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Comparative perspectives on human reproductive behavior

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Cyclic changes in women's sexual desire are consistent with an ancestral pattern in which hormonal shifts around ovulation prime behavioral patterns. We use comparative primate data to evaluate the plausibility of a prominent hypothesis in evolutionary psychology, that cyclic variation in women's preferences for high-quality men leads them to seek out extra-pair sex at times of high conception risk. Our review suggests little reason to invoke substantially different reproductive strategies for human females versus other monogamous primates, which are distinguished behaviorally and morphologically from species that have adapted to female promiscuity. While cuckoldry clearly exists in human pair bonds, we conclude that its potential to transform female sexual strategies, or male morphology, has been overemphasized.

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A central concern in evolutionary psychology is how human sexual behavior has been shaped by our evolutionary past. Debates in the current literature focus on how and why female sexual behavior varies across the menstrual cycle and, in particular, whether women maintain specific adaptations for eliciting genetic or phenotypic benefits from outside of a primary monogamous relationship. Empirical examination of human sexual behavior is challenging, typically involving self-reports and isolated examination of highly specific features of human mating psychology. The evolutionary significance of these patterns may be best understood by examining analogous systems in other primates. Here, we evaluate the plausibility of recent evolutionary arguments by placing empirical data from human evolutionary psychology within a broader primate context.

Psychologists and anthropologists often emphasize the flexibility and variety of human sexual behavior. Human mating, like that of other large-brained, anthropoid primates, is less dependent on hormonal and pheromonal control than that of most mammals. Sexual behavior in anthropoids can occur throughout the ovarian cycle, is exhibited even by gonadectomized animals, and is sensitive to individual experience and multimodal sensory cues [1•]. Non-conceptive sex is widespread, and serves a range of social functions not directly related to reproduction [2,3].

Dixson [4] categorizes primate mating systems on the basis of two primary considerations: firstly whether females normally mate with one or multiple males within a cycle, and secondly whether sexual relationships are generally long-term and exclusive, or short-term and promiscuous. Our closest living relatives, chimpanzees and bonobos, take short-term, promiscuous mating to an extreme. Chimpanzee females can mate with more than twenty males in a day, participating in 400 — 3000 copulations per conception [5,6]. Nothing remotely similar has ever been described in any human society.

Instead, human reproduction is notable for the centrality of the pair-bond, defined as an enduring, preferential, affiliative relationship between two individuals, that includes a sexual component [7•,8]. By this definition pair-bonds can be polygynous, polyandrous, or monogamous, need not be lifelong, and may even involve some degree of extra-pair mating. Such bonds, however, are fundamentally 'the opposite of promiscuity' [9]. The maintenance of enduring, preferential breeding bonds in the context of a larger multi-male, multi-female social group, though a human universal, is unusual among primates, and unique among the living apes [10,11].

Although both primate sexual behavior and its underlying neuroendocrine regulation are diverse, a number of specific behavioral and physiological features have predictably evolved in response to particular mating contexts. These features are valuable and reliable clues from which to infer the evolutionarily history of sexual behavior for a species.

Cyclic changes in sexual behavior

Although many studies have failed to detect periovulatory shifts in human sexual behavior [4,12], the most comprehensive efforts, measuring reproductive hormones across entire cycles in large samples of women, have documented small increases in the frequency of intercourse and the intensity of female sexual desire in fertile versus infertile phases [13,14•,15]. These changes are more pronounced in unpartnered than in partnered women [16]. Cyclic shifts in the ovarian hormones estrogen (upregulating sexual attraction and motivation) and progesterone (downregulating) are implicated in these behavioral changes, consistent with the general pattern in nonhuman primates [17]. Sexual behavior is, nonetheless, distributed more evenly across the cycle in humans than in other primates.

Many studies have also documented changes in women's preferences for particular mate characteristics (e.g., symmetry, masculine features) between fertile and non-fertile periods [18•]. Gangestad *et al.* [19] proposed that shifts in preferences facilitate fertilization by men of high genetic quality, a strategy that could conflict with the selection of highly-investing partners. Consistent with this hypothesis, studies find cyclic changes in women's evaluations of attractiveness for short-term mating, but not long-term relationships [18•]. Women rating their partners as less sexually desirable found more fault with them on higher fertility days of the cycle, whereas the reverse was true of women with desirable partners [20]. Some have argued that cyclic shifts in preference are psychological adaptations to motivate partnered women to seek out extra-pair fertilizations, and that this 'dual-mating' strategy is common enough to have selected for male traits promoting sperm competition [21–23]. Though the dual-mating hypothesis has received the most attention, viable alternatives exist. Variation in estradiol within and between cycles may enhance sensitivity to cues of desirable male traits when conception risk is highest without specifically promoting extra-pair mating [24]. Alternatively, small changes in mate preference that accompany within-cycle shifts in estradiol may be non-adaptive by-products of mechanisms that lead higher fertility women to be more selective of mates than lower fertility women [25•].

The hypothesized dual-mating strategy contrasts with the mixed mating strategies of promiscuous primates, such as baboons and chimpanzees. In these species, mating with many partners minimizes potential risk to a female's offspring by providing each male a probability of paternity [26,27]. Among anthropoids, multi-male mating is strongly correlated with the occurrence of genital swellings, which often extend outside the fertile period [28]. Sexual swellings may facilitate a mixed mating strategy because they signal an increased probability of ovulation without precisely identifying its timing. Females can attract many males to mate with them over the swellling's duration while mating more restrictively with the highest quality or most competitive males during the immediate periovulatory period [28]. Despite superficial similarities to the dual-mating strategy proposed for humans, mixed mating strategies in promiscuous primates are predicted to evolve under conditions of high infanticide risk and in conjunction with exaggerated signals of fecundity.

Extended sexuality

High rates of sex outside of the fertile window also characterize socially monogamous pairings in a variety of taxa, including primates [29]. As monogamy often involves male parental investment, females may initiate sex frequently to reassure a paired male of his paternity and to prevent desertion [29]. This 'mate retention hypothesis' is tentatively supported for humans by evidence that women are more likely to initiate sex in the luteal phase (after ovulation) when they perceive weak investment from their partners [30•].

Copulations occur throughout the cycle in the typically monogamous marmosets, tamarins, and gibbons [31–34]. While some females in these species have more than one partner, monogamously-paired female gibbons mate more frequently and for longer durations than polyandrous females [35], consistent with the mate retention hypothesis. Because human communities put bonded pairs in contact with other fertile adults more than in these other species, the mate retention hypothesis predicts that women should initiate especially high rates of in-pair sexual activity outside of the fertile period.

Periovulatory shifts in sexual behavior among tamarins and marmosets are driven primarily by increased female proceptivity and decreased resistance at midcycle [31–33]. Similarly, to the extent that men can detect ovulation, it appears that they rely on women's behavioral signals, or to potentially subtle vocal or scent cues [36]. These contrast with the striking visual advertisement of cycle status observed in promiscuous primates.

Behavioral cues potentially offer females greater flexibility to manipulate the information they provide to males, but there is little evidence that monogamous primates use them to secure fertile matings with outside males. In the instances when the ostensibly monogamous primates form polyandrous partnerships, fertile matings are strongly biased toward the primary or dominant partner [34,35,37]. Furthermore, facultative polyandry in these species appears to function to elicit higher investment for offspring rather to gain genetic benefits from the secondary male [38,39]. Thus, there is little evidence for a direct analog to the dual-mating strategy in nonhuman primates, and social monogamy coupled with paternal investment may be sufficient to explain extended sexuality in humans.

Nevertheless, extra-pair copulations are a persistent feature of monogamous systems. Rates of extra-pair paternity are reported to be high in socially-monogamous lemurs (44% *Cheirogaleous medius* [40]; >50%, *Phaner furcifer* [41]), low in one callitrichid (none detected, *Saguinus mystax*