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Adaptations to Ovulation

Implications for Sexual and Social Behavior

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ABSTRACT—*In socially monogamous species in which males heavily invest in offspring, there arises an inevitable genetic conflict between partners over whether investing males become biological fathers of their partners' offspring. Humans are such a species. The ovulatory-shift hypothesis proposes that changes in women's mate preferences and sexual interests across the cycle are footprints of this conflict. When fertile (mid-cycle), women find masculine bodily and behavioral features particularly sexy and report increased attraction to men other than current partners. Men are more vigilant of partners when the latter are fertile, which may reflect evolved counteradaptations. This adaptationist hypothesis has already generated several fruitful research programs, but many questions remain.*

KEYWORDS—*mating; evolutionary psychology; attraction*

Human sex can result in conception only about 20% of the time: from 5 days before ovulation to the day of ovulation. Yet unlike in humans' close primate relatives, human females lack conspicuous sexual swellings that vary across the cycle, and people have sex throughout the cycle. Continuous receptivity, however, need not imply that women's sexual interests or preferences remain constant. Indeed, it would be surprising if selection had not forged psychological adaptations in one or both sexes to be sensitive to conception risk—and recent research confirms this expectation. The ways people are sensitive to it provide keys to understanding how selection shaped human sexual relations. In short, romantic relationships take shape out of people's adaptive design for cooperating with partners—often lovingly—in pursuit of shared interests, in conjunction with each sex's adaptive design for pursuing its own interests (or those of same-sex ancestors) that conflict with those of partners.

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EVOLUTIONARY BACKGROUND: MATE CHOICE FOR GENES

Over evolutionary time, natural selection sifts through available genetic variants, saving those that promote success within a species' niche and discarding others. Our genes are typically "good genes" that have passed a test of time. But some aren't. Genes mutate. Though each gene is copied correctly 99.99+% of the time, sperm or eggs commonly contain one or more new copying errors. Because mutations typically have minor effects (much as slight impurities in a tank of gas subtly compromise car performance), most survive multiple generations before being eliminated. On average, an individual probably has several tens if not hundreds of mutations. Additionally, although the world to which humans must adapt is constant in many ways (e.g., its gravitational fields), in other subtle-but-profound ways it is not. Pathogens constantly evolve to better thrive in the human body, and humans must change merely to keep pace. Despite selection on thousands of ancestral generations to resist pathogens, humans do not possess sure-fire defenses against them.

The ubiquity of maladapted genes may explain why sex evolved. A gene mutated in an asexual, cloning organism persists in all descendants. Sexual organisms pass on just half of their genes to offspring, and what may make sex worthwhile is that offspring need not get all maladapted genes; some offspring get fewer than either parent.

Through good fortune and bad, not everyone has the same number of maladapted genes. The best way to minimize maladapted genes in offspring is to mate with someone lacking them. While mate choosers cannot directly compare DNA copying errors in suitors, they can do so indirectly—for precisely the reason that choosing mates with good genes is important: Genes affect their bearers' performance. Selection ensures that mate choosers evolve to be attuned and attracted to elements of performance that are sensitive to poorly adapted genes within the species—whether it be growth, the ability to physically dominate or outwit others, or possessing "good looks."

TRADE-OFFS BETWEEN MATERIAL AND GENETIC BENEFITS

In relatively few species do both females and males intensively nurture offspring. Humans may be one. While questions remain about how and to what extent men nurture their own offspring in foraging societies, in most societies men and women typically form socially monogamous pairs and men attempt to direct resources (meat, protection, direct care, money) to mates and offspring. Chimpanzees, bonobos, and gorillas don't share this pattern and are probably poor models of human sexual relations. As many bird species form social pairs, however, theories about their mating may offer insight into how selection shaped human sexual psychologies.

Many socially monogamous birds are not sexually monogamous. On average across species, 10 to 15% of offspring are fathered by males other than social partners—so-called “extra-pair” males. Multiple reasons that females seek extra-pair mates are being investigated, but one is that male assistance in raising offspring doesn't eliminate selection pressure on females to obtain good genes. Not all females can pair up with males with high genetic fitness. Those who don't could potentially benefit from getting social partners' cooperation in raising offspring but getting other males' genes. This pattern has been elegantly demonstrated in the collared flycatcher. A large male forehead patch advertises good genes. Females don't prefer large-patched males as social partners, as they work less hard at the nest. Small-patched males, however, are more likely to be cuckolded and large-patched males the biological fathers. Indeed, females time extra-pair copulations to occur during peak fertility, favoring paternity by extra-pair partners.

More generally, in socially monogamous species in which pairs have males as close neighbors, an inevitable conflict between the sexes arises. All else being equal, females mated to males not possessing the best genes could benefit by getting genes from someone else. At the same time, selection operates on investing males to prevent cuckoldry (e.g., by mate guarding or being able to recognize offspring not their own). Selection hence operates on each sex against the interests of the other sex; thus “sexually antagonistic adaptations” evolve. Depending on which sex evolves more effective adaptations (which may depend on ecological factors affecting the ease with which males guard their mates, the relative value of good genes, the amount of assistance males give females, etc.), the actual extra-pair sex rate may be high (20% or more) or low (5% or less). Even when it is low, however, the genetic conflict exists and sexually antagonistic adaptations may evolve.

THE OVULATORY-SHIFT HYPOTHESIS

We (Gangestad & Thornhill, 1998) proposed to look for human adaptations that are footprints of these selection forces, based on the fact we began with: Women are fertile during a brief window

of their cycles. If ancestral females benefited from multiple mating to obtain genetic benefits but at some potential cost of losing social mates, selection may have shaped preferences for indicators of those benefits to depend on fertility status: maximal at peak fertility and less pronounced outside the fertile period. Cycle shifts should furthermore be specific to when women evaluate men as short-term sex partners (i.e., their “sexiness”) rather than as long-term, investing mates (Penton-Voak et al., 1999). The logic is that costs do not pay when benefits cannot be reaped.

Over a dozen recent studies show that female preferences clearly do shift. At mid-cycle, normally ovulating, non-pill-using women particularly prefer physical symmetry, masculine facial and vocal qualities, intrasexual competitiveness, and various forms of talent.

The scent of symmetrical men. Asymmetry on bilateral traits that are symmetrical at the population level (e.g., finger lengths, ear dimensions, wrist width) reflects developmental instability, perturbations due to mutations, pathogens, toxins, and other stresses. Developmental instability, in turn, could affect numerous other features of men, including their scent. In four studies, men wore tee-shirts for two nights and women rated the attractiveness of the shirts' scents. All studies found that, when they were fertile, women particularly preferred the scent of symmetrical men (see Fig. 1). When women were not fertile, they had no preference for symmetrical men's scents. Although the chemical mediating this effect has not been identified, data and theory suggest the existence of androgen-derived substances, the scent of which women evaluate more positively when fertile.

Masculine faces. Male and female faces differ in various ways. Most notably, men have broader chins and narrower eyes (due to development of the brow ridge). Men vary, however, in the extent to which they possess masculine facial features. Women's preference for more masculine faces is more pronounced when they are fertile than when they are infertile, particularly when they

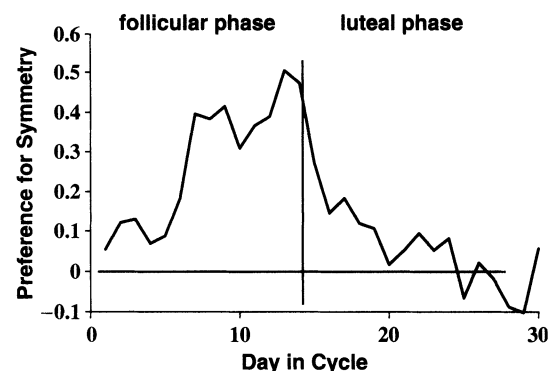


Fig. 1. Women's preference for the scent of symmetrical men as a function of their day in the cycle ($N = 141$). The vertical line corresponds to women's average day of ovulation. The follicular and luteal phases precede and follow ovulation, respectively. Each woman's ratings of scent attractiveness (a sum of ratings of pleasantness and sexiness) were measured against men's physical symmetry. Data are compiled from three separate studies: Gangestad & Thornhill (1998), Thornhill & Gangestad (1999), and Thornhill et al. (2003).

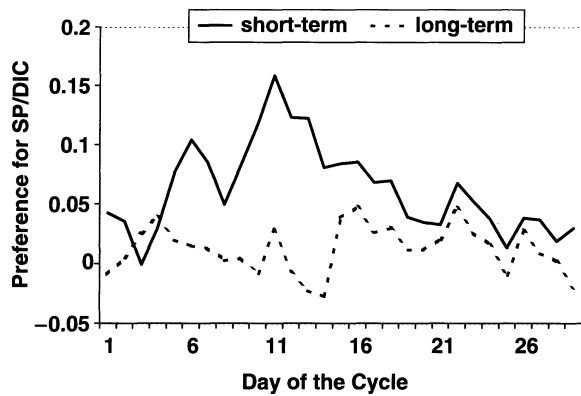


Fig. 2. Women's preference for men who display social presence (SP) and direct intrasexual competitiveness (DIC) as short-term partners (solid line) and as long-term partners (dotted line), as a function of day of their cycle ($N = 238$). From Gangestad et al. (2004).

rate men's sexiness, not their attractiveness as long-term mates (e.g., Penton-Voak et al., 1999; Johnston, Hagel, Franklin, Fink, & Grammer, 2001).

Behavioral displays of social presence and intrasexual competitiveness. We (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004) had women view videotapes of men being interviewed for a potential lunch date. Men independently rated as confident and who acted toward their male competitors in condescending ways were found more sexy by women when the women were fertile than they were when the women were not fertile (see Fig. 2).

Vocal masculinity. When rating men's short-term attractiveness, women find masculine (deep) voices more attractive at mid-cycle than they do at other times (Puts, 2005).

Talent versus wealth. Haselton and Miller (in press) found that, when faced with trade-offs between talent (e.g., creativity) and wealth, women choose talent more often when fertile than they do when nonfertile, but only when evaluating men's short-term mating attractiveness.

All of these characteristics may well have been indicators of good genes ancestrally. Not all positive traits are sexier mid-cycle, however. Traits particularly valued in long-term mates (e.g., promising material benefits) do not appear to be especially attractive to fertile women. For instance, follow-up analyses showed that while the women in the Gangestad et al. (2004) study found arrogant, confrontative, and physically attractive men particularly sexy mid-cycle, their attraction to men perceived to be kind, intelligent, good fathers, and likely to be financially successful—traits particularly valued in long-term mates—didn't change across the cycle. And men judged to be faithful were rated as less sexy mid-cycle than at other times (see also Thornhill et al., 2003).

SHIFTS IN WOMEN'S SEXUAL INTERESTS

Patterns of women's sexual interests also shift across the cycle. In one study, normally ovulating women reported thoughts and

feelings over the previous 2 days twice: once when fertile (as confirmed by a luteinizing hormone surge, 1–2 days before ovulation) and once when infertile. When fertile, women reported greater sexual attraction to and fantasy about men other than their primary partners than they did at other times—but their level of attraction to primary partners at this time was no greater than it was when they were infertile (Gangestad, Thornhill, & Garver, 2002; cf. Pillsworth, Haselton, & Buss, 2004).

In fact, however, the ovulatory-shift hypothesis expects a more finely textured pattern. On average, ancestral women could have garnered genetic benefits through extra-pair mating, but those whose primary partners had good genes could not. Selection thus should have shaped interest in extra-pair men mid-cycle to itself depend on partner features; only women with men who, relatively speaking, lack purported indicators of genetic benefits should be particularly attracted to extra-pair men when fertile. We (Gangestad, Thornhill, & Garver-Apgar, 2005) tested this prediction in a replication and extension of Gangestad et al. (2002). Romantically involved couples participated. Again, individuals privately filled out questionnaires twice, once when the female was fertile and once during her luteal phase. Men's symmetry was measured. Once again, women reported greater attraction to extra-pair men and not their primary partners when fertile. Effects, however, were moderated by the symmetry of women's partners. At high fertility, women with relatively asymmetrical partners were more attracted to extra-pair men—and less attracted to their own partners—than when they were infertile. No such effects were found during the luteal phase. Controlling for relationship satisfaction, another important predictor of women's attraction to extra-pair men, did not diminish the effect of partner symmetry. (See also Haselton & Gangestad, in press.)

MALE COUNTERSTRATEGIES ACROSS THE CYCLE

If women have been under selection to seek good genes mid-cycle, men should have been under selection to take additional steps to prevent them from seeking extra-pair sex at this time. Multiple studies indicate that they do so by being more vigilant, proprietary, or monopolizing of mates' time during those times (e.g., Gangestad et al., 2002; Haselton & Gangestad, in press).

There are several candidate cues of fertility status men might use. Three studies found that men find the scent of ovulating women particularly attractive (e.g., Thornhill et al., 2003) and one found that men judge women's faces more attractive mid-cycle. If women's interests change across the cycle, their behavior might too. Whatever the cues, women are unlikely to have been designed through selection to send them. As noted at the outset, women do not have obvious sexual swellings mid-cycle, and they have sex throughout the cycle. These features may well be due to selection on women to suppress signs of fertility status. Men, nonetheless, should be selected to detect byproducts of

fertility status not fully suppressed. Consistent with this idea, we (Gangestad et al., 2002) found that enhanced male vigilance of partners mid-cycle (as reported by women) was predicted by enhanced female interest in extra-pair men and not their partners. Men may be particularly vigilant of their partners mid-cycle, when their partners least want them to be.

ADDITIONAL OVULATORY ADAPTATIONS AND BYPRODUCTS

Women's preferences and biases may shift not only toward certain men, but away from clearly undesirable mating options (e.g., incest, rape; e.g., Chavanne & Gallup, 1998). Fessler and Navarrete (2003) assessed women's disgust in several domains: maladaptive sex such as incest and bestiality, food aversiveness, and filth. Only disgust to maladaptive sex rose with fertility.

Women can identify male faces as male more quickly when fertile (e.g., Macrae, Alnwick, Milne, & Schloerscheidt, 2002). This effect is perhaps a byproduct of greater salience of masculine features in male faces associated with their preference when women are fertile. Adaptive ovulatory shifts in preferences, sexual interests, and biases may produce a variety of other byproducts.

CONCLUSION

In any socially monogamous species in which males heavily invest in offspring, there is an inevitable genetic conflict between partners over where the female obtains genes for her offspring. Changes across the ovulatory cycle in women's and men's behavior may contain telltale signs of this conflict.

Many questions remain unanswered. Which female mate preferences strengthen mid-cycle; which don't? Is the pattern consistent with the good-genes hypothesis? Some preferences may be for compatible genes, ones that complement those of the mate chooser (e.g., dissimilar major histocompatibility complex [MHC] genes). Are preferences for compatibility maximal mid-cycle (see Thornhill et al., 2003)? How do male-partner features (e.g., symmetry, MHC dissimilarity) or relationship characteristics (e.g., satisfaction) affect female sexual interest mid-cycle? Do cycle shifts endure across women's reproductive lifespan? Are they robust across human populations? How, precisely, do men behave differently toward fertile partners and what cues mediate changes? Do women resist partners' proprietary actions more mid-cycle? What proximate mechanisms (e.g., hormones) mediate cycle shifts? (Changes in female preferences for the scent of symmetrical men are best predicted by corresponding changes in women's testosterone [positively] and progesterone [negatively], but other candidates [e.g., estrogen, luteinizing hormone] are possible.) Do men's hormones (e.g., testosterone) fluctuate in response to female partners' ovulatory status?

An evolutionary approach uniquely views ovulation as a highly important event around which psychological adaptations

might evolve. Alternative nonevolutionary approaches could not have predicted a priori or accounted for these findings. More generally, then, the ovulatory-shift hypothesis illustrates the heuristic value of an adaptationist perspective, guiding researchers to explore domains otherwise unexplored and generating fruitful predictions not offered by other approaches.

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