competitive and women have evolved to be subservient. Led to debates regarding gender roles
Donald Symons	The Evolution of Human Sexuality (1979)	Uses the notion of asymmetrical parental investment to help explain sex differences in reproductive behaviour
Sarah Blaffer Hrdy	The Woman That Never Evolved - 1981	Shifts the balance towards females and suggests they are equally as competitive as men and less coy than generally suggested
Jerome Barkow	Darwin, Sex, and Status - 1989	Demonstrates the importance of the male obsession with status and its role in relation to sexual selection. Aimed at social scientists
Helena Cronin	The Ant and the Peacock - 2010	Examines altruism through the lens of evolution and considers the importance of female choice in evolution of both sexes
David Buss	The Mating Mind - 2000	Provides strong evidence-based conclusions regarding differences (and similarities) in reproductive behaviour between the sexes
Geoffrey Miller	The Evolution of Desire - (1995; 2003; 2016)	Suggests sexual selection rather than natural selection led to the evolution of human intellect and, in particular, language
Christopher Ryan and Cacilda Jetha	Sex at Dawn - 2010	Proposes we are not naturally pair bonding species. Led to a lively debate concerning human sexual behaviour
Frederick Toates	How Sexual Desire Works - 2014	Brings a modern understanding of motivation theory into the debate. Also brings two system theory into the understanding of sexual desire

Table 1: Summary of ten important works on the relationship between evolution and reproductive behaviour.

Among others Fred Toates has dismantled the old idea that animals (including humans) are simply driven by internal factors such as hormones and replaced it with the notion that learning and hormones modulate the power of the incentive to exert a 'pull'. This is more subtle and allows for the development of wanting (mediated by dopamine) and liking (mediated by endogenous opioids) being different phenomena that can become out of kilter.

This approach in How Sexual Desire Works, allows Toates to combine psychological and biological mechanisms in understanding desire. In addition to providing as good an understanding as you will find of the current state of affairs with regard to sexual desire it examines this difference between wanting and liking in relation to the development of desire and explains how the brain has evolved a hierarchical system of processing. Toates argues persuasively that we have evolved two different systems. System 1, which is evolutionarily old, is driven by what is physically present whereas system 2 is a more recently evolved add-on involving conscious reasoning. At times there can be disharmony between the systems which has implications for desire and sexual behaviour. So, at times, system 1 is saying give in to temptation while system 2 is urging restraint. Using this understanding in relation to incentive salience Toates is able to help elucidate why we often have internal conflict about desire and sexual behaviour. It helps us to understand how guilt has an effect on sexual behaviour and also gives credence to the concept of sexual addiction. That is, as with other addictive states it is possible to want sex (dopamine driven) without liking it (opioid driven) anymore.

Conclusions

Based on the readings briefly discussed above we feel that there has been much progress, both in terms of theory and of evidence, in our understanding of sexual and reproductive behaviour since Darwin's theory of sexual selection was introduced in 1871. We can now state with some confidence that there are four reasons why we can predict there are likely to be differences between men and women in reproductive behaviour. First, a man can, in theory, create many babies in the time that a woman creates one. Second, while women are fertile for a limited number of years, men are fertile until old age. Third, women invest more time and effort than men in the production of offspring. Fourth, only men can be cuckolded (bringing up another man's child). The impact of these factors on sex difference in behaviour varies somewhat between different human populations, but evidence suggests similarities between these populations are greater than differences. Despite this, the variation in the nature of human romantic relationships suggests we are an adaptively flexible species. Progress has not been linear, but in some ways spiral, revisiting questions from a wider range

of angles. There are still debates, for example, as to the degree to which we are an innately pair-bonding species. Because both sexes faced largely identical adaptive challenges during our evolutionary history, we are more similar than different. When it came to reproduction however the sexes faced somewhat different challenges. Hence it is this area where we are likely to find subtle, yet predictable, differences in responses. Finally, when it comes to sexual motivation, we have evolved two systems; an evolutionary ancient one which is stimulated by what is immediately present and a more recently evolved one which attempts to attenuate this older system. This attenuation is not, however, always successful, often later leading to feelings of guilt and regret. In other words, we (and in particular men) are often prone to giving in to our more ancient 'drives' that require immediate gratification (System 1) rather than weighing up the overall long-term costs and benefits of our actions (System 2). This means that System 2 is more likely to lead to the formation of an enduring bond based around reciprocated romantic love. Sadly System 2 is often jettisoned when it comes to sexual relationships because the signals of immediate gratification are so salient. In the words of Woody Allen, "Sex without love is a meaningless experience. But as meaningless experiences go it's pretty damn good".

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