

Women's Sexual Strategies: The Evolution of Long-Term Bonds and Extrapair Sex

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Because of their heavy obligatory investment in offspring and limited offspring number, ancestral women faced the challenge of securing sufficient material resources for reproduction and gaining access to good genes. We review evidence indicating that selection produced two overlapping suites of psychological adaptations to address these challenges. The first set involves *coupling*—the formation of social partnerships for providing biparental care. The second set involves *dual mating*, a strategy in which women form long-term relationships with investing partners, while surreptitiously seeking good genes from extrapair mates. The sources of evidence we review include hunter-gather studies, comparative nonhuman studies, cross-cultural studies, and evidence of shifts in women's desires across the ovulatory cycle. We argue that the evidence poses a challenge to some existing theories of human mating and adds to our understanding of the subtlety of women's sexual strategies.

Key Words: dual mating, evolutionary psychology, ovulation, relationships, sexual strategies.

Hoggamus higgamus, men are polygamous; higgamus hoggamus, women monogamous.

—Attributed to various authors, including William James

William James is reputed to have jotted down this aphorism in a dreamy midnight state, awaking with a feeling of satisfaction when he found it the next morning. The aphorism captures a widely accepted fact about differences between women and men: Relative to women, men more strongly value casual sex (Baumeister, Catanese, & Vohs, 2001; Buss & Schmitt, 1993; Schmitt, 2003). James's statement, however, is clearly an oversimplification. The existence of a greater male

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desire for casual sex does not mean that women are "monogamous" and men are not. There is abundant evidence that women, as well as men, desire long-term committed relationships; but there is also an emerging literature revealing a hidden side of women's desires suggesting that women have also evolved to pursue short-term or illicit affairs. The purpose of this article is to review these lines of evidence and other recent findings pertaining to the evolution of women's sexual strategies.

Although humans are unique among other animals because of the diversity of their sexual behaviors (Dixson, 1998; Kinsey, Pomeroy, & Martin, 1948; Kinsey, Pomeroy, Martin, & Gebhard, 1953), we argue that a great deal of the evidence indicates two overlapping suites of psychological adaptations in women: those for securing long-term, cooperative social partnerships for rearing children and those for pursuing a "dual-mating strategy" in which women secure a social partner and engage in selective sexual affairs to gain access to good genes for offspring.

The Evolutionary Psychological Approach

The perspective we have taken in writing this review is that of evolutionary psychology. Evolutionary psychology is founded on the idea that an explicit consideration of the adaptive problems faced by our ancestors can lead to new discoveries and can organize and explain existing knowledge. We use this perspective as a framework for understanding the literature, and thus we begin by discussing recurrent features of the social and physical environment in which human mating strategies evolved, and we organize empirical discoveries in terms of the adaptations that may have evolved in response to these environmental challenges.

There are several core assumptions of evolutionary psychology that bear on our analysis. First, the working hypothesis of most evolutionary psychologists is that the mind contains many specialized adaptations akin to the different organs of the body (Barrett & Kurzban, 2006; Buss, 1995; Tooby & Cosmides, 1992); each organ in the body has a specific function, and so too should the mechanisms of the mind. Because mating decisions play a central role in reproduction, and thus in human evolution, our expectation is that there will be many richly specified adaptations underlying women's sexual behavior. Indeed, some of the best evidence supporting this expectation includes recent discoveries of specific changes in women's preferences and behaviors across the menstrual cycle, and this evidence plays a key role in our review.

A second assumption is that the mechanisms of the mind were forged by natural selection operating over hundreds of thousands of years, and

thus there will sometimes be mismatches between the outputs of these evolved mechanisms and the challenges present in the modern world. For example, humans have a well-documented tendency to easily develop fears of snakes and spiders, but not of some modern dangers that are much more perilous, such as fast moving automobiles (Öhman & Mineka, 2001). Another example is our preference for foods high in sugar, salt, and fat (Pinel, Assanand, & Lehman, 2000). In the ancestral environment, where food availability was unreliable, this preference probably helped to ward off starvation; in the modern world, these preferences lead to afflictions such as heart disease and diabetes. Human sexual behaviors were also forged in environments that were different in many ways from the environment of today. The availability of reliable contraception and technologies that assist in reproduction, for example, are modern inventions, and thus one would not expect psychological adaptations to have evolved to take into account the contingencies they present. Thus, although contraception has given women more practical freedom, women's minds may still treat sex as if it would have the reproductive consequences it had in ancestral conditions.

Lastly, the criterion for selection was reproductive success—how well the bearer of an adaptation and her descendants reproduced—regardless of how happy, well-adjusted, or even how healthy this made her. Thus, the goals women seek to achieve in their lives today, including their own subjective happiness, may not be served well by evolved adaptations. One possibility in presenting this evolutionary analysis of mating adaptations is that women may come to better understand the logic of their desires and perhaps make more informed decisions about whether to follow them.

The Evolution of Mating Strategies

Parental Investment Theory

Trivers's theory of parental investment proposes that males and females in sexually reproducing species should possess somewhat different psychological adaptations surrounding sex and mating (Trivers, 1972). Parental investment is investment in producing or caring for offspring. Investment in one offspring reduces the budget remaining for allocation to others, including future offspring. Human females, like the females of most other species, must invest heavily in each child produced. The human 9-month pregnancy, longer than expected based on mammalian patterns of gestation length relative to body size, requires an increase in caloric intake of 8%-10% (Dufour & Sauther, 2002). Lactation, which among modern hunter-gatherers persists for an average of

2.5 years (Lancaster, Kaplan, Hill, & Hurtado, 2000), is even more demanding and can increase energetic needs by up to 26% (Dufour & Sauther, 2002). Males have a much smaller obligatory investment. In principle, a human male can reproduce after investing only the time it takes for a single act of copulation.

Parental investment theory predicts that the higher investing sex should be more selective than the lower investing sex in choosing mates and more restricted in sexual activity. Women's reproductive investments are heavy, and they are necessary for offspring survival; in subsistence-level economies, for example, an infant orphaned by its mother before weaning is unlikely to survive (Hill & Hurtado, 1996; Mace, 1999; Sear, Allal, & Mace, in press). The death of a father also impacts child survivorship but is much less likely to be fatal. Because of the critical role their investment plays in reproduction relative to that of men, women should exact high standards before choosing a mate.

The lower investing sex, on the other hand, should be more open to opportunistic, low-investment matings. As Symons (1979) argued, an ancestral man who secured even one additional mating outside of his long-term relationship could have increased his reproductive success markedly, perhaps even by 50% or 100%. For women, increasing numbers of partners would not necessarily have increased offspring number; indeed, there were substantial costs that would have counteracted any benefits of having more partners, including risks of contracting sexually transmitted diseases and incurring the wrath of jealous partners.

Men can and do invest heavily in their offspring, however, and when they do so, they should also be highly selective in choosing mates (Kenrick, Sadalla, Groth, & Trost, 1990). Nonetheless, the difference in obligatory investment creates differences between the sexes, such that women, on average, desire greater material investment from partners than do men, and men, on average, seek to increase their overall partner number more so than do women.

The Heavy Burden of Raising a Human Child and the Need for Biparental Care

Humans are unique among our closest living relatives, the great apes and other primates, in the sheer amount of parental investment that is necessary to rear offspring to reproductive age, a situation that has led to a somewhat uneasy alliance between women and men. As a point of comparison, chimpanzee offspring from birth are able to hold onto their mothers' backs as they traverse the forest in search of food, are weaned at about 4 years of age, and are fully self-sufficient by about 5 years of age. Chimpanzee mothers have only one offspring about every 5 years,

thus rarely caring for more than one dependent offspring at a time (Lancaster et al., 2000; Silk, 1978). Female chimpanzees may sometimes attempt to get additional food resources from males in the troop, but they need not rely upon such resources to successfully raise their offspring, and it does not appear to be a significant factor in their reproductive success (Hemelrijk, Meier, & Martin, 1999).

Human offspring, on the other hand, are born relatively helpless, unable even to lift their own heads or unfold their hands until almost the 3rd month of life, and they remain dependent on their caregivers for a much longer time than any other primate. Among modern hunter-gatherers, for example, children do not begin to produce as many calories as they consume until approximately 15 years of age (Hill & Hurtado, 1996; Lee & Kramer, 2002), remaining dependent during that time on the provisioning of others. Human mothers in natural-fertility contexts (like those of most modern hunter-gather groups) wean their children at approximately 2.5 years of age, and have one child every 3 to 4 years (Lancaster et al., 2000; Mace, 1999; Panter-Brick, 1991)—a much greater rate of reproduction than chimpanzees. Women thus spend much of their adult life caring for multiple dependent offspring simultaneously, a commitment of time and energy unparalleled by any other primate. The problem of finding enough resources to meet women's own needs and those of several dependent children is one of the major challenges to reproductive success.

When children are unlikely to survive without investment beyond what can be provided by mothers alone, there can be selection for fathers to also invest in their offspring (Birkhead & Møller, 1996; Geary, 2000; Zeh & Smith, 1985). Human males are unique among the great apes in the extent to which they invest in their mates and offspring (Geary, 2000; Marlowe, 2000, 2001). This investment, however, entails a tradeoff, since a man who spends his time and energy providing paternal care cannot spend that time and energy seeking additional mating opportunities. Because male investment is not biologically obligatory, men may engage in a variety of strategies designed to minimize their costs while increasing their reproductive output, including fooling other males into investing in their offspring through cuckoldry (Gangestad & Simpson, 2000), pursuing opportunistic low-investment mating opportunities either in place of or in addition to a long-term relationship (Buss & Schmitt, 1993; Clark & Hatfield, 1989; Symons, 1979), and abandoning current mates and existing children in order to pursue other mating opportunities, particularly as their partners age and their future reproductive potential declines (Betzig, 1989). Because of the conflict for men between investing in parenting effort and mating effort,

women face the threat of being left without the resources needed to successfully raise their children. Ancestral women needed to be sensitive to how well a man could invest in her and her children, and also how likely he would be to continue to do so for the duration of time it took to raise a child to maturity.

Gaining Access to Good Genes

Genetic benefits. Material resources and investments of time are not the only factors affecting offspring. A child who is born weak or sickly, who is genetically vulnerable to parasitic infestations, or who is born cognitively impaired will require greater investment to raise and will be less likely to be reproductively successful when mature. Among modern foragers, the mean female reproductive success, measured as the number of offspring surviving to age 15, is only 3.11 (Marlowe, 2001). Because ancestral women produced relatively few offspring across their lifespan, evolutionary forces should have pushed women toward pursuing a strategy that ensures offspring quality, part of which will be determined by the genetic make-up of her mate and the genes he transmits to her offspring.

In evolutionary biology, the term *good genes* refers to genes that enhance offspring viability or reproductive success (Kokko, Brooks, Jennions, & Morley, 2003; Kokko, Brooks, McNamara, & Houston, 2002). There are at least three types of genetic benefits women could acquire through mates and transmit to offspring (following Gangestad, Thornhill, & Garver-Apgar, 2005a; Greiling & Buss, 2000): intrinsically good genes, compatible genes, and diverse genes.

Intrinsically good genes. All modern human beings are evolutionary success stories because they are descendants in an unbroken chain of ancestral humans who were themselves reproductively successful. However, in each new generation, the errors that occur during genetic copying produce genetic mutations. Some errors are devastating and are removed from the population because they result in the death of their bearer before reproductive age. Others are mildly deleterious and probably result in individuals who are slightly less intelligent, slightly less attractive, or slightly less athletic (reviewed in Keller, in press). These mutations can persist for many generations. The consequence is that all humans have hundreds of mildly deleterious mutations with cumulative effects on fitness (Fay, Wyckoff, & Wu, 2001). The number of these mutations present in each individual will vary and selection will thus favor mate choice adaptations that are sensitive to indicators of low mutation load and lead people to perceive such indicators as sexually attractive (e.g., Keller, in press; Keller & Miller, 2006; Miller, 2000; Rowe & Houle, 1996; Thornhill & Gangestad, 1999a).

The environment is also constantly changing, and the genes that conferred benefits in one generation (e.g., that conferred resistance to parasites in that environment) often are not optimal in the next (as the parasites themselves evolve around the genes of their hosts; Hamilton & Zuk, 1982). Therefore, selection will also favor adaptations sensitive to overall condition (e.g., body size, apparent health), as this will indicate the presence of genes well adapted for current environmental conditions (Thornhill & Gangestad, 1999b). There are several hypothesized intrinsic good genes indicators in humans, including certain facial and body features (Perrett et al., 1999), certain body scents (Thornhill & Gangestad, 1999b), and intelligence (Miller, 2000), which we review below.

Compatible genes and diverse genes. Good genes can also be defined in the relative sense as those that combine well with the genes of the other parent—*compatible genes*. For example, for certain genes related to immunity called the major histocompatibility complex (MHC), offspring benefit from receiving different genes from each parent (greater variation in an individual's MHC genes is thought to make it harder for pathogens to mimic a host's biochemistry and thus go undetected), and thus mates with different MHC genes are more compatible than those who have similar MHC genes (Penn, 2002; Wedekind, Seebeck, Bettens, & Paepke, 1995). Lastly, as a bet-hedging strategy, it may have benefited women to have multiple partners whose genes differ from each other (*diverse genes*) so that women's offspring also differ from each other and thus are not susceptible to the same disease threats (Jennions & Petrie, 2000). This may have been particularly important in environments in which disease threats were high and there was a significant risk that all of a woman's offspring could be wiped out by a single disease.

Coupling and Dual Mating

We propose that selection has produced two overlapping suites of psychological adaptations that address the challenges faced by women of obtaining the resources necessary for reproduction and of obtaining the best genes for their offspring. We do not propose that these suites of adaptations are the only ones selection has shaped, but we do contend that they explain a great deal of women's mating behaviors. The first set of adaptations involves *coupling*—the formation of social partnerships for providing biparental care (Pillsworth & Haselton, 2005). Theoretical considerations, universals in mating behaviors, and evidence of specialized psychological adaptations all support the hypothesis that coupling is a major component of women's evolved sexual strategies.

The second set of adaptations involves *dual mating*. Ancestrally, women may have received the greatest fitness benefits if they were able

to secure a monogamous long-term partnership with a man who displayed both investment cues and indicators of genetic quality. However, because men who are sexually attractive are in greater demand and have more opportunities for extrapair mating, they may shift their efforts away from parenting and toward securing additional sexual opportunities, making them less attractive as long-term mates (Faurie, Pontier, & Raymond, 2004; Hughes & Gallup, 2003; Perrett et al., 1999; Thornhill & Gangestad, 1994). Faced with such tradeoffs, ancestral women may have benefited by forming a social partnership with a man she judged to be a reliable investing partner, while surreptitiously seeking good genes from another man through extrapair sexual encounters (Gangestad & Simpson, 2000; Gangestad & Thornhill, 1997; Greiling & Buss, 2000; Pillsworth & Haselton, 2006). We consider adaptations for coupling and for dual mating in turn.

The Evolution of Coupling

Selection Pressures Favoring Coupling

Men benefit from investing in their own offspring. Theoretically, a woman could obtain resources from a variety of social partnerships, particularly kin relations (Gaulin, McBurney, & Brakeman-Wartell, 1997; Laham, Gonsalkorale, & von Hippel, 2005; McBurney, Simon, Gaulin, & Geliebter, 2002; Van den Berghe & Barash, 1977). Among most of the world's peoples, however, women form cooperative relationships with unrelated men—generally the putative fathers of their offspring—as a means of obtaining the resources needed to raise offspring (Betzig, 1989; Brown, 1991; Lancaster, 1991; Murdock, 1967). One reason for this pattern is that, unlike any other individual, a biological father has just as much genetic interest in a particular child as does the mother. The mother's own kin are only, at most, half as related to her children as is the father; unrelated individuals have no genetic interest whatsoever in her children, and in evolutionary terms are a woman's reproductive competitors. This makes the father a valuable ally in terms of his willingness to incur costs in order to acquire necessary resources, protect mother and offspring from predators or dangerous conspecifics, and, in later years, help children learn to navigate a complex social world and master the tasks necessary for survival (Geary, 2000; Marlowe, 2000).

Father absence affects offspring survival. The impact of father absence on child mortality also provides evidence of the importance of fathers. In a study of the Aché in Paraguay, Hurtado and Hill (1992) found that children between the ages of 1 and 5 years old were more

than twice as likely to die (2.6 times) if their fathers were dead than if they were alive. The effect of father absence due to divorce or desertion was even more pronounced, with children in the same age range being 2.9 times as likely to die in those households than in father-present households. Some researchers have argued that men's investment is unnecessary for offspring survival and that much of male provisioning (e.g., through hunting) is actually directed at obtaining additional mating opportunities rather than providing for their existing children (Hawkes, 1991; Hawkes, Rogers, & Charnov, 1995). Evidence from East African and Amazonian hunter-gatherer populations, however, demonstrates that fathers do provide critical investment, albeit via less showy means than hunting big game (Marlowe, 1999a, 1999b; Wood & Hill, 2000). In a study of the Hadza in Tanzania, Marlowe (2003) demonstrated that, whereas men did not preferentially provide meat to their own offspring due to norms of food-sharing with other members of the village, better hunters did provide more overall calories to their own offspring than did less-skilled men. These calories were provided from less conspicuous and less widely shared sources than meat, such as honey, and played a critical role in child success, particularly during the nursing years. During those years, women's foraging returns declined and their energy requirements increased. Marlowe found that provisioning by fathers compensated for mothers' reduced ability to acquire calories themselves. Similarly, in a meta-analysis of paternal investment using the Standard Cross-Cultural Sample of 186 diverse societies, Marlowe demonstrated that, although male provisioning varies substantially between populations, it never declines to zero (as female provisioning does in some societies), and that even modest amounts of additional provisioning by men can have important consequences for offspring survivorship, and hence women's reproductive success (Marlowe, 2000).

Extended sexual cohabitation affects pregnancy success. The immunological challenges of pregnancy may have favored long-term mating in humans. Fetal tissue shares only 50% of its genetic material with the mother and is often recognized as a foreign body by the mother's immune system and thus subject to attack. One result of immunological attack is preeclampsia, a severe form of gestational hypertension that occurs in about 10% of all human pregnancies. In extreme cases it may lead to epileptic seizures and possibly result in the death of the fetus (Martin, 2003). Because the risk of preeclampsia usually decreases with subsequent pregnancies, it has long been thought to be a risk only of first pregnancies. However, when studies examined the effect of different fathers on the risk of preeclampsia, it was found that regardless of the overall number of children borne, the critical predictor of

preeclampsia was whether it was a woman's first child with that particular father. Women who became pregnant with a new partner experienced the same risk of preeclampsia as women who were in their first ever pregnancy (Dekker & Robillard, 2003; Robillard, Dekker, & Hulsey, 1999). The risk of preeclampsia was also correlated with the duration of the sexual relationship with the father. Women who conceived for the first time within the first 4 months of sexual cohabitation had a 40% risk of preeclampsia, whereas those who conceived after a year of sexual cohabitation had only a 5% risk (Robillard et al., 1994). Lengthy sexual cohabitation may not only reduce the risk of disease, but may also have positive effects on the fetus. When conceptions occurred after a year of sexual cohabitation, pregnancies were marked by increased fetal weight relative to placental weight, an indication of fetal health (Robillard et al., 1994). This evidence suggests that the mother's immune system may learn over time not to reject the genetic material of a long-term sexual partner (Robertson, Bromfield, & Tremellen, 2003; Robertson & Sharkey, 2001) and suggests an additional benefit of forming long-term sexual relationships.

Coupling Is Universal

Patterns of marriage. Marriage occurs in almost all human cultures (Brown, 1991; Murdock, 1949, 1967), and although marriage traditions on the surface are variable, they all reflect a pattern in which individuals seek to form relatively long-term parenting partnerships with one or more individuals. Polygyny—one husband with two or more wives—is the legally permitted system in 82% of the world's cultures (Murdock, 1967) but is actually practiced by a minority of individuals, as only the wealthiest men in a society are able to afford the costs of having more than one wife. The balance of the population forms socially monogamous couples or does not partner at all (Borgerhoff Mulder & Caro, 1983; Kuper, 1982; Murdock, 1949, 1967).

Those who can afford more than one wife do not necessarily violate the notion of forming social pairs. The polygyny threshold model (Orlans, 1969; Verner & Willson, 1966) predicts that when there is variation in the amount or quality of resources held by males—such as the size or quality of the territory a male bird can defend—some females will do better to share the abundant resources of a single mate than to have sole access to the scant resources of a poorer mate. Similarly, if the function of the social pair for humans in the ancestral past was to provide the resources necessary to successfully raise offspring, a man who was able to acquire more resources could have provided sufficient investment for more than one partner (Borgerhoff Mulder, 1988, 1990). Men

and each of their partners may still have experienced the cooperative social bond that is likely designed to provide the resources for raising offspring.

When polygyny is practiced, husbands may feel bonded to one of their wives more than others. Thus, a more exclusive form of coupling may still be occurring at the psychological level. Among Fundamentalist Mormon polygamists, who are steeped in an ideological environment that strongly promotes multiple marriage and discourages exclusive emotional attachments, men struggle with unequal feelings of attachment toward their wives, often admitting that they prefer one over the others (Jankowiak & Allen, 1995). Wives, in turn, compete jealously for the attentions of their shared husband (Jankowiak & Allen, 1995).

Arranged marriage. In some cultures, marriages are arranged and individuals exercise little influence on the choice of their partner. Although this is a complex issue worthy of more research, for several reasons, we do not believe that the practice of arranged marriage poses a problem for the hypothesis that coupling is an important human adaptation. First, although arranged marriages are relatively common in the present day, they may not have been ubiquitous over human evolutionary history. In hunter-gatherer populations, for example, systems of arranged marriage are somewhat rare, and in those cases for which arranged marriages are the norm, the individuals to be married generally have a great deal of influence on the decision (Harris, 1995). Second, some evidence indicates that arranged marriages occur most often when family wealth is at stake, and thus these marriages may function, in large measure, as strategic financial alliances between clans or lineages rather than cooperative biparental partnerships (Parsons, 1984). Third, some studies suggest that autonomous choice enhances marital functioning. For example, in studies conducted in cultures in which both arranged marriage and "love matches" are practiced, relationship satisfaction and marriage quality, particularly for women, is higher in love matches (Lev-Wiesel & Al-Krenawi, 1999; Xiaohe & Whyte, 1990). Thus, there were likely advantages of individual choice, and therefore there are reasons to expect that a psychology for selecting a mate and maintaining a cooperative partnership would evolve.

The desire to form couples is resistant to ideologies to the contrary and is not constrained to the cultural practice of marriage. The Na of China, described in the ethnography by Hua (2001), have been held by many to be an exception to the universal practice of marriage. Hua describes the relationship ideology of the Na as one of casual sexual liaisons, or "visits," in which a man sleeps in a woman's bed and sires her children, but in which individuals do not form exclusive or long-term bonds, and in

which children do not know their fathers. Both women and men remain in their natal homes and siblings form the economic unit, with sisters tending the gardens and preparing the meals for the household, and brothers caring for the herds, maintaining the house, and providing material goods and protection for their sisters and their sisters' children.

One explanation for this pattern is that Na men face a low level of paternity certainty. The central economic activity for men is herding, an activity that takes them far away from home for what are often long periods of time. Thus, men may be more certain of their genetic relatedness to their sisters' children than to their lovers' children. The purported result is an ideology that is specifically opposed to exclusive romantic bonds and that strongly proscribes romantic or sexual jealousy. Both Hua's ethnography (2001) and the autobiography of a Na woman (Namu & Mathieu, 2003) claim that individuals behave according to the Na ideology: that fathers are unknown, sexual liaisons are casual, and jealousy does not exist. Despite these assertions, however, both sources actually provide evidence that men and women form emotional bonds and may remain in primarily exclusive relationships for extended periods of time. First-person accounts indicate that children often know who their biological fathers are, and that fathers provide resources in the form of gifts or work around the house. And, jealousy, far from being unknown, is common as both women and men struggle with their desires to form more exclusive bonds (Namu & Mathieu, 2003). Recent interviews with Na women confirmed that even among the older generation, long-term relationships were the norm and not the exception (Lulu Li, personal communication, October 5, 2004).

Falling in love is universal. Behaviorally, people around the globe appear to form relatively enduring social partnerships, both within and outside of the official bonds of marriage. The emotional correlate of these behaviors—romantic love—also appears to be universal. Many social scientists have argued that romantic love, or passionate love, is a recent cultural “invention” of the Western courtly age (e.g., Bloch, 1991; Person, 1991). However, two independent surveys of the ethnographic literature suggest otherwise. Harris (1995) outlined a set of seven core characteristics of romantic love drawn from 17 independent definitions of romantic love (e.g., Averill, 1985; Hatfield & Walster, 1978; Lee, 1988; Murstein, 1970; Peele, 1988; Shaver, Hazan, & Bradshaw, 1988; Sternberg, 1986; Tennov, 1979) and examined the ethnographic record for descriptions that matched the characteristics. The characteristics defined by Harris included the “desire for union or merger, both sexual and emotional,” the “exclusivity of the emotion for one particular per-

son," and a "reordering of motivational hierarchies of life priorities." Using this definition of love, Harris found evidence in the primary ethnographic literature for the existence of romantic love in each one of over 100 cultures, spanning every region of the globe. In an even broader survey using data from the Human Relations Area File (HRAF), Jankowiak and Fischer (1992) found positive evidence for romantic love in 89% of all cultures documented. For the remaining cultures, there were simply no relevant data; there was not a single instance of a culture in which love was shown to not exist.

Consistent with the behavioral evidence from the Na, romantic love as it has been characterized by these researchers is independent of the cultural practice of marriage. The cultures surveyed in these studies reflect the full range of variation in marriage ideology, including societies with arranged or polygynous marriage, collectivist societies that de-emphasize the role of the conjugal unit, societies that demand chastity before marriage and sexual fidelity within it, and those that accept and encourage short-term sexual relationships both before and after marriage. In all of these societies, individuals experience the desire to find a unique other and to form an exclusive, if impermanent, emotional bond with that person.

Psychological Adaptations for Coupling

Preferences for cues to dyadic cooperation. If the desire to form couples reflects adaptations for biparental care, traits that provide cues to the expected quality of that care ought to be of great importance when evaluating potential partners. For a cooperative partnership to succeed, partners must be able to work together, communicate effectively, reduce conflict, and share many of the same goals (Stanley, Markman, & Whitton, 2002). To this end, both women and men are expected to desire characteristics that indicate a partner's ability and willingness to cooperate. Women's and men's preferences in long-term partners have been measured in almost 40 societies—encompassing all regions of the world and a wide variety of social, economic, religious, and political systems—and in each of these societies, both women and men rated as most important those traits that directly affect a person's willingness to cooperate with others, such as kindness and reliability (Buss, 1989; Pillsworth, 2006), and the traits that are likely to act as cues to pair-specific cooperation, such as an "interesting personality," "sense of humor," and "mutual affection" (Buss & Barnes, 1986; Li, Bailey, Kenrick, & Linsenmeier, 2002). Preferences for other qualities that do not carry the same importance for the formation of social bonds, such as virginity and religiosity, show much greater variation both between cul-

tures and between the sexes within cultures (Buss, 1989; Pillsworth, 2006).

Preferences for resources. Material resources are also important to women and their offspring. Men vary in their ability to provide these resources, and thus women should possess adaptations designed to evaluate and to prefer cues indicating men's ability to acquire them. In studies of the characteristics that people prefer in long-term romantic partners, relative to men, women more strongly preferred traits such as "good earning capacity," "college graduate," "good financial prospect," and "ambitious and industrious" (Buss, 1989; Buss & Barnes, 1986). Although there is variation in the magnitude of the sex difference in preferences for resources, the sex difference appears to be universal across societies (Buss, 1989; Gangestad, Haselton, & Buss, 2006; but see Eagly & Wood, 1999).

Recently Li and colleagues (Li et al., 2002) further examined women's preferences for resources by creating an experimental context in which women's choices were constrained. Women from university and community populations in the United States were given a limited budget of "mate dollars" to spend in designing their ideal long-term romantic partner. For each mate dollar spent on a specific characteristic, the partner they were designing would increase by ten percentile units on that trait. Thus, if a woman spent ten mate dollars on a single characteristic she would design a mate at the 100th percentile—the top mate on that characteristic (e.g., the richest, kindest, or most humorous man in the world). If a woman spent zero mate dollars on a trait, her mate would be the lowest on that characteristic in the population. When women's budgets were most constrained (i.e., they had the fewest mate dollars to spend), they devoted the greatest proportion of their budget to a man's ability to acquire resources and his intelligence, in spite of the fact that they would have less to spend on other characteristics, such as creativity or friendliness. Li and colleagues interpreted this pattern as indicating that the ability to provide resources is a "necessity" in mate choice, whereas other characteristics are relative luxuries (Li et al., 2002). Cues to dyadic cooperation, such as kindness and sense of humor, also emerged as necessities for both women and men (Li et al., 2002).

For most of human history, people were unable to accumulate resources in the form of currency or durable goods. Thus ancestral women also needed to be able to predict, in the absence of observable wealth, which men would be most likely to be good providers in the future. Studies of modern hunter-gatherers' foraging returns further indicate that ancestral men probably did not reach their peak level of productivity until relatively late, for example, in their mid-30s (Hill &

Kaplan, 1999), suggesting that the observation of a young man's foraging returns may have provided an imperfect estimation of his potential quality as a provider. One possible cue to a man's future access to resources, instead, may be social status or prestige, as these traits indicate social resources available to an individual. In foraging groups, like those that existed over most of evolutionary history, cooperation, sharing, and the exchange of favors can be critical to survival (Cosmides & Tooby, 1992; Kaplan & Hill, 1985; Winterhalder, 1997). It is likely that individuals with higher status are in a better position to engage in beneficial exchanges with others in the population (Moore, 1983). Furthermore, in many societies social status is inherited and status hierarchies remain stable across many generations, making it a reliable predictor of a young man's future ability to acquire resources (Geary & Flinn, 2001). As with traits that indicate direct access to resources, relative to men, women more strongly prefer high social status and prestige in potential partners (Buss, 1989; Li et al., 2002).

Commitment skepticism. A man's access to resources is not useful to a woman if he is not also willing to commit them to his partner and her children. This is a nontrivial concern, because men faced trade-offs between parenting effort directed toward long-term mates and mating effort directed outside of long-term partnerships. According to Error Management Theory (Haselton & Buss, 2000), there should be systematic biases in assessing others' intentions when the costs of making different types of errors are asymmetric. In the case of assessing a man's interest in long-term relationship commitment, Haselton and Buss hypothesized that it was more costly for an ancestral woman to falsely infer commitment in a prospective mate and risk being abandoned than it was to err on the side of skepticism and risk missing an opportunity to conceive (an opportunity that would have been relatively easy to replace).

Several sources of evidence support this hypothesis. First, when evaluating the intentions conveyed by male courtship behaviors, such as kissing, buying jewelry, or saying "I love you," American men and women give somewhat different assessments. Men infer that these behaviors are more indicative of long-term commitment than do women (Haselton & Buss, 2000). Second, when asked at what point in a relationship they would be likely to have sex with their partner for the first time, women in most cultures report an average preference for a longer period of time than do men (Schmitt, 2003; Schmitt, Shackelford, & Buss, 2001). Third, women are less likely to consent to sexual intercourse, or activities that might lead to sexual intercourse, with a stranger (Clark & Hatfield, 1989; Schmitt, 2003). Fourth, women display skepticism by often requiring large economic investments before

consenting to either marriage or sexual intercourse. This is a common practice throughout the world, and in many cultures women or their families may expect men to provide some form of bridewealth, for example in the form of cattle or an expensive engagement ring (Borgerhoff Mulder, 1995; Goody, 1973). Being skeptical of men's intentions, delaying sexual intercourse, and demanding large initial economic investments allow women to better evaluate the true intentions of potential partners and make less costly errors.

Jealousy. Another threat to a woman's long-term partnership is that of other women. "Mate poaching," or intentionally attempting to attract another person's partner, is a common strategy used by both men and women around the globe (Schmitt, 2004; Schmitt & Buss, 2001). For women more than for men, the risk of infidelity lies in the possibility that a mate may abandon the alliance entirely or divert investments to a reproductive rival. This may be particularly likely if a man falls in love with another woman. Dozens of studies have confirmed that, on average, women are more upset than are men by the thought of their partner becoming emotionally involved with someone else (see Buss, 2000; Buss & Haselton, 2005; Sagarin, 2005 for reviews; also see Harris, 2003, for a critique of this evidence).

When is Coupling Disfavored?

Unstable environments. Long-term social partnerships may not always be available, or they may not present the best reproductive opportunities for women. In unstable environments, in which the availability of resources varies significantly from year to year or season to season, it can be difficult for women to predict how much potential mates will be able to invest in offspring. In addition, unstable environments may lead to increased competition for resources and higher levels of male-male violence and mortality (Durham, 1976; Gat, 2000; Manson & Wrangham, 1991). At the same time, it may be too costly for women to delay reproduction in the search for a high-investing mate, particularly if women's own health and longevity are compromised by harsh conditions (Johnstone, 1997; Kokko et al., 2002; Promislow & Harvey, 1991). According to life history theory (Bonner, 1965; Hill, 1993), women who are exposed to harsh environments in their childhood may facultatively adjust their reproductive strategies to favor a more short-term oriented strategy, in which there is little expectation of male provisioning after conception (Belsky, Steinberg, & Draper, 1991; Chisholm et al., 1993; Stearns, 1992). Women pursuing this strategy may engage in sexual activity at an earlier age, be more willing to have sexual intercourse early in their relationships, place less emphasis on emotional attach-

ments before sexual intimacy, decrease the duration of relationships, place greater emphasis on immediate resource extraction from sexual partners, and place greater emphasis on indicators of good genes, including physical attractiveness. Several researchers have demonstrated an association between a childhood environment that includes cues to relationship instability—including harsh parenting, father absence, and socioeconomic stress—and short-term oriented adult mating behaviors (Belsky et al., 1991; Geronimus, 1996).

Data from inner-city teen mothers in the United States further supports the hypothesis that uncertain environments may elicit this alternative, short-term reproductive strategy (Geronimus, 1996, 1997, 2003). Due to the high rates of violence, mortality, and incarceration among young men, the sex ratio in these environments is heavily imbalanced—there are more women of reproductive age than there are men. Cross-culturally, sex ratio imbalances like these predict not only an increase in single motherhood, but specifically in teen pregnancy (Barber, 2000, 2003). Women's health also declines rapidly, and delaying reproduction can mean failure to reproduce at all. In response to these conditions, girls tend to reproduce early, while their bodies are still strong. In a review of American pregnancy data, Geronimus (1997) found that in poor socioeconomic conditions, infants of teen mothers had higher birthweights and lower mortality rates than those born to women in their 20s and 30s; among middle-class women the pattern was reversed. The rapid decline in birth outcomes among impoverished women suggests that accelerated reproduction could have carried fitness advantages in some ancestral conditions.

Father absence. The absence of an investing adult male in early childhood is another possible cue that may shift women's reproductive strategies. Draper and Harpending (1982) proposed that the presence or absence of a biological father in the home during early development provides girls with information about the reproductive environment they will likely encounter in adulthood. In fact, girls who grew up in father-absent homes are more likely than girls who grew up in homes with a father present to engage in the short-term mating behaviors described above, and they are more likely to begin reproduction early (Ellis et al., 2003). In a study looking at the effect of father absence on girls' orientation toward early parenthood, researchers found that girls who grew up in father-absent homes showed greater interest in infants, measured by time spent looking at images of infants compared to other images, at an earlier age than girls whose fathers has been present in the home (Maestripieri, Roney, DeBias, Durante, & Spaepen, 2004). Father absence also affects physiological maturation. Many studies have docu-

mented a relationship between father absence and early age of menarche, (see Ellis, 2002, 2004, 2005 for reviews). Although the specific mechanism through which the presence or absence of a biological father affects women's sexual strategies remains a matter of debate, the effects of father absence are consistent and suggest that women are sensitive to cues that predicted the success of varying strategies in ancestral environments (Ellis, 2004).

Dual Mating

Selection Pressures Favoring Dual Mating

Offspring success depends in part upon the quality of genes inherited from parents. Because half the child's genes come from its father, but it is the mother who bears the majority of the obligatory costs of reproduction, it is likely that there was strong selection for discriminating mate choice among women on the basis of indicators of good genes. Although the best outcome for an ancestral woman may have been to form a long-term social relationship with a partner who could both invest heavily and transmit good genes to offspring, several sources of evidence indicate that women probably faced trade-offs in mate choice, and that gaining access to investment and good genes through the same partner was often not possible.

Fluctuating asymmetry (FA) is the degree to which bilateral features of an organism deviate from perfect symmetry (e.g., right and left wing lengths in birds and right and left finger lengths in humans). FA reflects developmental instability resulting from the disruptive effects of environmental or genetic anomalies and hence FA may serve as a summary indicator of mutation or maladapted genes (e.g., Møller, 1997). Across species, greater FA is associated with lower fecundity and survival (Møller, 1997). In humans, FA is negatively associated with sexual attractiveness in men (e.g., Scheib, Gangestad, & Thornhill, 1999), and therefore symmetrical men can and often do pursue a strategy that emphasizes mating effort at the expense of parenting effort. For example, symmetrical men have a greater number of lifetime sex partners, more sexual affairs, and are chosen more often by women as affair partners (Gangestad & Thornhill, 1997). Thus, although highly symmetrical men may be physically attractive, they may not make the best long-term mates.

Social perception studies provide further evidence of trade-offs in women's mate choices. There are a variety of hypothesized fitness indicators in humans, including several features associated with testosterone such as muscularity and facial masculinity. Across several

studies, Frederick and Haselton (2006) found that women rated images of muscular men as being higher in sexiness and dominance but lower in fidelity than nonmuscular men. Similarly, Roney, Hanson, Durante, and Maestripieri (2006) found that women preferred facial photographs of men who were high in testosterone as short-term mates, but not as long-term mates. Using the same set of photographs, and with no other information, women also rated men who had scored high on a measure of interest-in-infants as more attractive as long-term mates, but not as short-term mates, further suggesting the trade-off between investment and heritable quality (Roney et al., 2006).

Trade-offs in mate choice are also seen in other socially monogamous species. When sexually mature, male collared flycatchers develop a patch of white feathers on their foreheads. Offspring of males with large forehead patches tend to be in better condition (as measured by standard body weight assessments) compared to their half-siblings (Sheldon, Merila, Qvarnström, Gustafsson, & Ellegren, 1997), and hence forehead patch size is thought to be an indicator of good genes. Males with larger forehead patches, however, invest less time feeding offspring in their nests, and thus they may be less desirable as social partners than those with smaller forehead patches (Qvarnström, 1999; Qvarnström, Pärt, & Sheldon, 2000).

Behavioral Evidence for Dual Mating

Extrapair mating is common in socially monogamous species. If the risks are sufficiently low relative to the genetic benefits to be gained, females in species that practice biparental care may select long-term social males who display investment cues while seeking good genes through extrapair matings. In the collared flycatcher, for example, an average of 15% of the eggs in a female's nest are sired by males other than her social mate, and, as predicted by the good genes theory, males who display larger forehead patches account for more extrapair fertilizations than males with smaller patches (Sheldon & Ellegren, 1999). Moreover, females whose social mates have relatively small patches are more likely to engage in extrapair copulations, especially when they are most fertile (Michl, Torok, Griffith, & Sheldon, 2002; Sheldon, Davidson, & Lindgren, 1999). Recently, Wolff, Mech, Dunlap, and Hodges (2002) found that even in the prairie vole, a rodent studied as a rare model of mammalian monogamy, females will seek copulations with other males when their social partners are tethered and thus are prevented from mate guarding. In the study, almost half of mated females chose to mate with a different male when given the opportunity, and 25% of them deserted their previous mate for a new mate.

Extrapair paternity in humans. Women in all parts of the world engage in voluntary extrapair sex. In the U.S., for example, 15%-20% of women report that they have had extramarital sex at some point in their lives (Laumann & Mahay, 2002). Although systematic underreporting of infidelity is likely, female adultery is listed as a primary cause of marital dissolution cross-culturally, suggesting that it is not a rare occurrence (Betzig, 1989). Furthermore, rates of human extrapair paternity are substantial. Anderson (2006) reviewed paternity data from around the world, comprised of tens of thousands of paternity tests and including samples from indigenous populations in Venezuela and Brazil, European populations, South African populations, and several samples from the United States, among others. He found that extrapair paternity rates ranged from an average of about 1.7% among men whose paternity was not in question but was assessed for other reasons (e.g., in medical screenings), to rates as high as 55.6%, with an average of about 30%, among men who actively sought paternity testing (Anderson, 2006).

Evidence of male counteradaptation to female infidelity. In the ancestral environment, the fitness costs to a man who was cuckolded were large—including the loss of his own reproductive opportunity and the investment of his resources in the offspring of a rival male. Thus, researchers have hypothesized that men will be sexually jealous of their mates. Many studies have shown that men express more distress than do women in response to the thought of their partner engaging in sexual intercourse with another man (Buss, 2000; Buss, Larsen, Westen, & Semmelroth, 1992; Buss et al., 1999), and real or suspected infidelity is a leading cause of domestic violence and spousal homicide around the world (Daly & Wilson, 1988; Daly, Wilson, & Weghorst, 1982; Figueredo & McCloskey, 1993; Peters, Shackelford, & Buss, 2002; Rude, 1999).

Men also engage in greater mate retention efforts when the threats of infidelity are highest. In a study of mate guarding in a Trinidadian village, Flinn (1988) found that men spent more time in the presence of their wives and engaged in more agonistic interactions with unrelated men when their wives were in the most fertile years of their lifespan. Similarly, Buss and Shackelford (1997) found that American men's mate retention tactics—including expressions of jealousy, increased monitoring of their partners' behavior, and increased expressions of love and commitment—were positively correlated with two indicators of their partners' reproductive potential: age and attractiveness. Several other studies have found that men are more jealous and possessive, as well as more loving and attentive, when their partners are near ovulation in the menstrual cycle, the time at which men's paternity is most threat-

ened (Gangestad, Thornhill, & Garver, 2002; Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006). One would not expect the evolution of anticuckoldry adaptations in men if women were inclined to be perfectly faithful. Thus, male sexual jealousy and mate retention tactics suggest a history of female infidelity.

Evidence of male adaptations to sperm competition. Sperm competition occurs when the sperm of two males occupy the reproductive tract of the same female at the same time, and thus compete to fertilize her eggs. One physiological adaptation to sperm competition is large testis size, a trait that is correlated with the mating system of a species (see Dixon, 1998, for a review). Chimpanzees live in multimale, multifemale troupes, and females will mate with almost all the males in the troupe when fertile. As a result of the high degree of sperm competition, chimpanzees have a very large testis relative to their body size. Conversely, gorillas live in harems, controlled by a single dominant male. Females mate almost exclusively with the dominant male when fertile, leading to very low levels of sperm competition and small testis size relative to their body size. In humans, the ratio of testis size to body size is intermediate between primates who show high levels of sperm competition and those with low levels of sperm competition (Harcourt, Harvey, Larson, & Short, 1981; Harcourt, Purvis, & Liles, 1995; Møller, 1988). Although human testis size does not approach that of chimpanzees, it is comparable to primate species in which there is a moderate degree of sperm competition, including orangutans (Utami, Goossens, Bruford, de Ruiter, & van Hooff, 2002). Thus, the data suggest that some level of sperm competition in humans has probably occurred.

Psychological Evidence for Dual Mating: Preferences for Good Genes Indicators

The benefits of preferring partners with qualities desired in long-term social partners can be gained throughout the cycle, whereas the good genes benefits of mating with partners displaying fitness indicators can be gained only when women are fertile within the cycle (near ovulation). Thus, the dual-mating hypothesis predicts that women should express greater preferences for good genes indicators when they are near ovulation relative to other cycle phases. As we detail below, this prediction has been confirmed in dozens of studies across many hypothesized fitness indicators. In each of these studies, researchers limited their samples to normally ovulating women (those not taking the contraceptive pill or any other form of hormone-based contraceptive).

The scent of symmetry. Body and facial symmetry are statistically associated with male attractiveness, but differences in symmetry itself

cannot be assessed with the naked eye (Scheib et al., 1999). Thus, women must use some other cue when choosing symmetrical men as sex partners (Gangestad & Thornhill, 1997). Scent plays a role in women's mate preferences (e.g., Herz & Inzlicht, 2002); thus, the effects of symmetry on male sexual attractiveness could be mediated by differences in male scent. Four studies have examined whether women can discriminate between the scents of men who vary in symmetry. In each study, women were asked to rate the scents of T-shirts worn by men they had not seen. In three of the studies, women rated the shirts worn by more symmetrical men as more attractive, but only when the women were near ovulation within the menstrual cycle (Gangestad & Thornhill, 1998; Rikowski & Grammer, 1999; Thornhill & Gangestad, 1999b). In the remaining study, there was also a modest relationship between male symmetry and female preferences averaging across fertile and infertile cycle phases, but preferences for symmetry were strongest among women in the fertile phase of the cycle (Thornhill et al., 2003). Taken together, these results suggest that, although symmetry may be moderately preferred generally, women prefer symmetry most when they are fertile within the cycle, possibly because of the association between features correlated with symmetry and good genes.

Facial masculinity. Facial masculinity is another hypothesized fitness indicator. Masculine features are influenced by testosterone, a hormone that is correlated with immune functioning (Muehlenbein & Bribiescas, 2005). Thus, researchers have theorized that only males in good condition can physiologically afford to display masculine features, making those features honest indicators of good genes (Folstad & Karter, 1992). Across several studies, when women were presented with images of faces that had been digitally altered to appear more or less masculine (e.g., by altering the width of the jaw and the size and placement of the brow), women in the high-fertility phase of the cycle preferred more masculine faces than women in the low-fertility phase of the cycle (Johnston, Hagel, Franklin, Fink, & Grammer, 2001; Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999). In one study, women rated faces for attractiveness separately as short-term and long-term mates. The ovulatory preference for masculine faces was only apparent when women were rating men as short-term mates; facial preferences in long-term mates did not vary across the cycle (Penton-Voak et al., 1999). This pattern is consistent with the existence of adaptations in women for seeking good genes through extrapair sex or other short-term sexual liaisons.

Dominance. Men who are more competitive with other men and who behave in a more socially dominant manner tend to have lower FA, and

therefore behavioral dominance may also be a cue to good genes (Simpson, Gangestad, Christensen, & Leck, 1999). Gangestad, Simpson, Cousins, Garver-Apgar, and Christensen (2004) coded the social presence and intrasexual competitiveness of men who were videotaped while ostensibly competing for a lunch date with an attractive woman. The researchers then showed the videos to women, who rated the men as potential long- or short-term partners. Women in the ovulatory phase of the cycle rated the men displaying more social presence and competitiveness as more attractive than did women in nonovulatory phases of the cycle, but, again, only when they evaluated the men as short-term sexual partners and not as long-term mates (Gangestad et al., 2004).

Havlicek, Roberts, and Flegr (2005) took body odor samples from men who varied in dominance (measured using a personality test). Women in the fertile phase of the cycle rated the scents of the dominant men as more attractive than women in other cycle phases. This effect was considerably stronger in women who already had long-term mates as opposed to those who were single, suggesting that the effect could be driven by adaptations specifically for extrapair mating.

Vocal characteristics. The sounds of male and female voices are highly sexually dimorphic (Klatt & Klatt, 1990), and men with lower voices report having a greater lifetime number of sex partners than men with higher voices (Puts, 2005). Both of these facts suggest that vocal characteristics have been sexually selected. In two recent studies, researchers manipulated vocal recordings to make them sound more masculine or more feminine by lowering or raising their pitch. In each study, women in the fertile phase of the cycle expressed greater preferences for masculine voices than did women in the nonfertile phases of the cycle (Feinberg et al., 2006; Puts, 2005). In one of the studies, women rated the voices separately for their attractiveness in short-term and long-term mates; the effect of cycle phase on attractiveness ratings was again greatest for ratings of short-term sexual partners (Puts, 2005).

Body morphology. Height is also sexually dimorphic and has been linked with reproductive success in men (Mueller & Mazur, 2001; Nettle, 2002). Pawlowski and Jasienska (2005) showed women images of male and female couples that varied in their differences in height, with some of them depicting couples of nearly equal height, and others depicting couples with great disparity in height, with either the man or the woman being taller. The researchers found that women in the fertile phase of the cycle, more so than women in other cycle phases, preferred images in which the difference between the men and women was greater, with the man being taller than the woman. As with behavioral and vocal dominance, this effect was strongest when women evaluated

the men as short-term mates.

Ovulatory shifts in preferences are observed only for hypothesized good genes indicators and not for traits valued in long-term mates. Although many studies have found the predicted ovulatory shifts in women's preferences, it is important to show that these preference shifts are specific to likely indicators of good genes and not the qualities women desire in long-term social partners. A recent study by Gangestad and colleagues did just this (Gangestad, Garver-Apgar, Simpson, & Cousins, in press). Using the same videotapes from the behavioral dominance studies (Gangestad et al., 2004; Simpson et al., 1999), men were first rated by one set of women for ten perceived qualities women might desire in extrapair and/or long-term social mates, such as faithfulness, physical attractiveness, and social presence. A second set of women rated the attractiveness of the men as short-term and long-term partners. The dual-mating hypothesis predicts that women in the fertile phase of the cycle should prefer the qualities desired in short-term mates more than women in infertile phases of the cycle. The hypothesis further predicts that preferences for qualities desired in long-term mates should be independent of cycle phase or preferred less when women are most fertile.

Consistent with the existing literature, men's perceived arrogance, confrontational behavior, muscularity, and physical attractiveness predicted their attractiveness as short-term mates better than their attractiveness as long-term mates, whereas their faithfulness, warmth, intelligence, potential to be a good father, and potential for financial success predicted men's attractiveness as long-term mates better than as short-term mates. And, as predicted by the dual-mating account, the traits preferred more by women in the fertile phase of their cycle were also those preferred more in short-term mates: arrogant, confrontational, muscular, and physically attractive, as well as socially respected. The only other trait that was differentially preferred by low- and high-fertility women was faithfulness, but high-fertility women actually preferred it *less* than low-fertility women.

In a related study, Haselton and Miller (2006) presented women with a task in which they were to choose between two types of men, separately as long-term and as short-term mates. The first type was described as having received monetary wealth through luck (e.g., being left a small fortune by his adoptive parents), whereas the other was described as being very talented but poor (e.g., being a talented business man who had lost all of his money in an unfair lawsuit). Haselton and Miller predicted that women would trade off wealth for creative intelligence when they were most fertile, as showy displays of talent or

intelligence may be indicators of good genes (see Miller, 2000). They supported this prediction: Women in the fertile phase of the cycle preferred talent over wealth, especially when they chose men as short-term mates.

In sum, ovulatory shifts in women's mate preferences appear to be limited to likely indicators of good genes; preferences for the qualities women particularly value in long-term social partners—including resources, kindness, and fidelity—are not preferred more when women are most fertile.

Effects of context on shifts in women's mate preferences. Several effects of context on women's preferences also support the dual-mating account. First, as described above, when women have rated men separately as short-term and long-term mates, women's preferences shift more when they evaluate short-term mates. This suggests that shifts in preferences do not function as a means for seeking out long-term social partners; rather, these shifts may have led ancestral women to seek extrapair matings with men possessing sexually attractive indicators of good genes. Second, women already involved in long-term relationships have a greater overall preference for facial masculinity than do single women (Little, Jones, Penton-Voak, Burt, & Perrett, 2002). Similarly, Havlicek et al. (2005) found a greater ovulatory shift in women's preference for dominant male body odor in mated women than in single women. Third, women who are themselves more physically attractive may be able to demand more in mates, and hence they may not have to trade off good genes indicators for investment to the same extent as less attractive women. Evidence shows, as expected, that more attractive women prefer more masculine faces than less attractive women (Little, Burt, Penton-Voak, & Perrett, 2001; Penton-Voak et al., 2003). Lastly, a woman's ability to control resources may cue a strategy in which she does not need to seek resources through a long-term social mate, and thus she can elevate her preference for indicators of good genes. Recently, Moore and colleagues (Moore, Cassidy, Law Smith, & Perrett, 2006) showed precisely this pattern. Women's wealth and control of resources were associated with preferences for attractiveness over resources in mates (Moore et al., 2006).

Psychological Evidence for Dual Mating: Shifts in Women's Sexual Desires

Shifts in extrapair desire. The dual-mating account also predicts that women's sexual desires should change across the menstrual cycle. The costs of extrapair mating, including those imposed by jealous partners, extend throughout the cycle, whereas the genetic benefits of extrapair

mating can only be obtained when women are fertile. Thus, women should feel attracted to, flirt with, and occasionally have sex with men other than their primary partner more often when in the fertile phase of the menstrual cycle than in other phases of the cycle. Extrapair mating behaviors are relatively rare and often cloaked in secrecy, and thus are difficult to measure. The desires that underlie these behaviors, however, may be much more common, particularly in women whose primary partners lack cues to good genes.

Several researchers have documented that women's attraction to men other than their primary partner changes over the cycle (Gangestad et al., 2002; Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006). In one of these studies, for example, normally ovulating women completed questionnaires assessing their sexual desires and behaviors every day for 35 days, thus capturing an entire menstrual cycle. Whereas women's general sexual desire did not change across the cycle, near ovulation women were more attracted to and flirted more with men other than their primary partner than during other times in the cycle (Haselton & Gangestad, 2006). Another study assessed women's extrapair desires in laboratory sessions scheduled during high- and low-fertility points in the cycle, confirming ovulation with hormone tests (Gangestad et al., 2002). In this study, women's desires for their primary partners did not change across the cycle, but, again, their attraction to other men did: It was strongest near ovulation.

Shifts in desire are contingent on indicators of intrinsically good genes. The dual-mating account further predicts that these shifts should be strongest for women who would have experienced the greatest fitness gains through extrapair mating, that is, those women whose own partners do not show indicators of good genes. Three studies have confirmed this prediction. In one study, the strength of a woman's ovulatory increase in extrapair desires was predicted by her partner's asymmetry: Only women with relatively asymmetrical partners showed increases in extrapair desires at midcycle (Gangestad, Thornhill, & Garver-Apgar, 2005b). Moreover, in this study, women with relatively symmetrical partners actually showed an increase in attraction to their own long-term mates at midcycle (Gangestad et al., 2005b). Two other studies showed that women's assessments of their social partners' sexual attractiveness moderated shifts in extrapair desires, such that women who perceived their partners as least sexually attractive showed the greatest shifts in extrapair attraction (Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006). In these studies, the women who rated their partners highest on sexual attractiveness showed no evidence of an increase in extrapair desires near ovulation. Women's assessments of

their partner's long-term attractiveness (e.g., possession of resources; Pillsworth & Haselton, 2006) and their satisfaction in their relationships (Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006) did not predict cyclic shifts in extrapair attraction, indicating that the predicted effects were specific to partner sexual attractiveness. In sum, shifts in desire are experienced by the women who, according to the good genes theory, would have the most to gain through extrapair sex.

Shifts in desire are contingent on compatible genes. In addition to intrinsically good genes, women could engage in extrapair mating to gain access to diverse genes or compatible genes. In humans, there is no specific evidence that women engage in extrapair mating simply for the purpose of diversifying the genes of their offspring. Although this hypothesis cannot be fully ruled out, the specific nature of the shifts in women's mate preferences (for some traits more than others) and extrapair desires (for the partners of some men more than others) are hard to reconcile with the genetic diversity hypothesis.

There is some evidence, however, that women engage in extrapair mating to gain access to compatible genes. The major histocompatibility complex (MHC) is a set of genes contributing to immune function (see, e.g., Knapp, 2005). Unlike other genes, MHC alleles are expressed codominantly, which means that offspring express each of the two alleles at a given locus (one from their father and one from their mother). Diversity in MHC genes is thought to give offspring a greater ability to combat a wider range of pathogens. Thus, some men will have MHC genes that are more compatible with a woman's own genes than will others—specifically, those men with different genes than her own.

Couples tend to be more dissimilar in their MHC than would be expected if pairing were to occur randomly, suggesting that MHC related preferences operate in mate choice (Garver-Apgar, Gangestad, Thornhill, Miller, & Olp, 2006; Ober & Aldrich, 1997). Although it is somewhat mixed, there is also evidence that women prefer the body scents of MHC dissimilar others (Santos, Schinemann, Gabardo, & Bicalho, 2005; Wedekind & Furi, 1997; Wedekind et al., 1995; but see Thornhill et al., 2003), as do men (Thornhill et al., 2003; Wedekind & Furi, 1997; but see Santos et al., 2005). One recent study indicates that women with partners who are relatively similar in their MHC may seek compatible genes through extrapair mating. Garver-Apgar et al. (2006) assessed the MHC genes of women and men in long-term relationships. They found that the amount of MHC similarity between a woman and her mate positively predicted the number of affairs the woman had while in the relationship, controlling for relationship length and the woman's general interest in casual sex. These women also showed shifts

in extrapair desires across the 1-month duration of the study: They were attracted to men other than their long-term mate when they were most fertile within the cycle. In sum, women's dual-mating strategy may have evolved both for securing intrinsic good genes and compatible genes through extrapair partners when such benefits are not available from long-term mates.

Discussion

Coupling

We have argued that a great deal of evidence, including data from many recent studies, indicates that women possess adaptations for forming long-term social bonds with mates. Relative to other primates, human offspring require large investments of time and material resources to reach reproductive maturity. Fathers' reproductive interests are closely aligned with those of their offspring, and so the investment of fathers may have been particularly important, leading to the evolution of biparental care. Among the sources of evidence suggestive of adaptations for coupling are the universality of romantic love and marriage and the existence of female preferences for cues indicating that long-term partners will be willing and able to invest in offspring.

Dual Mating

In concert with this cooperative strategy, there may have evolved an antagonistic strategy in which women seek better genes for their offspring from men other than their primary partner, while attempting to maintain their alliance with their long-term mates (dual mating). Available mates will vary in mutation load and some individuals will have genes better adapted to current environments; thus, there has likely been selection for preferences for fitness indicators and the evolution of perceptions of such indicators as sexually attractive. In ancestral conditions, if long-term mates did not manifest these cues, women may have gained reproductive benefits from seeking sex with other men. The sources of evidence for dual-mating adaptations include nontrivial rates of extrapair paternity around the globe and the specificity of women's desires. Women more strongly prefer purported indicators of good genes when they are most likely to conceive within the cycle, and when they are considering a man as a potential short-term sexual partner. Because men with these traits may be less likely to invest in offspring, women do not strongly prefer these traits in long-term partners. Women also experience greater sexual desire for men other than their primary partners during the ovulatory phase of the cycle and particularly if their

partners lack cues to good genes. The specificity of these findings appears to support the dual-mating hypothesis and pose a challenge to some general theories of human mating strategies (see below).

Comparison With Existing Theories of Women's Sexual Strategies

Comparison with existing evolutionary theories. The arguments we have presented are consistent with other evolutionary theories of women's sexual strategies. In sexual strategies theory, for example, Buss and Schmitt (1993) proposed that humans pursue both long-term and short-term strategies. According to this theory, because of men's lower obligatory investment, short-term strategies occupy a larger share of the strategic repertoire of men as compared to women. Women, according to the theory, could pursue short-term strategies for a variety of reasons, including gaining access to resources and switching from one long-term mate to another. Buss and Schmitt speculated that women could also use short-term strategies to gain access to good genes, but they conceded that the evidence available at the time could not test this hypothesis.

Our analysis is consistent with sexual strategies theory. The studies we have reviewed confirm that women, too, can gain benefits from short-term mating. However, our analysis also suggests two significant updates. First, the balance of the evidence would seem to now suggest that short-term mating in women evolved, at least in part, to solve the problem of gaining access to good genes. Second, rather than *short-term* mating per se, the evidence seems to point to the evolution of *extrapair* mating—the psychology that leads women to have short-term affairs may be activated when they already occupy long-term partnerships. Thus, in addition to a temporal distinction between strategies, theories should distinguish between strategies that involve one sexual partner and those involving cotemporal sex with more than one mate (also see Greiling & Buss, 2000). Our review suggests that the latter distinction may play a larger role in defining variation in the strategies women pursue (but see Belsky et al., 1991; Ellis et al., 2003).

Our analysis is also consistent with strategic pluralism theory (Gangestad & Simpson, 2000). Like sexual strategies theory, strategic pluralism theory proposed that women and men pursue a variety of different mating strategies, but the theory emphasized that the strategies women and men pursue should be contingent on cues indicating the fitness costs and benefits of different courses of action. Strategic pluralism theory predicted, for example, that sexually attractive men should shift their efforts away from parenting and toward securing additional mating opportunities. Although the theory arguably focused more on the

strategies of men than of women, strategic pluralism theory also articulated the prediction that women would engage in extrapair sex for gaining access to good genes—a prediction that has now garnered substantial support.

Long-term mating only? Some theorists have claimed that human reproductive strategies are designed only to be cooperative (see, e.g., Miller, Putcha-Bhagavatula, & Pedersen, 2002; Pedersen, Miller, Putcha-Bhagavatula, & Yang, 2002; Roughgarden, Oishi, & Akçay, 2006). These researchers propose that short-term mating, when it occurs, is a result of novel circumstances or maladaptive misfires of evolved mechanisms (e.g., Miller & Fishkin, 1997; Miller et al., 2002). We agree that cooperative strategies form a major part of the repertoire of human mating strategies. At the same time, however, there is growing evidence of specific adaptations for engaging in sex outside of a long-term partnership. In particular, it is hard to see how misfires would lead to the specific pattern of shifts in women's desires across the menstrual cycle.

Evidence of sex-specific adaptations? Eagly and Wood (1999; Wood & Eagly, 2002) have argued that sex differences result not from different selection pressures acting on the minds of men and women, but solely from the differential placement of women and men into social roles (in combination with bodily differences between the sexes). This idea is difficult to reconcile with the evidence we have reviewed. For example, abundant evidence indicates that there would have been substantial fitness advantages accruing to women who sought material investment from mates. It is unlikely that women's mating psychologies would be immune to such selection pressures. This view is also not consistent with much of the new evidence of specific adaptively patterned changes in women's preferences across the menstrual cycle. For example, social roles cannot account for specific shifts in women's extrapair attractions—shifts that track women's menstrual cycles and their partners' symmetry, sexual attractiveness, and MHC similarity. The fact that these preferences are tied to cycling hormones that are different in women and men clearly indicates that these adaptations differ between the sexes.

Comparison with popular understandings of evolutionary perspectives on sex differences. Some authors have taken issue with evolutionary approaches to sexual strategies by claiming that they consign the sexes to stereotypical, simplistic, and fundamentally conflicting behaviors. Like the purportedly Jamesian aphorism, evolutionary theorists are said to claim, simply, that men are designed for short-term mating and women are designed for long-term mating (e.g., Angier, 1999). We hope that the data we have reviewed in this paper will help to put these

notions to rest. Researchers have been actively studying the plurality of strategies pursued by women and men and seeking to understand both sex differences and within-sex diversity. Moreover, the existence of a strategy in one sex often implies some behavioral similarity in the other. Women could not have evolved to seek long-term committed relationships if men would never comply, nor could they have evolved to seek extrapair liaisons in the absence of willing male partners.

Implications for Research on Men

Understanding women's strategies should inform research on men. If we are correct that coupling played a crucial role in the evolution of human mating strategies, there should be many specialized adaptations for long-term partnerships that are shared by women and men. Some of these have already been discovered—for example, long-term mate preferences (e.g., Buss, 1989) and patterns of attachment and bonding (Fraley & Shaver, 2000; Gonzaga, Keltner, Londahl, & Smith, 2001; Hazan & Shaver, 1987; Hendrick & Hendrick, 1994; Kirkpatrick, 1998). There should also be adaptations specific to men's adaptive challenges. For example, marriage and the birth of a child are correlated with lower testosterone in men. One interpretation of this pattern is that testosterone decreases as a mechanism for promoting parenting effort and reducing mating effort (Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002).

The dual-mating hypothesis leads to the expectation that men will be equipped with evolved counterstrategies that combat the risk of cuckoldry. Although the evidence is somewhat mixed (e.g., Harris, 2003), there may be a dedicated psychology in men that leads them to be sexually jealous and to engage in mate guarding (see, e.g., Buss & Haselton, 2005). Because paternity is threatened during the narrow window of fertility within women's cycles, men may also be sensitive to ovulatory cues. Indeed, although it may be in women's interests not to advertise such cues to preserve freedom of choice, several studies indicate that men find women's body scents near ovulation most attractive (Doty, Ford, Preti, & Huggins, 1975; Singh & Bronstad, 2001; Thornhill et al., 2003). Researchers could also examine whether men are sensitive to changes in women's behaviors across the ovulatory cycle, including their flirtation with other men (Haselton & Gangestad, 2006) and the degree to which they "dress to impress" (Haselton, Mortezaie, Pillsworth, Bleske-Rechek, & Frederick, 2007).

Other Female Mating Adaptations and Mating Behaviors

Our review is not comprehensive. Because of our theoretical orientation and space constraints, we have focused only on studies of hetero-

sexual women, and we have not reviewed the literature on lesbian and bisexual women—a literature that is required for a complete understanding of women's sexuality. We have also concentrated on two suites of female adaptations that we believe to play a central role in women's behavior, but there are many other adaptive problems we have not addressed. For example, a burgeoning area of research is that in which adaptations for inbreeding avoidance (Fessler & Navarrete, 2004; Lieberman, Tooby, & Cosmides, 2003) and rape avoidance (Bröder & Hohmann, 2003; Chavanne & Gallup, 1998) have been examined. Another promising area of research would be to explore the ways in which women's sexual strategies, and the conflicts and congruencies of interest with a social mate, change across the lifespan.

One of the most intriguing areas for future research concerns *erotic plasticity* in women. Recent discoveries have revealed that women's sexual orientation changes more across the lifespan than does men's (Baumeister, 2000; Diamond, 2003). Women are also sexually aroused by sexual images of both women and of men, regardless of their stated sexual orientation (Chivers & Bailey, 2005; Chivers, Rieger, Latty, & Bailey, 2004), whereas men tend to be aroused only by sexual images of one sex or the other (Chivers & Bailey, 2005; Chivers et al., 2004). These findings present another "hidden side" of women's desires that should be explored.

Conclusion

Ancestral women were limited in the number of offspring they produced, their investments were necessarily heavy, and fertility within in the menstrual cycle is fleeting—lasting only a few days each month. Women's sexual behaviors were also situated in complex social environments that included reproductive competitors, allies, their other children, their social mates, and, possibly, extrapair mates. It would be remarkable if these forces had not created a richly specified psychology that is sensitive to cues indicating reproductive opportunities and that could guide women's behavior toward strategies that exploited them. Indeed, women's sexual behaviors are diverse, varying within local environments and across the globe. Underlying this variation, however, there are shared psychological adaptations—perhaps, involving both coupling and dual mating. Research on these adaptations adds to our understanding of the texture and subtlety of women's sexual strategies.

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