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The Evolutionary Psychology of Human Mate Choice: How Ecology, Genes, Fertility, and Fashion Influence Mating Behavior

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The recent incorporation of sexual selection theories into the rubric of Evolutionary Psychology has produced an important framework from which to examine human mating behavior. Here we review the extant empirical and theoretical work regarding heterosexual human mating preferences and reproductive strategies. Initially, we review contemporary Evolutionary Psychology's adaptationism, including the incorporation of modern theories of sexual selection, adaptive genetic variation, and mate choice. Next, we examine women's and men's mating preferences focusing on the adaptive significance of material, genetic and fertility benefits, and their relationship to environmental characteristics. Following this, we consider human mate choice in relation to non-adaptive preferences. This discussion ends with a look at context effects for individual differences in mate-preferences and reproductive strategies.

KEY WORDS: Sexual selection, fitness indicators, mate choice, mating preferences, mating strategies, parental investment

From colorful birds and dancing bees to Sinatra's crooning, Betty Davis's eyes, and Monty Python's satires, various phenotypic traits serve as signals to others. *Aposematism* (warning coloration) in butterflies, for example, cautions predators that the butterfly is poisonous (Joron, 2002). Other elaborate coloration may signal genetic quality, immune function, and environmental condition in birds—thus, attracting mates who are seeking healthy sires for offspring (Houle & Kondrashov, 2002). A bee's dance indicates the location of nectar and pollen (Nieh, 2004), while among humans the rhythm and intensity of an adolescent Wodaabe male's dance indicates physical prowess and vigor, a criterion used in female mate choice in many species (Kokko, Brooks, Jennions, & Morley, 2003). Whatever the signals, evolutionary processes shaped them to help individuals survive or reproduce, with the ultimate unconscious adaptive goal of the proliferation of one's own genes.

Theories of signal evolution are fairly recent, and new discoveries about animal signaling are made almost daily (see Bradbury & Vehrencamp, 1998; Kokko, Brooks, McNamara, & Houston, 2002). Evolutionary science has come a long way since the dawn of Darwin's dangerous idea in 1859. While the theory of natural selection revolutionized the understanding of non-human behavior fairly early, its application to human behavior has been a long, arduous journey with frequent misunderstandings of Darwinian adaptationism, as well as its sociopolitical implications (Plotkin, 2004; Segerstråle, 2000). After sorting through these misunderstandings, the past two decades have seen a torrent of research on human behavior, drawing from diverse fields such as anthropology, behavior genetics, ecology, economics, evolutionary biology, game theory, genetics, neuroscience, psychology, sociology, and zoology (Buss, 2005).

The Darwinian revolution in human behavior has led recently to *Evolutionary Psychology* (EP)—an insightful consilience of behavioral and biological research—from which scientists have begun to explore the psychological adaptations that constitute human nature and their evolutionary origins. Mostly, these scientists have followed the basic tenets of natural selection theory, focusing on *inclusive fitness theory* (practical adaptations for replicating selfish genes) and *stabilizing selection* (adaptations optimized to show low variance). In recent years, however, another group of scientists have incorporated sexual selection and signaling theory into their research (e.g., Boone, 1998; Gintis, Smith, & Bowles, 2001; Hawkes & Bliege Bird, 2002; Miller, 2000a, 2000b). This paradigm shift has led to a different flavor of adaptationism, in which genes can proliferate based on their power to impress others through signals, rather than on their ecological utility, and in which genetic variation between individuals is amplified rather than reduced. In this text, we will examine human heterosexual mating strategies using the full range of modern Darwinian theory, including natural selection, sexual selection, and signaling theory. Due to limited space, we will describe EP's approach only briefly and refer the reader to other texts in this volume that describe EP in more depth.

As we attempt to integrate a variety of fields of knowledge, it is important to define commonly used terms in sex research to minimize confusion (see Kauth, 2005). (We will define terms related to evolutionary theory throughout the text). Here the term "sex," used as a noun, refers solely to the biological distinction between males and females of a species, defined by gamete size relative to each other; "sex" as a verb refers only to the act of penile-vaginal intercourse. Social distinctions between males and females are referred to by the term "gender," relating the former to those social behaviors and physical characteristics associated with masculinity and the latter with those associated with femininity. When referring to members of one sex across different species, we will use the terms "male" and "female." When referring to human males and females, we will use the terms "man" or "woman." "Sexual orientation" refers to the sex to which one is attracted: "heterosexual" (other-sex attraction), "homosexual," (same-sex attraction), or "bisexual" (attraction to both sexes). Use of these terms as adjectives does not imply an identity. "Heterosexuality," "homosexuality," and "bisexuality" refer to classes of social and sexual behaviors or sexualities, and also do not imply a self identity. "Mating" refers to those biological and social behaviors that lead to sexual intercourse. This text will focus on heterosexual (male-female) attraction and mating and will not consider the characteristics or circumstances of homosexual or bisexual attraction and mating.

In the first portion of this text, we will describe the current EP understanding of sexual selection: Outlining basic sexual selection theory and exploring a genetic perspective on the development of sexual reproduction itself, including theories of pleiotropic mutation and fitness indicators. We will then shift to our main focus: Exploring how ecological and social factors interact with evolved mating patterns, preferences, and strategies to shape human heterosexual behavior. We propose that heterosexual mating behavior varies adaptively in response to key ecological factors, such as local topography, climate, flora, fauna, pathogens, and parasites. In addition, mating behavior will vary adaptively in response to social factors, such as kinship structure, population density, operational sex ratio, and cultural traditions—all of which affect people's strategies for finding, attracting, seducing, retaining, and protecting mates. Although the interplay of these factors is still far from being understood (Gangestad & Simpson, 2000), a review of the current empirical research may illuminate how seemingly disparate mating strategies make sense from a unified Darwinian standpoint. That is, despite its superficial complexity, variability, and mystery, human mating behavior shows a high degree of cross-historical, cross-cultural, and cross-environmental stability at a more abstract level of description, which can be understood through sexual selection and signaling theory.

EVOLUTIONARY PSYCHOLOGY'S ADAPTATIONISM

EP takes an adaptationist perspective on behavior, exploring how selection has shaped behaviors via behavioral mechanisms as solutions to various adaptive problems over evolutionary time. From the contemporary EP perspective, humans may be seen as cultural Einsteins with bodies shaped for a Flintstone world: that is, organisms well-adapted to a slow-paced, relatively unchanging Pleistocene lifestyle, yet not matched to the rigors of the rapidly changing modern world. Since these adaptations were thought to result from repeated past selection during prehistoric human evolution on the Pleistocene African savannah, EP has focused on challenges faced by early humans in this *environment of evolutionary adaptedness* (EEA). Evolutionary psychologists have searched for human universals shared across time and cultures, mechanisms that probably evolved before our ancestors left Africa some 60,000-80,000 years ago. With their focus on universals, evolutionary psychologists typically view individual differences as little more than noise in the system (Tooby & Cosmides, 1992). As a whole, EP has been fruitful in understanding many apparent universal mechanisms, such as those related to cheater detection (Cosmides & Tooby, 1992), landscape preferences (Orians, 1986), food choice (Profet, 1992; Sherman & Hash, 2001), alliance formations and group dynamics (Price, 2005), and personality (Buss, 1998; Figueredo, Sefcek, Vasquez, Brumbach, King, & Jacobs, 2005). EP has also offered a coherent perspective on the causes of physical and mental illness (Wakefield, 1992; Williams & Nesse, 1991).

Recent advances in population and quantitative genetics and in understanding the forces of selection (balancing, stabilizing, disruptional, directional, and sexual selection) have begun to undermine the assumption that there is no adaptive genetic variation. There is now ample genetic evidence from paternally inherited Y-chromosome (NRY), maternally inherited mitochondrial DNA (mtDNA), and nuclear DNA analysis to show that the underlying genetic differences between individuals are real, heritable, and adaptively relevant. Furthermore, contemporary understanding of gene expression, gene-environment interactions, and regulator genes (genes that orchestrate the expression of other genes) suggests that even small genetic differences between individuals may express themselves as large phenotypic differences. This idea has led to insights concerning genetic disease susceptibility across individuals and lineages (Cavalli-Sforza, Menozzi, & Piazza, 1994; Williams & Nesse, 1991) and differences in mental traits such as intelligence (Rowe, 2005) and personality (Allik & McCrae, 2004). Thus, EP is developing a more sophisticated understanding of heritable genetic differences between individuals—differences that may be important in human sexuality and mate choice.

The original EP approach has been challenged by sexual selection theory. Miller (2000a), for example, has revived Darwin's most interesting mechanism of change: sexual selection (Darwin 1859, 1871). In brief, *natural (non-sexual) selection* tends to create adaptations that are efficient, modular, and universal (showing low genotypic variance, phenotypic variance, and heritability), so EP tended to focus on traits with these properties. However, many intriguing psychological phenomena show the opposite properties—high cost, low modularity, large individual differences, and high heritability. For example, personality shows high individual variation both within and between populations, with genetic contributions (determined through twin and adoption studies) accounting for 30 - 60% of the variance (Bouchard, 1994). This kind of heritable variability is what one would expect from complex traits that were shaped by sexual selection. Many theorists, including Darwin, have suggested that sexual selection has played a major role in shaping the behavior of modern humans. EP has begun to incorporate the broader insights of sexual selection theory, which should be supremely relevant to understanding human sexuality.

Sexual Selection and Mate Choice

Sexual selection refers to the traits that arise from competition among individuals for access to mates. Darwin (1859) focused especially on sexually attractive ornaments (e.g., peacock tails) and sexually competitive weapons (e.g., elk antlers) that seem to decrease individual survival prospects in relation to the larger ecology. Although the peacock's tail signals genetic quality and parasite resistance, it actually decreases longevity and increases the likelihood of death due to predation (Petrie, Halliday, & Sanders, 1991). Rather than a "struggle for existence" against environmental factors, sexual selection reflects a struggle between the individuals of one sex to attract, copulate with, and produce viable offspring with the other sex (Darwin, 1859). Curiously, Darwin noted that sexually selected traits were typically more complex and elaborate in males than in females of most species that he studied. He theorized that these sex differences (dimorphisms) were due to females being choosier about their mates and males competing more intensely for mates. We now know that Darwin was correct. When mate choice occurs, females typically do the choosing. Trivers' (1972) *parental investment theory* predicts that the sex that invests more time and energy in nurturing offspring (higher "parental investment") will be the limiting reproductive resource in the population, and so should be choosier about their mates. Conversely, the less-investing sex (typically males) should compete more intensely for access to the choosy, reproductively valuable sex (typically females). Support for this theory is found both across species and cross-culturally within species and shows that parental investment patterns strongly determine the degree to which many sexually selected traits develop in organisms. In sex-role-reversed species, for example (species where males are the principle child-raisers), we find choosier males and more competitive, ornamented females. However, higher female parental investment is the norm across almost all sexually reproducing species, especially mammals such as humans, where females carry the fetus internally and produce milk to feed newborns.

Sexually selected traits are shaped through two different processes. First, sexually selected traits may be shaped through mating competition within a sex (called "intrasexual competition"). Males, for example, may compete directly to copulate with fertile females or compete indirectly for food, territory, nest sites, or social status that may increase their access to fertile females. In either situation, females are not exactly "choosing" from among male competitors, but acquiescing to sex with the male that holds the food, territory, or nest site that they need in order to reproduce.

Second, sexually selected traits may be shaped through reproductive mate choice, directly favoring sex with an individual who displays particular traits. Mate choice need not be conscious, rational, or deliberative. Mate choice refers to *both* conscious and unconscious processes that may be either psychological, physiological, or both (Miller, 1998). In the ultimate sense, mate choice occurs whenever an organism shows a higher likelihood of mating with an individual by virtue of that individual's perceivable traits. If the sexually favored trait is heritable, the trait will be passed on to offspring. If both the trait and the preference for the trait are heritable, a positive feedback loop called "runaway sexual selection" may develop, such that in subsequent generations both the preference for the trait and the trait itself become more pronounced (Miller, 1993; Fisher, 1958/ 1999). If the selected traits consistently occur in one sex and preferences for the traits occur in the other sex, then sex differences in the trait tend to develop. For example, mate choice by female stalk-eyed flies has led to males evolving much longer eye-stalks, because males with longer eye-stalks are preferred, whereas males show no preference for females with long eye-stalks. Usually, the sexual ornaments favored by mate choice carry useful information about the bearer's genetic and phenotypic quality, but they are also aesthetically pleasing and attractive to the observer (Waynforth, Delwadia, & Camm, 2005). The attractiveness of the trait is due in part to the adaptations of the displayer and to the adaptations of the beholder (Symons, 1995).

In some species (such as socially monogamous birds and humans), both sexes are fairly choosy.

Mutual mate choice leads to small or absent sex differences in ornamental traits, because each sex uses the trait as a mate choice criterion and the trait and trait preference evolve equally in both sexes. Miller (2000a) has argued that brain size and intelligence in humans is an outcome of mutual choice.

Fitness Indicator Theory

Theories about the evolution of sexual reproduction may help explain why specific sexually selected traits have evolved. Although the origin of sex remains obscure, there are two leading theories that explain the benefits of sexual reproduction in terms of the genetic mixing that it entails. The *parasite theory* and the *repair theory* each suggest that sex evolved to bring long-term evolutionary benefits to selfish genes—mixing them up either to resist fast-evolving parasites or to dilute harmful mutations (Ridley, 1993).

The repair theory emphasizes that without the genetic mixing allowed by sexual reproduction a non-sexual lineage would accumulate ever more harmful genetic mutations with no hope of diluting or repairing them. This is why non-sexual species of plants and animals almost always go extinct within a million years. By contrast, sexual reproduction produces offspring that carry different combinations of inherited mutations—by chance, some will have a higher mutation load (inheriting the worst genes from each parent), but some will have a lower mutation load (inheriting the best genes from each parent) (Michod, 1997). The increasingly well-supported repair theory views sex as an anti-mutation defense (Ridley, 2001) echoing Plato's notion that love is a way of making life whole again.[1] Within the context of sex itself being an anti-mutation defense, it makes sense for mate choice to focus on evaluating the mutation load (genetic quality) of potential sexual partners in order to minimize the number of harmful mutations inherited by one's offspring. Thus, sexual ornaments evolve to proclaim genetic quality.

This is where *fitness indicator theory* comes in. As a branch of sexual selection theory, fitness indicator theory suggests that many sexual ornaments and weapons serve as honest signals of an individual's physical, psychological, and/or genetic quality and, thus, ability to attract mates, deter sexual rivals, or deter predators. These traits may not contribute directly to survival or reproduction, but they contribute indirectly by influencing the behavior of other animals. Examples of fitness indicators include the peacock's tail (to influence mate choice by peahens), long eye-stalks in male stalk-eyed flies (to intimidate sexual rivals), a conspicuous jumping behavior called "stotting" in gazelles (to advertise abundant energy and deter predators from chasing) and, as some authors argue (e.g., Miller, 2000a), human courtship displays such as dancing, music-making, and artistic and poetic expression.

Of course, all animals might prefer to look super-fit and receive the mating benefits. What keeps the fitness indicators honest and accurate as signals of quality? Zahavi (1975) realized that high-cost indicators will remain honest and accurate if low-quality animals cannot afford to produce them. Reliable fitness indicators cannot be faked by individuals in poor condition, because they are costly to the individual in terms of metabolic energy (e.g., for a peacock to grow a quality tail), risk (e.g., a bright cumbersome tail makes a peacock susceptible to predation), and time (e.g., to grow a truly magnificent tail). In addition to fitness quality, robust fitness indicators also demonstrate "developmental stability"—the trait's ability to resist perturbations by genetic mutations, parasites, diseases, and accidents (Kowner, 2001). Many sexual ornaments show a high degree of bilateral symmetry, which would be difficult to achieve if developmental accidents affected right- and left-side growth differently. Developmental stability can also be demonstrated by growing traits that show radial symmetry, precise uniform coloration, or precise repetition of complex patterns—as evident in much bird plumage.

Zahavi's (1975) *handicap principle* proposes that fitness indicators should be costly enough to impose a "handicap" on the organism in order to demonstrate that the individual has sufficient resources to survive having the trait. An example of the handicap principle is testosterone in males. Testosterone increases musculature and aggressiveness, which may aid competition for mates, but it also has many negative effects, such as suppressing immune functioning and increasing susceptibility to prostrate cancer and male pattern baldness in humans. Too much aggressiveness, recklessness, or risk-taking can lead to injury or death, especially among young males (Wilson & Daly, 1985). An extreme example is "'roid rage"—the hair-trigger aggressiveness that body-builders feel after taking anabolic steroids that mimic male sex hormones. Thus, males, such as Tom Cruise, who display markers for high testosterone, such as upper body musculature, a square jaw, and body hair and who are not otherwise debilitated or dead (although arguably misinformed about modern psychiatry), are reliably advertising their genetic and phenotypic quality.

In sum, fitness indicators do the voodoo that they do so well because they are *condition-dependant*: that is, only individuals in good condition, with good genes, can produce a high quality indicator. Conversely, individuals with high mutation loads are compelled to show off their poor quality fitness indicators. If fitness is faked, the receiver will find out by having poor-quality offspring; competitive peers will find out through size-comparisons; the gazelle will be made dinner; and the object of poetic affection may decide that your hyperbole is showing. Thus, in principle, both sexes have incentives to favor mates who display high-quality fitness indicators and to avoid mates who display low-quality indicators. In practice, males are typically choosy about female fitness indicators only when they invest substantial effort and resources in child-rearing, as do socially monogamous birds and humans. Female choice for male fitness indicators is much more common across species.

Many studies have shown that offspring tend to survive and reproduce more successfully if they are sired by a father who displays high quality indicators, such as body size in gladiator frogs (Kluge, 1981), wing symmetry in scorpion flies (Thornhill, 1992), tail symmetry in barn swallows (Møller, 1992), eyespot symmetry and train length in peacock tails (Petrie et al., 1991), tail length in red-collared widowbirds (Pryke, Andersson, & Lawes, 2001), color saturation in bird plumage (Folstad & Karter, 1992; Hamilton and Zuk, 1982), facial coloration in the uakari monkey (Miller, 2000b), and eye stalk length in stalk-eyed flies (Burkhardt & de la Motte, 1988). Other studies have examined behavioral traits as fitness indicators that predict mating success and offspring viability; these include call duration in grey tree frogs (Gerhardt, Tanner, Corrigan, & Walton, 2000; Welch, Semlitsch, & Gerhardt, 1998), song complexity in thrush nightingales (Amrhein, Korner, & Naguib, 2002) and nightingale grasshoppers (Klappert & Reinhold, 2003), frequency and duration of courtship display in dung beetles (Kotaiho, 2002), and nest building in widowbirds (Savalli, 1993) and bowerbirds (Borgia, 1985, 1995). Apparently, sexual selection through mate choice often favors sexual ornaments that can function as reliable fitness indicators.

Mating Patterns and Sexual Dimorphism

An overview of human mating behavior requires at least a brief description of mating patterns and mating (reproductive) strategies. (For a thorough review, see Alcock, 2001). A *mating strategy* is an organized set of behavioral adaptations that guide an individual's mate preferences and allocation of mating effort. These strategies may be *long-term* (focusing on pair-bonding and parental effort), *short-term* (focuses on immediate copulation), or *mixed* (employing elements of both long-term and short-term mating strategies as conditions warrant). *Mating patterns* refer to the four common types of mateships: monogamy, serial-monogamy, polygamy, and polygynandry.

In *social monogamy*, one male and one female form a long-term pair-bond and mate for life, or until one of the pair dies. Contrary to popular opinion, exclusive monogamy is fairly rare across human populations. Only 16% of the world's pre-industrial cultures practice monogamous marriage exclusively (Schmitt, 2005). Monogamy is even rarer (about 3% of species) among nonhuman mammals (Kleiman, 1977). However, among birds, monogamy is the typical mating pattern found in 90% of species. Even so, *social* monogamy (living together and raising offspring together) need not imply *genetic* monogamy (producing only offspring that carry the partner's genes). Recent DNA paternity studies show that many female birds pursue extra-pair matings and produce offspring sired by males other than their long-term partner (Barash & Lipton, 2001).

Regardless of species, monogamy seems to arise most often when food is scarce and predators are common. In such environments, care by both parents is necessary to provide enough food and protection for the developing offspring. The need for biparental care in birds is accentuated by the typically helpless and vulnerable ("altricial") state of newborn birds. Many mammals are born able to walk, whereas most birds must mature in the nest before they can escape from predators. Other factors may also influence the higher rate of monogamy among birds compared to mammals. While female mammals are lactating to feed their offspring, they are usually infertile and unable to produce new offspring. In such situations, it may be in the male's interest to seek other fertile females, although it is in the female's interest to provide for her current young. Birds, however, do not lactate, so either parent is about equally suited to care for hatchlings.

A variation on lifetime monogamy is *serial-monogamy,* which refers to forming a pair-bond long enough to raise a few offspring (typically, for one breeding season) and then forming a new pair-bond later. Evolutionary psychologists such as Buss (2005) have argued that serial monogamy is the typical mating pattern among humans, with strict life-long monogamy enforced in some cultures through religious norms. Not surprisingly, the typical human pair-bond lasts roughly 5 years, about the same length of time that women in traditional cultures need to raise one child through pregnancy, breast-feeding, and toddler-hood (Fisher, 2004; Jankowiak & Fisher, 1992). Temporary pair-bonding is probably an adaptation to keep fathers close to home, where they can offer protection and resources to their partner and vulnerable offspring.

Although monogamy is rare among animals in general and rare among mammals specifically, polygamy is quite common. *Polygamy*—an individual of one sex mates with many individuals of the other sex—comes in two types: polygyny and polyandry. *Polygyny* occurs when one male mates or forms pair-bonds with more than one female concurrently. Typically, these males offer little parental investment beyond defending offspring from predators and infanticidal sexual rivals. In the animal kingdom, polygyny is the norm, occurring in about 90% of species and in 97% of mammals (Kleiman, 1977).

Polyandry is the female version of polygamy: one female has many male mates. This mating pattern is very rare, occurring in only a few known species of birds, insects, and sea horses, and in a few human cultures in Nepal, Tibet, Sri Lanka, and India. Polyandry arises when food is very scarce, predators are very dangerous, and there are fewer viable females in the environment relative to males. Thus, raising offspring requires collaborative investment by several males—often brothers or other close kin, consistent with kin selection and inclusive fitness theory (Dixson, 1998).

The final mating pattern is *polygynandry*, or promiscuity, wherein no pair-bonds are formed. Polygynandry usually arises when males share a territory that overlaps with the foraging territories of several females, as in the common chimpanzee. In such a system, a status hierarchy exists, and the dominant or *alpha* male gets most of the mating opportunities. However, the *beta* males sometimes find opportunities to copulate and produce offspring (Gagneux, Gonder, Goldberg, & Morin, 2001). In polygynandrous societies, paternity is confused, since any male who has mated with a female has a chance of being the father of her offspring. Consequently, males who have mated with a female are much less likely to harm her offspring (Goodall, 1986).

Each mating pattern is associated with different kinds and distributions of sexually selected traits. Monogamy leads both sexes to evolve sexual ornaments; polygyny leads males to evolve larger ornaments; polyandry leads females to evolve larger ornaments; and promiscuity (which involves the least amount of mate choice) leads both sexes to be fairly unornamented.

In mating patterns such as polygyny, where some individuals have many offspring and some have none, there is fierce competition among the males for females and for female-attracting resources. Thus, polygynous males may evolve extraordinary ornaments and weapons. Among southern elephant seals, for example, the dominant male in a territory will sire approximately 85% of the offspring. As a result, male elephant seals have evolved to grow about three times larger than females (Seal Conservation Society, 2005). In monogamous species, where competition is less intense, males and females show smaller sex differences. Among the white-handed gibbons, body size and ornamentation are identical except for the white hands of the males.

Sexual dimorphism between species also helps to identify which mating pattern has been the species' norm over evolutionary time (Baker & Bellis, 1995). For example, male chimpanzees' testicle size is a whopping 3% of their total body weight, compared to .8% in human males and .02% in male gorillas. The promiscuous mating pattern of chimpanzees suggests that males with small testicles were selected against because they were unable to "wash out" the sperm of larger-testicled competitors. Among polygynous gorillas, one male controls a harem of females with little or no competition from other males, so there is little selection for large testicles and ejaculates. Male humans are between chimpanzees and gorillas in both testicle size and body size dimorphism; this supports the view that over evolutionary time humans have been *at least* mildly polygynous (Baker & Bellis, 1995). This point is further supported by genetic data concerning variation in Y chromosomes (genes passed only from fathers to sons), showing that just 19 male lineages have dominated in populating the world. One lineage within haplogroup C accounts for about 8% of the male population in Asia, suggesting that one male lineage, probably that of Gengis Khan, dominated mating within that region several hundred years ago (Zerjal, Xue, Bertorelle, xxx, xxx, xxx et al., 2003).[2]

Mate Choice Benefits and Mate Preferences

An evolutionary approach to mate selection suggests that mate choice criteria (i.e., mating preferences) should be related to reproductive fitness enhancing benefits (Miller, 2000b). These may be either *direct benefits* that increase the individual's reproductive success through classical Darwinian fitness by benefiting the individual and any offspring or *indirect benefits* that increase the individual's inclusive fitness by benefiting the reproductive success of individuals who carry copies of the individual's genes (Alcock, 2001). The ultimate evolutionary purpose of different mating preferences is the proliferation of one's genes through offspring and relatives within a given environmental context.

In addition to the broad distinction between reproductive benefits described above, mate preferences may focus on *material benefits* such as an individual's access to food or alliances (Buss, 2003a). Mate preferences may identify *fertility benefits* by recognizing a potential mate's signs of fertility and, thereby, increasing one's own reproductive output. Finally, mate preferences may focus on *genetic benefits,* by transmitting to offspring a well-adapted genotype relative to the environment and, thereby, increasing the reproductive success of one's offspring. Many mate choice criteria signal more than one type of benefit. For example, fluctuating asymmetry is thought to signal both an underlying genetic quality (as expressed through developmental stability) and current physical condition relative to ecological factors, such as nutrition and parasite load. In addition, fluctuating asymmetry signals fertility and material benefits. Indeed, as we will discuss below, fluctuating asymmetry is a commonly used trait by which humans gauge potential partners. It is important to note that mating preferences are not necessarily evaluated separately and that they may be relative to one's own traits. For example, Jones and colleagues (2005) has shown that women grouped by different physical and psychological traits predicted preferences for different qualities of a hypothesized males face. Essentially, every potential mate possesses hundreds or thousands of traits that each add to or decrease their overall mate-value, a measure of general attractiveness. Evaluation of a mate's fitness depends upon the individual's ability to detect a fitness signal produced by the potential mate.

Although this body of literature is still emerging, we believe that it is appropriate to include a discussion about female fertility preferences and male material and genetic benefits preferences. We also propose that some mating preferences do not signal true adaptive benefits. Rather, some preferences focus on *non-adaptive benefits* that may simply be byproducts of other selected mechanisms. Because of the difficulty in exploring this perspective within a classic EP framework, we have organized the remainder of this text in the following manner. First, we will describe general female mating preferences in relation to parental investment, genetic benefits, fertility, and long-term versus short-term mating strategies. Next, we will describe general male mating preferences in relation to parental investment, genetic benefits, fertility, and long-term versus short-term mating strategies. Finally we will conclude with a discussion about non-adaptive genetic benefits for both females and males.

WOMEN'S MATING PREFERENCES

Biologically, the costs associated with mating differ for each sex, with greater costs attributed to females. Thus, an evolutionary approach to female-male mating strategies expects that at some level the sexes will differ with regard to the types of benefits desired in a partner. Both females and males have the opportunity to increase their inclusive fitness by seeking material, genetic, and fertility benefits in potential mates. However, many apparent mate choice differences between the sexes are differences in degree, rather than kind, and may be more or less equivalent, depending on whether a long-term or short-term mating strategy is employed. Long-term mating strategies are expected to focus on signals of parental ability, while short-term mating strategies should focus on genetic and fertility benefits for any offspring produced.

Material Benefits: A Woman's Perspective

Compared to other species, human males are rare in the amount of investment they give to both mates and offspring. Even so, amount and quality of male investment varies and may be largely determined by his paternity certainty: i.e., how confident he is that the offspring produced by the female are actually his (Hrdy, 1999). It is likely that sexual selection has shaped women's mate choice to focus on male traits that indicate parental investment, but the likelihood of parental investment can be difficult to identify in a potential mate. Consequently, women must rely on several cues to infer a man's potential for commitment and investment. One set of cues signal a man's access to material resources. In evaluating these cues, the woman is asking herself, "Does he *have* the resources to invest in me and my offspring?" Another set of cues suggests a man's willingness to invest. In essence, the woman is asking, "Given that he has the resources, what is the likelihood that he *will* use them to aid me and my children?"

Can He Invest?

The material benefits that a male partner can provide include direct access to food, allies, and protection for self and offspring, each of which may also contribute to parental investment. Women may assess a man's ability to provide material benefits by observing his current resource holdings, future resource potential, ability to defend accrued resources, and social status (Shackelford, Schmitt, & Buss, 2005). Theoretically, any valued resource that a woman can procure from a man will increase her inclusive fitness. However the type, quantity, and quality of resources that are beneficial depend on the particular ecological context (Schmitt & Buss, 1996; Hrdy, 1997; Holden, Sear, & Mace, 2003).

In human societies where men control wealth and resources, women benefit from mating with men who have plentiful resources (Hrdy, 1997). In several African nations where men invariably control material resources, the primary way that women get access to land and cattle is through marriage (Hakansson, 1994). However, in more egalitarian societies, where wealth is more evenly distributed and/or women contribute considerably to the resources of the family (Warner, Lee & Lee, 1986), women may gain an advantage by choosing mates based on characteristics that indicate genetic or fertility benefits. Cross-cultural studies have demonstrated that women from more egalitarian societies, such as Finland and Sweden, place less importance on financial resources in their male partners (women have their own resources) than do women from more gender-role rigid societies, such as Japan or India (Buss, 1989).

Resource holdings, of course, may change throughout one's lifetime. Therefore, women looking for a long-term relationship are unlikely to choose a mate based solely on his current resources. Rather, a man's current resources serve as a proxy for his relative status within a given population and an indicator of future resource acquisition (Buss, 1989). Women's preference for men with resources is not only based on the direct benefit that she receives, but also in part on the benefit provided to her children. For example, among the Gabbra of Kenya, sons of men with the most camels had more female partners relative to same-sex competitors, and these privileged sons acquired their first wives earlier in life, suggesting that Gabbra women choose their mates based in part on the man's material resources: i.e., the number of camels owned (Mace, 1996). A similar pattern of women's preference for males with material resources has been shown across many societies (Buss, 2003b).

Will He Invest?

From an evolutionary perspective, a man's provisioning of food resources can be seen as contributing to parental effort to increase the likelihood of offspring survival or to mating effort to increase the likelihood of copulation. Thus, women should exhibit preferences for men who not only have the ability to accrue resources but also demonstrate a willingness to share with her and her children. Provisioning of resources may take the form of sharing food, territory, or alliances.

A typical example of a man's provisioning of food sources to his mate(s) and offspring involves meat sharing from hunting. Hunting and food sharing from hunting serves several functions, including costly signaling of hunting prowess, signaling social status, obligating reciprocity, attracting mates, and making political alliances (Patton 2005; Wiesser, 2002; Wood & Hill, 2000). The tactic a man chooses in provisioning food is determined in part on his life stage: e.g., a young man trying to procure a first wife, or a high-status man trying to maintain status for nepotistic advantage (Wiesser, 2002; Wood, & Hill, 2000). Although men in traditional hunter-gatherer societies often hunt for meat, they also gather food when hunting is not productive or social conditions change. For example, Marlowe (2003) has shown that Hadza husbands of Tanzania will gather nutritious foods for their nursing wives who are less able to acquire food themselves.

Consistent with the "showoff hypothesis," hunting may also contribute to mating effort (Hawkes, 1996). Hawkes has noted that better hunters have more mating partners and offspring. Heath and Hadley (1998) have expanded this notion by considering the male's overall wealth. They reported that wealthy men will invest their wealth in mating effort by channeling resources toward other potential mates. However, poor men with meager resources tend to invest what resources they have in parental effort (Marlowe, 1999).

Much evidence suggests that the amount of food that males contribute to a family unit varies greatly across cultures (Kelly, 1995). One factor that affects channeling food resources is simply the abundance of food in the environment. Several studies have now shown that the amount of food men direct toward to their partners and offspring is associated with geographical latitude: that is, the colder the climate (where food resources are scarcer and more difficult to procure), the more meat/food men contribute to daily subsistence. Rates of food channeling range from about 20% of the daily subsistence for Hadza men in Africa (approximate latitude: 3° - 4° S) to 100% for Chipewyan men in Canada (approximate latitude between 55° - 60° N). Ecological context affects not only the men's ability to direct resources but also affects women's preferences. Thus, women in colder climates seek more resources from mates than do women in warmer climates.

Women may also make mate choices based on a man's ability to provision territory to offspring. In patrilineal societies that practice primogeniture (first-born sons inherit their father's estate), first sons tend have greater reproductive success than their younger brothers (Strassmann & Clarke, 1998; Mace, 1996). In this context, women's mate preferences are for land-owning men, rather than for men without land.

Political alliances are another material resource that a woman may seek from a man. Political alliances may be indicated by a man's social status and same-sex alliances. For example, Patton (2005) has described how meat is used to establish political alliances among the Conambo of Ecuador. Due to their history of warfare and male homicide, sharing is used to establish political and social alliances and indebt reciprocity. Motivation to avoid warfare and intrasexual violence may help to explain strong male coalitions and reciprocal altruism across human societies (Tooby & DeVore, 1987; see also, Muscarella, this volume). Among the !Kung of Botswana, men who do not share meat from a hunt lose social status and prestige (Lee, 1979), suggesting that communal meat sharing contributes to status and reputation. Thus, it is reasonable to infer that women make mate choice decisions based on how well a male can form strong same-sex alliances (Kauth, 2000; Muscarella, 2000). In fact, considerable research has indicated that women prefer men with high social status compared to the general population (Buss, 1989).

Social status may also indicate a man's ability to protect both his mate and his offspring from attacks by predators or hostile men (Buss, 2003b). Predators have been a major threat to humans over our evolutionary history. Women, especially when pregnant, and children were vulnerable to attack by predators, resulting in injury or death (Barrett, 2005). It is therefore likely that women chose mates based on their ability to provide protection from predators. Also, given the disparity in body size and strength, women have been at risk of physical domination and violence by men, resulting in oppression, injury, unwanted pregnancy, or death (Smuts, 1985; Thornhill & Palmer, 2000). Studies by Figueredo, Bachar, & Goldman-Pach, (1996) and Figueredo, Corral-Vedugo, Frias-Armenta, Bachar, White, McNeill et al. (2001) have noted that male kin density—the number of male kin within an easily traveled distance—are principle factors in deterring spousal abuse in samples from Madrid and Mexico. The need for physical protection has likely been a significant factor in shaping women's mate choice.

A cue to a man's ability to defend his mate from predators is the presence of strong male alliances and access to weapons. Physical strength, hunting ability, and athletic prowess may also indicate a man's ability to protect his mate and offspring from environmental dangers (Barber, 1994; Smuts, 1985). Several studies have found that women prefer men who are larger than themselves and are physically strong (Buss & Schmitt, 1993). Pierce (1996) found that women preferred to mate with men who are taller than themselves, more than men preferred to mate with women who are shorter than themselves.

Genetic Benefits

Few topics in EP have captured as much attention in the popular press as findings regarding physical attractiveness in sexual partners. Although many characteristics that individuals find attractive in sexual partners come as no surprise to the average person, EP has added a foundation of ultimate causation to the study of sexual attraction. We can state with varying degrees of certainty that many physical characteristics that men and women find attractive serve as cues to "good genes" and/or high fertility in the other sex. In the following section, we explore physical and mental characteristics associated with sexual attractiveness and women's mate preferences.

Fluctuating Asymmetry

Fluctuating asymmetry is the degree to which bilaterally symmetrical features deviate from each other. Typically, these measures come from measuring differences in paired traits on the face or body. A plethora of studies across many species have documented that a variety of environmental stressors interacting with genetic processes affect the phenotypic expression of symmetry. Both environmental stressors (e.g., pollution, parasites, malnutrition, and blunt traumas) and genetic stressors (e.g., inbreeding and mutations) have been shown to increase fluctuating asymmetry, which is associated with higher instances of health risks in males and females (Scutt, Manning, Whitehouse, Leinster, & Massey, 1997) and overall lower fitness (Thornhill & Gangestad, 1999). Studies of preferences for low fluctuating asymmetry, utilizing visual and olfactory stimuli, have suggested that symmetry (the reverse of fluctuating asymmetry) is considered "attractive." Several studies have evaluated ratings of facial attractiveness using color and black-and-white photos among different cultures and found that more symmetrical faces are rated as most attractive (e.g., Mealey, Bridgstock, & Townsend, 1999). Even infants spent more time gazing at symmetrical faces than asymmetrical faces (Langlois & Roggman, 1990).

Beyond beauty, symmetry may be considered just plain sexy. Thornhill and Gangestad's (1999) initial t-shirt study found that women during the most fertile periods of their menstrual cycle who were not taking hormone-based contraception preferred the scent of t-shirts worn by more symmetrical men, even going so far as to report that some of them smelled "sexy." This study and many others (e.g., Mealey et al., 1999; Grammer & Thornhill, 1994; Scheib, Gangestad, & Thornhill, 1999) have demonstrated that while people, including infants, find symmetrical faces most attractive, this effect is strongest in adult women's ratings of men's faces. Thornhill and Gangestad have suggested that sexual selection for "good genes," as demonstrated by low male fluctuating asymmetry, is strong because the amount of parental investment required from men for reproduction is lower than for women. This idea is supported by the many important negative correlates of fluctuating asymmetry in men, including muscularity, lower metabolic rate, larger body size, greater number of sexual partners, and earlier age at first intercourse. By contrast, high fluctuating asymmetry is related to serious illness among Brazilian men (Waynforth, 1998) and negative sperm parameters leading to infertility (Manning, Scutt, & Lewis-Jones, 1998).

Major Histocompatibility Complex and Body Scent (or Pheromones)

The immune system employs the *major histocompatibility complex* (MHC) genes to recognize foreign organisms. Recent research suggests that body odor, which is influenced by MHC genes, is another characteristic that women use to evaluate potential sexual partners. (For a detailed discussion of pheromones, see Kohl, this volume). During the infertile phase of their menstrual cycles, women on average prefer the scent of men who have heterozygous MHC alleles (Thornhill, Gangestad, Miller, Scheyd, McCollough, & Franklin, 2003). Such heterozygosity has been positively related to ratings of a man's facial attractiveness and perceived facial health (Roberts, Little, Gosling, Perrett, Jones, Carter et al., 2005), even when MHC similarity between the female raters and male participants were partialled out. Whether women prefer MHC dissimilar or similar men is under debate. Thornhill and colleagues found no association between women's preference and MHC-dissimilarity, regardless of current point in their ovulatory cycle. However, Wedekind and Furi (1997) and Wedekind, Seebeck, Bettens, and Paepke (1995) found that women rated body odor of MHC-dissimilar men most pleasant, unless they were taking oral contraceptives. Thornhill has suggested that these conflicting findings are due to methodological issues (e.g., small sample size, homogeneity of ethnicity) in the first two studies.

Overall, such findings suggest that different mechanisms are at work in relation to women's mate choice for MHC. First, the relative preference for heterozygous men might decrease the likelihood of mating with a man who comes from an inbred population, or MHC might simply be spuriously correlated with any preference (Roberts et al., 2005). However, the extreme polymorphisms associated with MHC and lack of correlation between MHC homozygosity and general allelic zygosity (Carrington, Nelson, Martin, Kissner, Vlahov, Goedert et al., 1999) suggest that this is not the case. Second, direct benefits of a man's MHC allele heterozygosity for female reproductive success may outweigh any indirect effect on offspring heterozygosity, suggesting that a focus on parental ability and health may be more of a focus than offspring condition.

Personality and Mental Traits

Although sex differences are not a necessary result of sexual selection, they are one indicator that sexual selection for a trait has almost certainly occurred. Sex differences in personality are apparent among humans and non-human animals (Budaev, 1999). Here, personality will be only briefly considered. For more information on personality traits and their relationship to sexual attraction and behavior, see Schmitt in this volume.

Sex differences in personality are hypothesized to have arisen due to differential parental investment by each sex. Parental investment theory (Trivers, 1972) predicts that males will devote more energy to mating effort and females will devote more resources to parental investment. Thus, it is not surprising that males are rated higher in personality domains subsumed under the behavioral approach system, such as social dominance, sensation seeking, extraversion, and risk-taking. These characteristics presumably provided survival and reproductive advantages to males in our evolutionary past. However, females score higher on nurturance/love, which presumably also provided reproductive advantages to females and their offspring (Budaev, 1999; MacDonald, 1998; Buss, 1997).

Although some researchers have suggested that different personalities evolved to fill a diverse array of social niches (Figueredo & King, 2001; MacDonald, 1998), recent evidence suggests that personality types are not equally advantageous. Figueredo, Sefcek, and Jones (2005) have found that the "ideal" partner personality type for potential romantic partners includes high openness, conscientiousness, extraversion, agreeableness, and low neuroticism. Mirroring these results, Vasquez (2004) has found that women who rated themselves high in mate-value (a global measure of traits relevant to mate-choice) also identified themselves as having this "ideal" personality. Little research has directly addressed the reproductive fitness associated with various personality traits, although some studies suggest that greater fertility and longevity is associated with the personality traits described above (e.g., Wischmann, Stammer, Scherg, Gerhad, & Verres, 2001; Eaves, Martin, Heath, Hewitt, & Neale, 1990; Friedman, Tucker, Tomlinson-Keasey, Schwartz, Wingard, & Criqui, 1993; Schwartz, Friedman, Tucker, Tomlinson-Keasey, Wingard, & Criqui, 1995; Friedman, 2000; Tucker & Friedman, 1996). Personality traits that are *disfavored* by potential partners are associated with a variety of aging-related disorders, including cardiovascular and bone diseases, arthritis, Type

2 diabetes, certain cancers, as well as frailty and functional decline (Kiecolt-Glaser, McGuire, Robles, & Glaser, 2002).

Recently, Miller (2000b) has made the argument that other human mental traits such as intelligence, creativity, artistic expression, musical aptitude, and sense of humor also function as sexual signals or fitness indicators. Indeed, men and women have demonstrated a preference for specific mental characteristics in sexual partners. Buss (1989) has provided cross-cultural evidence that both sexes value traits such as intelligence, kindness, and generosity in a long-term partner, suggesting that mutual mate choice is also at work.

If mutual mate choice is indeed influencing mental characteristics, this may help to explain variability in intelligence, even though intelligence is highly heritable (e.g., Miller, 1997). Recall, that in order to be reliable fitness indicators, traits must demonstrate high individual differences; traits may be highly heritable if they "tap into genetic variation in fitness," because fitness itself seems to be a heritable characteristic (Miller, 2000b). Although brain size correlates with intelligence (Rushton & Ankney, 1996), creating a large brain is costly for the organism in terms of metabolic energy necessary to support the brain, time necessary to produce it, as well as the physical difficulty and health complications of squeezing through a small pelvic opening during delivery. Intelligence is also correlated with other fitness indicators, in particular, body symmetry (Furlow, Armijo-Prewitt, Gangestad, & Thornhill, 1997). Prokosch, Yeo, and Miller (2005) have found evidence that general intelligence (*g*) reflects developmental stability. Furthermore, the finding that humans assortively mate with others of similar intelligence, which should increase variability in intelligence in the general population, lends weight to the idea that indicators of *g* are used as indicators of fitness (Rushton 1989; Rushton & Bonns, 2005).

Miller (2000b) has further argued that "creativity may have evolved as a sexually selected indicator of proteanism ability, youthful energy, and intelligence" (p. 411). Here is another case of a fitness indicator that is reliable because it is difficult to fake. Creative displays capitalize on novelty, a trait that is characteristic of many species, from bower-birds to chimps, and seems especially important to humans. Although creativity may provide some survival advantages in terms of creative problem-solving, the major utility of creativity likely lies in the reproductive benefits that it confers to an individual. Anyone who has ever been to a rock concert or an art exhibition has likely noticed this. For example, some of the most prolific fathers and notorious "ladies' men" in recent American history have been musicians like Screamin' Jay Hawkins, who reportedly fathered over 70 children, and artists like Picasso, whose sexual exploits are legendary. Women who select men on the basis of creativity may not benefit from parental investment, because creative displays consume time and energy. However, women who select creative mates are likely to increase their inclusive fitness through production of creative sons and daughters who share their mother's preference for creative displays.

A good sense of humor can be viewed as another facet of creativity and is a trait that is consistently preferred in romantic partners. Preference for a good sense of humor has often puzzled evolutionary theorists who have focused on traits that provide a functional advantage from a natural selection perspective. However, when considered from a sexual signaling point of view, a preference for a good sense of humor makes sense. Being funny and entertaining is often the result of making novel or unexpected associations and has the potential outcome of putting people at ease, reducing social conflict, and creating good will. Anyone who has suffered through failed attempts at humor can attest to the difficulty of faking such displays. Several lines of evidence suggest that individuals who are funny and entertaining are also likely to be intelligent, energetic, likeable, and youthful (Miller, 2000b). In a recent unpublished study, Miller (2003) found that a good sense of humor is significantly and positively correlated with numerous fitness indicator traits, including intelligence, health, facial and body masculinity, extraversion, happiness, and perceptions of parental ability. Furthermore, a good sense of humor is preferred in a mate regardless of the type of relationship, although as predicted fertility based on menstrual cycle timing increased the effect. In a recent study relating humorous cartoons to brain activation, both women and men showed similar activation in the semantic processing areas of the brain (Azim, Mobbs, Jo, Menon, & Reiss, 2005). Women, however, showed more activation of both executive processing and reward areas. The study investigators argued that this implies that women have lower expectations than men with regard to humor and experience greater pleasure when those expectations are exceeded.

Fertility Benefits

By fertility benefits, we mean those traits that signal a potential mate is capable of reproduction and is not sterile. In traditional EP, female choice for fertility benefits has been virtually ignored. One potential reason for this omission is that in males markers associated with fertility (e.g., facial dominance caused by testosterone) are typically intertwined with markers for "good genes" (e.g., symmetry), making them difficult to decouple (Fink, Manning, Neave, & Grammer, 2004). Regardless, we see merit in examining female preferences from a fertility perspective, apart from the traditional genetic benefits.

The link between testosterone levels and sex drive is well-established for males in a variety of species (Rhoden & Morgentaler, 2004). Additionally, limited and indirect evidence link testosterone levels in males to higher fertility. Much of this evidence comes from studies of nonhuman species such as Zucker rats (Hemmes & Schoch, 1988), Mongolian gerbils (Clark & Galef, 2000), and Japanese quail (Ottinger, Duchala, & Masson, 1983). In the case of Japanese quail, decreases in serum testosterone associated with age are correlated with a decline in fertility and mating behavior. Other studies have demonstrated that prenatal manipulations of testosterone levels correlate with the frequency mating behavior and higher fertility in adulthood (Hemmes & Schoch, 1988; Ottinger, Duchala, & Masson, 1983).

In humans, testosterone levels also decline with age, and evidence suggests that prenatal testosterone levels correlate with frequency of adult mating behavior (Baker & Bellis, 1995). In addition, men's testosterone levels fluctuate throughout the year, with the highest levels coinciding with the autumnal equinox. Birth rates peak about nine months later, perhaps due to seasonal increases in sex drive. The ultimate cause for seasonal variation in human sex drive and birth rates is hypothesized to be greater survival rates of infants born with the longest possible interval before the subsequent winter (Baker & Bellis, 1995). To our knowledge, there is no direct evidence to show that women prefer men when their testosterone levels are highest. However, this may be a limitation in methodologies in measuring testosterone levels, as levels fluctuate throughout the day.

Other indirect evidence for the role of testosterone on male fertility comes from a variety of biometric sources. Typical masculine (testosterone induced) features include a pronounced brow-ridge and large jaw and nose (Johnston, Hagel, Franklin, Fink, & Grammer, 2001). Preferences for these masculine characteristics are more pronounced when women are at their most fertile period of their menstrual cycle or are considering a partner for a short-term relationship (Gangestad, Thornhill, & Garver-Apgar, 2005). Female preference for masculine and symmetrical features has been attributed to Hamilton and Zuk's (1982) contention (based on Zahavi's "handicap principle") that only healthy organisms can produce and maintain secondary sex characteristics that are both symmetrical and exaggerated. Thus, women's preference for typical masculine features is correlated with seeking "good genes" and with short-term mateships.

Waist-to-hip ratio (WHR), or waist circumference divided by hip circumference, is a general measure of circulating androgens in the body. Due to a low-level of testosterone and estrogen in the bloodstream, prepubescent boys and girls have similar WHR's, approximately .85 - .95 (DeRidder, Bruning, Zonderland, Thijssen, Bonfrer, Blankenstein et al., 1990). At puberty, increased levels of circulating testosterone cause a fatty build up on the chest and waists of boys, causing them to retain a high WHR, between .85 - .95 (Zaadstra, Seidell, Van Hoord, ta Velde, Habbema, Vrieswijki et al., 1993). In girls, however, estrogen causes fatty build-up on the thighs, hips, buttocks, and breasts, leading to a woman's classic "hour-glass" figure and increased breast size. Although more research on WHR ratio has been conducted in women than men, several studies support this biometric marker as a criterion used in women's mate choice, with the cross-cultural preference for a man's WHR approximating .90 (for a review, see Weeden & Sabini, 2005).

Some researchers have argued that it is not a man's WHR ratio that women are assessing, but rather waist-to-chest ratio. *Waist-to-chest ratio* (WCR) is correlated with a mesomorphic, muscular, body type. Maisey, Vale, Cornelissen, and Tovée (1999), for example, have examined WCR, body mass index (BMI; a measure of body fat composition), and WHR as predictors of women's judgments of attractiveness. WCR was the only significant variable in a linear model, accounting for 56% of the variance, whereas BMI and WHR were not significant predictors. Overall, it seems that women prefer men with a triangular body shape, which while related to WHR and BMI is probably more indicative of WCR or shoulder-to-waist ratio (Franzoi & Herzog, 1987; Salusso-Deonier, Markee, & Pedersen, 1993), indicating high muscularity and low fatness.

Other studies have indicated that the ratio between the second (2D; index finger) and fourth (4D; ring finger) digit of the hand is associated with testosterone levels, dominance, and male attractiveness (Roney & Maestripieri, 2004). The 2D:4D digit ratio is thought to be a measure of prenatal androgen level and is suspected in the production of many male-typical traits that come online during adolescence (Manning, 2002). In adults, this digit ratio is sexually dimorphic, with men typically showing a lower 2D:4D ratio than women. Testosterone levels have been correlated with 2D:4D ratios in English and Spanish samples. Studies have found 2D:4D ratios to have negative and significant correlations with male fertility (Manning, Barley, Walton, Lewis-Jones, Trivers, Singh et al., 2000), myocardial infarction (Manning, 2002), athletic ability (Manning & Taylor 2001), courtship behavior (Roney & Maestripieri, 2004), and number of children fathered (Manning et al., 2000).

Testosterone-induced masculine features are also associated with the likelihood of impregnating a woman. Shackelford, Weekes-Shackelford, and LeBlanc (2000) have found that women who were in relationships with "attractive" (masculine) men reported a greater likelihood of orgasm during coital sex than did women who mated with less attractive men. Baker and Bellis (1995) have correlated coital orgasm with likelihood of conception. Here, detection of "good genes" seems to be directly related to sexual frequency, pleasure, and fertility. For a detailed discussion on sexual pleasure, see Abramson, Pinker, and Mercer, this volume.

MEN'S MATING PREFERENCES

Contrary to our founding fathers' declaration, all men are not created equal, at least in terms of reproductive fitness. Like women, men employ different mate selection preferences to enhance their reproductive success. Although short-term mating strategies, which focus on signs of female fertility, may warrant little consideration of a woman's parenting ability, adoption of a long-term mating strategy should activate a man's evolved preference for female traits that signal maternal investment and good mothering. Such traits may include nurturance, foraging ability through gathering, and domestic investment (e.g., textile production and willingness to invest in her mate and offspring).

Material Benefits: A Man's Perspective

In many species, males vastly differ from females in reproductive potential. In humans, for example, the orgasm of one lucky man could theoretically inseminate at once all females within the city limits of Tucson, AZ (female population approximately 250,000), whereas a woman can only successfully gestate a limited number of fetuses at one time. To further add to this disparity, for men the consequences of a "poor" choice in mate that leads to unhealthy offspring would at minimum mean the loss of a few seconds of time (how embarrassing!) and a few ounces of semen. However, for a woman, the minimum cost for a "poor" mate choice is potentially a nine-month pregnancy and years of child-dependent care. This cost discrepancy is the basis for *sexual strategies theory* (Buss & Schmitt, 1993), which stipulates that given the disparity in reproductive cost men on average will place more stock in quantity of sexual partners than quality compared to women who typically focus on quality of partners. Unlike most animals, human males typically make a significant parental investment in their offspring. Consequently, men tend to engage in long-term mateships with sexually attractive and receptive female partners, while perhaps peppering these pairings with a few short-term matings on the side.

Due to the large high-production cost of gametes, metabolically costly internal fertilization, and necessary lactation, females of all mammalian species bear the largest costs of reproduction. By default, females make the greater parental investment, from production of eggs to weaning an infant. Because of this disparity of investment, human males should have evolved mechanisms that detect the fertility benefits of potential female mates. In addition, because men bear less reproductive costs than women, men should have evolved mechanisms to detect the degree to which women are willing to invest emotionally and materially in his children, given that he may not be around. Sperm may be cheap, but it still has costs associated with its production that a man may not be willing to write-off. As well, conception has genetic benefits that a man may wish to retain, even if he is not involved in raising his offspring.

Men must rely on their female mate to make smart decisions in allocation of resources among offspring in order to maximize the reproductive success of both parents. By choosing a mate who is adept at resource acquisition and allocation, a man benefits his own reproductive interests without doing the work himself. Just as women seek mates who can provide for them, men also seek mates who are able to provide for them and their offspring. Women have been shown to provide their male partners with gathered goods, clothing, and investment in their offspring (Kelly, 1995). Theoretically, women also provide their mate with emotional support and affection and an outlet for men to express support, which are known to have positive effects on men's health and longevity (Brown, Nesse, Vinokur, & Smith, 2003). A mate may also increase a man's social status and even help attract other female partners (Kauth, 2000). Hence, a psychology that focuses not only on the classic fertility benefits but also on material and genetic benefits is likely to have evolved.

Although the exact factors associated with a woman's provisioning are uncertain, climate appears to play a role in leading men to value such provisioning, when it is necessary. The relative scarcity of resources within an environment is likely to influence what type and how much provisioning women offer their partners. The colder the climate, the more likely it is that women will provide essential resources to their partners, such as clothes, food storage, and tool repair. In most human societies, women gather available foodstuff and typically provide significant nourishment to their families and mates (Kelly, 1995). The amount of time that women in traditional cultures spend gathering food is negatively correlated with the amount of meat her husband provides (Hurtado, Hill, Kaplan, & Hurtado, 1992). It follows that if a man has his choice of long-term partners, he will prefer a woman who is industrious (Buss, 1989). A woman's ability to provide gathered food is especially beneficial if her husband is a poor hunter. At times, the food that women forage will directly benefit her mate and, at other times, gathered food benefits him indirectly by provisioning for their children (Kelly, 1995). Ache men of northeastern Paraguay spend approximately 6.7 hours a day in subsistence activities (Hill & Hurtado, 1989) and share about 84% of their hunting spoils outside of their immediate family (Hawkes, 1991); whereas Ache women spend approximately 8 hours a day in childcare activities and 4 hours a day foraging, sharing only 58% of gathered goods outside of the family.

Another example illustrates how men may evaluate female-based resources in mate-choice. Among the "Nebraska" Amish, men preferentially paired with women who lived near her kin group, even though the farms were passed along the male line (Hurd, 1985). The Amish are characterized by their reciprocity of labor and material help, both in food and textiles. Thus, by living near both his and her kin, a man doubles the resources he can rely on in times of need.

Throughout our evolutionary past, women have been the primary textile producers. Spinning and weaving textiles is the type of work that has been consistently conducive to childrearing demands (Barber, 1994). As humans moved out of Africa and into colder climates, clothing became increasingly essential (Kelly, 1995). Consequently, men's mate choice may be based in part on how well a woman can provide him with necessary clothing. Consistent with the examples above, men's emphasis on women's textile production should be greater in cold regions and lesser in the tropics.

Genetic Benefits

Relatively little work has examined what traits signal genetic quality in females. One reason for this is that traditional EP perspectives on human mating have drawn a sharp distinction between men's focus on fertility of their partner and women's focus on the parenting or genetic contributions of their partner. That is not to say that findings that support the notion of "good genes" sexual selection on male mate choice do not exist in the literature. Rather, these studies have been overshadowed by the obvious focus on female fertility. Here we explore the physical and mental characteristics that may be associated with female genetic quality and their implications on a man's mate choice.

Fluctuating Asymmetry

As noted earlier, fluctuating asymmetry is likely to serve as an indicator of developmental instability and is correlated with greater genetic, physical, and mental health in both men and women, suggesting a shared genetic structure among these traits. As in men, female fluctuating asymmetry is measured by examining the deviations between paired traits on the face and body. Asymmetry studies in women have examined the degree to which breast asymmetries are associated with health, fertility, and attractiveness (Manning, Scutt, Whitehouse, & Leinster, 1997; Scutt et al., 1997). Across studies using various measures, fluctuating asymmetry has been linked to negative health factors such as breast cancer (Scutt et al., 1997), as well as other health-risks and infertility (Møller, Soler, & Thornhill, 1995).

Several studies have demonstrated men's preference for symmetrical women. In one study, asymmetry was found to be inversely related to male judgments of attractiveness (Singh, 1995). Compared to women, men rate women's facial attractiveness as rapidly and harshly declining with age (Henss, 1991). In addition, older men more than younger men have been found to prefer the scent of symmetrical women when the women are at high risk of conception (as measured by timing of their ovulatory cycle) (Thornhill et al., 2003). It is known that chemicals similar to estrogen stimulate hypothalamic responses in men but not in women, suggesting that males may have an evolved mechanism to specifically detect ovulatory cues (Savic, Berglund, Gulyas, & Roland., 2001). Other studies suggest that men show olfactory sexual responses to *couplins* (sex pheromones) that may be present in the vaginal secretions of fertile women (Grammer & Jutte, 1997). However, these results are attenuated by other studies that have not found a relationship between the "scent of symmetry" among women's and men's mate preference (Thornhill et al., 2003; Thornhill & Gangestad, 1999). Other physiological measures such as neuroimaging techniques have found that "attractive" (symmetrical) women's faces stimulated reward-areas of the brains of male subjects, whereas average women and men's faces did not, suggesting that symmetrical is pleasing (Aharon, Etcoff, Ariely, Chabris, O'Connor, & Breiter, 2001). Taken together, such findings suggest that men's partner-evaluation mechanisms are tuned to facial symmetry, which declines with age. That symmetry increases when women are most fertile also supports the notion that symmetry is tied to male mate-choice and that women signal their fitness through symmetry.

Major Histocompatibility Complex and Body Scent (or Pheromones)

MHC genes have been found to influence men's perception of women's attractiveness via body scent. (For further discussion, see Kohl, this volume). Studies have found that men on average prefer the scent of individuals who possess MHC genes that are dissimilar to their own (Thornhill et al., 2003; Wedekind & Furi, 1997). Other studies have found a male preference for common versus rare alleles (see Thornhill et al., 2003). One reason for these findings may be that men's preference for common alleles serves as a mechanism to avoid *gestational drive* (Haig, 1996), a condition in which a maternal allele may cause a female to spontaneously abort a fetus that does not possess the same allele. Thus, selecting a partner with common MHC alleles may increase the likelihood that the pair shares the same allele, indirectly enhancing a man's fitness by decreasing the chance that his mate will spontaneously abort the fetus.

Personality and Mental Traits

Across cultures, men tend to prefer long-term mateships with women who are physically healthy and who desire a home and children (Shackelford, Goetz, & Buss, 2005). Buss (1989) has demonstrated that men in many cultures also prefer women who are kind and loyal. This finding may be related to men's desire for paternity certainty. Due to internal fertilization, a man can never be 100% certain that an offspring is his. However, kindness and loyalty may also reflect good mothering behavior.

Although many personality traits do not show sex differences, women typically score higher on measures of nurturance and love. Presumably, these traits have provided reproductive and survival advantages to women and their offspring (MacDonald, 1998; Buss, 1997). In addition, women on average have higher levels of neuroticism than men. People who are rated high in neuroticism tend to exhibit greater emotional liability. According to MacDonald (1995), neuroticism is associated with negative affect and avoidance behavior, or behavioral inhibition. Although neuroticism is negatively correlated with longevity and other indicators of "good genes," it may be a component of a low risk or long-term female mating strategy. Thus, men may benefit from neuroticism in a partner through lower risk of extra-pair copulation (EPC). We know of no studies to date that have tested this hypothesis. The higher prevalence of neuroticism in women suggests that the trait is not strongly selected against by men.

Fertility Benefits

Male mate choice in relation to fertility cues of potential partners has received the lions-share of attention, both from a researcher's standpoint and that of popular journalists. It is undeniable that there are certain physiological features that men focus on when seeking mates. A glimpse of the accounting books of plastic surgeons and cosmetic moguls makes this point. Most of these traits (e.g., full lips, rosy cheeks, breasts, WHR) signal estrogen and, hence, the woman's capacity to bear children. However, less-well popularized are those behavioral traits that also signal fertility. In this section, we will examine the current literature regarding markers of female fertility.

Estrogen

Numerous studies have found that men prefer "feminine" facial features in their potential mates, such as a small jaw, large eyes, small nose, and larger top-third than bottom-third of the face (Johnston et al., 2001; Perret, Lee, Penton-Voak, Rowland, Yoshikama, Burt et al., 1998; Perret, May, & Yoshikawa, 1994). Furthermore, men across cultures prefer women with a light-skin complexion relative to local skin tones (van den Berghe & Frost, 1986). General preference for lighter complexions may be linked to the lightening of skin-tone that occurs with higher estrogen levels and fertility (Perret et al., 1998). Higher levels of estrogen also increase the symmetry of female faces and breasts, cues of reproductive fitness (Oinonen, 2004).

Although women's preference for a .90 WHR in males has been documented, much more research has found a universal male preference for a .70 WHR in women, regardless of body-size (Singh, 1994; Streeter & McBurney, 2003; Furnham, Tan, & McManus, 1997). Women with a WHR outside the typical range of .60 - .80 have fewer children and a greater risk of chronic disease. In a more direct way, the hour glass shape may also signal that a woman has wide pelvic bones and is capable of easily giving birth (Singh, 1995). Other studies link these findings to BMI, arguing that the strong correlation between WHR and BMI in normal women is what drives the preference for a certain WHR (Tassinary & Hansen, 1998). These different findings may also be based on preferences as a function of local ecology. In nutritionally-stressed environments, body mass may be a better indicator of overall health because only women with a certain level of fat-reserves are fertile and able to carry a fetus to term. However, in well-nourished populations where everyone has relatively equal access to nutrition, WHR may be a better indicator (Westman & Marlowe, 1998).

Youth

Another universal male mate preference is youth (Buss, 1989). Buss has found that males on average prefer females who are 2.5 years younger than themselves, with ranges between two and seven years, depending on the culture. This finding is supported by recent U.S. Census data that shows that the largest proportion of heterosexual married and cohabitating couples include men who are 2-5 years older than their partners (36.3% and 28.6%, respectively) (Fields and Casper, 2001). Notably, preferred age differences increase as men get older, with men preferring women who are increasingly younger relative to their own age (Kenrick & Keefe, 1992). Other studies have reported that women at the age of peak fertility, roughly 19-25 years of age, are typically rated as most attractive by men. It is probable that men are not responding to youth itself; rather, men may be responding to the fertility benefits that young age implies. Youthful physical features such as facial neotony, clear skin, and strong hair-growth and behavioral traits such as novelty-seeking and playfulness signal fertility through the combined effects of estrogen. Because women have a narrow reproductive window compared to men, over evolutionary history men who impregnated young women would have had the greatest reproductive success. This is especially true of men who selected young long-term mates; these men would have reaped the benefits of his mate's peak fertility in the short-term and also would have enjoyed a longer period in which to produce more children by the same mate.

NON-ADAPTIVE BENEFITS

Sexually-selected traits may develop to signal material, genetic, and fertility benefits, but traits can also be favored just because they look good, smell good, or feel good. Darwin (1871) understood that pure aesthetics could play a large role in mate choice, even among animals with simpler nervous systems, such as insects and fish. His monist belief that culture, mind, and matter were not qualitatively separate realms of existence led to a materialist view of beauty and attractiveness. This view implied that animals capable of perception were capable of differential aesthetic responsiveness to objects in the environment, including potential mates.

Thus, if a fruit-eating species evolved to favor ripe fruit and fruit co-evolved to advertise its ripeness through bright red coloration, then the species may evolve a visual system that responds strongly to red coloration. Red becomes eye-catching, attention-grabbing, salient, memorable, and attractive. Once the fruit-eaters' visual system favors the color red, their mate choice systems may also favor red as a non-adaptive side-effect. Any mutations that increase the area or saturation of red coloration on the fruit-eater bodies will attract more attention from potential mates and will, thus, be favored through sexual selection. "Sexy" red patches will spread. This beauty-bootstrapping process has been called "sensory drive" (Endler, 1993), "sensory trap" (West-Eberhard, 1984), "sensory exploitation" (Eberhard, 1985; Ryan & Keddy-Hector, 1992), "signal selection" (Zahavi, 1991), and "the influence of receiver psychology on the evolution of animal signals" (Guilford & Dawkins, 1991).

Initially, the eye-catching red patches may not be correlated with "good genes" or good parenting ability. They may carry no fitness benefits to the individuals who favor them; they simply capture their senses, their attention, and their aesthetic taste. From one point of view, the red-badged show-offs are exploitive seducers who are manipulating their sexual victims, without offering any genetic or material advantages. From another point of view, the aesthetically addicted perceivers are forcing their suitors to evolve exciting new forms of beauty that are liberated from the workaday business of food-finding, gene-copying, and baby-rearing.

Several species show these sorts of non-adaptive, aesthetic preferences, probably due to sensory biases. Ridley (1981) has suggested that tails with multiple eye-spots, such as those of the peacock and the Argus pheasant, play upon a widespread responsiveness to eye-like stimuli in animal perception. Ryan (1990) has found that female frogs of some species prefer the courtship calls (deep "chuck" sounds) of male frogs if they are played back at artificially lowered frequencies, as if produced by extra-large frogs. Burley (1988) has shown that female zebra finches prefer males whose legs have been experimentally decorated with red or black plastic bands, although males with blue and green bands were rejected. Basolo (1990) has demonstrated that female platyfish prefer males with colorful plastic "swords" glued to the ends of their tails, suggesting that this preference pre-dated the evolution of similar ornaments among their close relatives, the swordtails.

Once a non-adaptive preference arises, it may turn into an adaptive preference through one of two processes: *Fisher's runaway process* and conversion into a fitness indicator. Fisher (1930) realized that a genetic positive-feedback loop could develop between aesthetic preferences and sexual ornaments. Suppose that peahens vary in the strength of their preference for long peacock tails, and peacocks vary in the length of their tails, and both of these traits are genetically heritable. The peahens that are choosiest about tail length will tend to mate with the longest-tailed males. Their offspring will tend to inherit both the genes for longer-tail preferences and the genes for longer tails. These two traits will become genetically correlated—appearing together more often than expected by chance, if random mating were happening. Now, if most peahens favor longer over shorter tails, the longer-tailed male offspring will attract more mates and sire more peachicks. These peachicks in turn will inherit their grandmother's tail-length obsession. Thus, the genes for longer-tail preferences and the genes for longer tails will both spread through the population as consequence of their genetic correlation. (The reasoning here looks a bit circular, but then all positive-feedback processes look a bit circular). Population genetics models show that Fisher's runaway process can drive aesthetic preferences and sexual ornaments to extreme forms (Pomiankowski, Iwasa, & Nee, 1991). Fisher's runaway process resembles the spread of fads and fashions: advertising creates demand (like a sexual preference), manufacturing fulfills the demand (like a sexual ornament), and a frenzy of consumption ensues (like runaway evolution) until next season's fashion tastes switch to a new preference.

The second process that hijacks non-adaptive sexual ornaments is their conversion into reliable fitness indicators. This process tends to happen as the trait's genetic and phenotypic costs and complexity increase. Louder, brighter, longer, more energetic signals generally work better to drive sensory responses. Therefore, an initially non-adaptive preference will favor signals that require more output energy and finely controlled patterning, rather than less energy and less patterning: that is, preferences will be biased to favor higher cost and higher precision. Genetic mutations, injuries, toxins, parasites, and starvation all tend to reduce an animal's ability to allocate physiological resources to its sexual ornaments, and disrupt the precise development of those ornaments. Therefore, poor genetic and phenotypic quality will undermine the cost and precision of sexual ornaments. A positive correlation will arise between genetic quality and ornament quality, even if no such correlation existed originally. Thus, a non-adaptive sexual ornament as it evolves higher cost and precision will convert into a good old-fashioned fitness indicator (Miller, 2000a). After that, ornaments can evolve to advertise "good genes" and/or good parenting abilities in the usual ways.

Why should we care about non-adaptive preferences that have converted to adaptive preferences? Understanding how sexual ornaments can develop from sensory biases can help us understand why they are so diverse across species, so numerous within species, and often bizarre in form. If ornaments evolved only through pure fitness indicator processes, we might expect the first multi-cellular animal after the Cambrian explosion (535 million years ago) to have evolved one good indicator that would be passed on conservatively to all descendent species. Maybe penis size, symmetry, and intricacy would suffice as universal fitness indicator among males. Then the females from all 350,000 beetle species, all 9,500 bird species, and all 4,500 mammal species would be uniformly penis-crazed. In the *phallus-über-alles* world, there would be no other sexual ornaments—no bright-gold beetles, no singing birds, no antlered mammals.

But, we do not live in such a world. We see a vast diversity of sexual ornaments, most of which probably first arose as non-adaptive traits that exploited the sensory biases and aesthetic tastes of the other sex—pure sexual ornaments came before indicators, sensory pleasure before useful information, and beauty before reliability. This fact may be why sexual attraction carries such a sense of ineffable mystery and irreducible charm: sexual selection has transformed the most acute sensitivities and deepest desires of our nervous systems into the real bodies and minds of our lovers.

ADOPTING A MATING STRATEGY: LONG, SHORT, OR MIXED

The desired traits in a sexual partner vary in relation to the reproductive strategy employed—long-term, short-term, or mixed mating strategy—which itself varies in relation to environmental factors. Research has documented across many species that long-term mating strategies typically focus on indicators signaling "good parenting" and material benefits (e.g., a male's ability and willingness to invest resources in any offspring produced) (Gangestad & Simpson, 2000; Miller, 2000b). By contrast, short-term mating strategies focus on genetic and fertility benefits (e.g., fluctuating asymmetry, health, vigor), and mixed-strategies combine both.

Differences in the costs associated with human mating suggest that on average men will seek out more sexual partners over their lifetimes and that, all else being equal, a short-term mating strategy will be employed (Gangestad & Simpson, 2000). Typically, women, who are more focused on long-term pairings due to their greater parental investment, value good parenting indicators more than do men, suggesting that sex itself is a reasonable proxy measure of behavioral differences in mating strategies. Consequently, men should ascribe more importance to cues of genetic health and fertility than to material benefits. Women, however, should give more importance to cues of material benefits in order to provide for themselves during pregnancy and lactation and to provide for resulting offspring (Buss, 1995). Following this logic, classic EP research has sought out mean differences between men and women's mating behavior, rather than within-sex variation (Gangestad & Simpson, 2000). This approach has examined women's preference for material and genetic benefit cues, while virtually ignoring women's utilization of male fertility cues. Conversely, research on male preferences has focused on fertility benefit cues in women, while ignoring preferences for material or genetic benefit cues.

As noted above, this research bias strikes us as a major limitation and an erroneous assumption. There is a growing literature that finds, for example, that women's short-term and mixed mating strategies are more prevalent than once thought, both across and within cultures (Gangestad & Simpson, 2000). Furthermore, cross-cultural differences in men and women's resource acquisition (i.e., foraging versus hunting) and ability to acquire and maintain resources suggest that men who seek long-term mates may base their preference in part on women's food acquisition abilities (e.g., industriousness and/or ambition) and on her kin-network (Buss, 1989; Hurd, 1985). In several meta-analyses, sex, although statistically significant as a predictor of seeking short-term mates (see Buss & Schmitt, 1993; Simpson & Gangestad, 1991), typically accounts for only 8%-25% of the variance in measures of socio-sexuality (e.g., interest in casual intercourse, willingness to engage in intercourse without commitment) (Gangestad & Simpson, 2000). This means that sex itself is not the only thing driving differences in socio-mating behavior. Indeed, Simpson and Gangestad (2000) have found that when looking at median scores 30% of men reported less favorable attitudes towards casual intercourse compared to women. Taken together, these results suggest that there may be conditional or mixed mating strategies employed by both sexes, and many of the factors accounting for such variation are due to ecological conditions, including availability of material resources, predatory conditions (including pathogen load), and genetic or parenting quality of the local mating pool. As well, different mating strategies are evident when considering menstrual cycle effects on women's mate choice (see below).

Contextual Effects on Women's Strategies

At first glance, the concept of women engaging in anything but a long-term mating strategy seems counterintuitive to an evolutionary perspective on mating. After all, a woman engaging in a short-term coupling runs the risk of becoming pregnant with little or no resources from her coital partner. Further, a woman who is partnered and engages in an extra-pair copulation risks both reputational damage, limiting her ability to acquire future mates, as well as losing her partner's resources if caught. Yet, cross-culturally, combined estimates of at least one act of marital infidelity are 20-50% for women and 30-60% for men (Buss & Shackleford, 1997a). Whichever estimate one accepts as representative, the fact is that women engage in extra-pair copulations, although unlike men they typically report an emotional attachment to their extra-pair partner (Glass & Wright, 1985).

Several hypotheses have been proposed to explain these findings. These include *mate-switching* hypotheses that are aimed at expelling (Greiling & Buss, 2000), replacing (Symons, 1979), or adding an extra mate for insurance against losing the current partner (Smith, 1984); *skill-acquisition,* aimed at honing skills used in mate attraction in order to acquire a high quality mate (Buss, 2003a), or to learn what it is the individual prefers in a mate through trial-and-error testing (Greiling & Buss); and *mate manipulation,* where a woman attempts to increase commitment from her partner by displaying obvious interest of other men (Greiling, 1993) or use sex as a means of revenge for her partner's infidelities. *Resource* hypotheses are aimed at confusing paternity and ensuring resources from many males (Hrdy, 1999), gaining immediate economic resources, such as trading sex for meat (Symons, 1979), gaining protection from hostile others (predators, unwanted men) (Smuts, 1985), or elevating status by mating with high-status males (Smith, 1984). In addition, *genetic benefits* ("good genes" or "gene-capture raid") hypotheses are aimed at producing children (from another mate) who will be more fit, perhaps by creating genetically diverse offspring who can better adapt to fluctuating environments (Smith, 1984) or by producing a "sexy son" who will be more attractive to women (Fisher, 1958).

Resource Uncertainty and Father Absence

Some of the most intriguing findings about women's mate choice over the past three decades seem to support hypotheses related to resource acquisition and genetic benefits. For example, it has long been noted that children of divorced parents often demonstrate a number of psychological effects associated with father absence (e.g., Santrock, 1977; Santrock, 1975). Typically, these effects are viewed as "negative" or socially deviant. However, from an evolutionary perspective, the majority of these effects can be seen as consequences of a short-term mating strategy, which may be adaptive given the fewer resources and lower parental investment that frequently accompany father absence (e.g., Belsky, Steinberg, & Draper, 1991; Chisholm, 1988). For example, in their evolutionary theory of socialization, Belsky, Steinberg, and Draper (1991) have posited that a variety of features of the family environment during the first seven years of life, including father absence, set daughters on a developmental trajectory toward early puberty and sexual behavior; in essence, the familial micro-environment serves as a litmus test of the macro-environment. Thus, the experience of being reared by a single mother leads a girl to adopt the optimal mating strategy for the ecological conditions that often accompany father absence. These conditions include the relative unavailability of suitable males for long-term relationships, lesser likelihood of investment from male partners that a girl might encounter in adulthood, fewer resources in general, and greater unpredictability of the environment. Familial stressors and especially father absence are correlated with a variety of physiological and psychological outcomes for women, including earlier menarche, earlier initiation of sexual activity, younger age at first birth, and higher incidence of affective disorders (Ellis, 2004).

Menstrual Cycle Effects

The effects of a woman's menstrual cycle on mate choice provide a glimpse into the traits that are most important from a genetic benefits perspective. During a woman's typical 28-day menstrual cycle, the likelihood of conceiving on days 6-16 averages between 15% and 45% for any single copulation (Jöchle, 1973). The "good genes" model would predict that during those 10 fertile days women's mating strategies should shift in four main areas: *mate search* (desiring, seeking out, and engaging in sex), *mate attraction* (shaping markers of attractiveness to be more pleasing to men), *mate choice* (desiring traits that signal "good genes" and fertility), and *resistance to sexual coercion* (decreasing the likelihood that the individual will be impregnated by an unwanted male).

Indeed, several lines of research support this view. For example, several studies have found that during days 6-16 women experience increases in sexual desire, self esteem, confidence, pleasure seeking, and flirtatious behavior (see Bullivant, Sellergen, Stern, Spencer, Jacob, Mennella et al., 2004, for review), distance traveled per day away from home (Chrisler & McCool, 1991), volunteerism (Doty & Silverthorne, 1975), sexual fantasies about men other than their current partner (Garver, Gangestad, Simpson, Cousins, & Christensen, 2002), and rates of extra-pair copulations with high fitness males (Baker & Bellis, 1995). Further, physiological markers such as facial (Oinonen, 2004) and breast (Manning, Scutt, Whitehouse, Galizia, Nagler, Holldobler et al., 1996) symmetry increase, WHR becomes closer to the .70 ideal (Kirchengast & Gartner, 2002), skin tone lightens, and pheromonal output increases (Singh & Bronstad, 2001). In addition, psychological markers such as general mood and subjective well-being improve (Dennerstein, Lehert, Dudley, & Guthrie, 2001) and creativity and verbal fluency increase (Krug, Mölle, Fehm, & Born, 1999), while aggression, antisocial behavior, and psychotic symptoms decrease, perhaps to accentuate the positive aspects of a woman's personality (D'Orban & Dalton, 1980). In the middle of all of this, men's attractiveness ratings of women's faces increase with increased fertility (Roberts, Havlicek, Flegr, Hruskova, Little, Jones et al., 2004).

Studies have also shown that during their most fertile period women prefer positive indicators of "good (male) genes," such as dominance (Garver et al., 2002), facial testosterone markers (Penton-Voak & Perett, 2001), intelligence and creativity (Miller, & Haselton, in press), humor (Miller, 2003), and low fluctuating asymmetry (Gangestad & Thornhill, 1998). Further, studies have found that women are more likely to orgasm (a potential sperm retention mechanism) at this time, especially with symmetrical men (Thornhill, Gangestad, & Comer, 2005). Resistance to sexual coercion, which can limit a woman's choice, may also kick-in at this time by avoiding situations where sexual coercion is likely to occur and having the ability to physically defend against coercion. Although women are engaged in more socialization during ovulation, they are less likely to go to secluded areas and to walk alone at night (Chavanne & Gallup, 1998). In addition, grip-strength (Petralia & Gallup, 2002), pain threshold, and sympathetic arousal increase, perhaps in readiness for a fight-or- flight response (Fillingim, 2003).

Although the jury is still out on which of these (or which combination of these) factors best explain the occurrence of short-term or mixed mating strategies in women, each offers some insight into how to maximize reproductive fitness. Studies on the menstrual cycle do not test the direct fitness payoff of the "good genes" model, but they suggest the presence of unconscious mechanisms shaped by selection to aid females in increasing their fitness. Taken together, these studies support the idea that females vary their mate selection strategy to maximize their reproductive fitness.

Contextual Effects on Men's Strategies

The advantage of a man engaging in short term or mixed mating strategies is immediately obvious. A single act of copulation is low-cost and can increase the number of offspring produced by the individual during his lifetime. Indeed, several studies have shown that men on average desire more sexual partners, consent to sex sooner, lower their "standards" (i.e., preferences in relation to short-term pairings) (Buss & Schmitt, 1993), and are more likely to visit prostitutes (Kinsey, Pomeroy, & Martin, 1948) than are women. All men, however, do not engage in such behavior. Nearly half of the men in samples that examine infidelity report having been faithful throughout their relationship (Buss & Shackleford, 1997a).

For men, several personal (e.g., material resources, physical attractiveness, mental attributes) and ecological factors (e.g., number and quality of same-sex competitors, mating strategies of local women) affect his mating strategy. As with girls from father-absent homes, boys reared in such environments will also show short-term mating tendencies at an earlier age. Draper and Belsky (1990) have noted that father-absent boys exhibit more masculine behavior than their father-present peers, including more aggressive tendencies, more risk-taking, and more competitive behavior. These behaviors are all indicators of greater mating effort and typically accompany lower parental investment tendencies in adulthood. It may be that these boys engage in such behaviors because of a shared genetic link with their fathers (i.e., they are in a father-absent home because their father was a short-term strategy kind-of-guy). However, their behavior may also be a response to the environment. Theoretically, if a man is in an environment where women require high-investment from a mate, then it pays for him to focus on parental effort (i.e., be a "dad"), even if he retains several partners in whom he invests. Whereas, in environments where women do not demand such investment, it pays for men to focus on short-term mating strategies (i.e., be a "cad").

Such logic also extends to the sex ratio, or number of women to men in a population. In environments where high quality men are a scarce commodity (e.g., places plagued by war), it may be in a woman's best reproductive interest to adopt short-term mating strategies or risk not reproducing at all—men in environments where they are highly valued can make the rules (Pederson, 1991). The opposite would hold true for female-scarce environments (e.g., the polyandrous societies of Nepal, Tibet, Sri Lanka, and India). Regardless of environment, it pays for a man who has substantial resources or power (e.g., kings, emperors, Donald Trump) to adopt a strategy focusing on mating effort. Further, if a lower quality male has the good fortune to attract a high mate-value mate, then it is in his best interest to focus on keeping her, rather than seeking out other mates. Due to the high value of women on the mating market, men are essentially limited by their own attributes and by female choice of those attributes.

Mate Retention: An Evolutionary Perspective

Assuming an individual has adopted a long-term mating strategy, attracting a mate is only the first-step in achieving reproductive success. Essential to this strategy is the concept of *mate retention*—behaviors designed to fend off rivals and prevent a partner's infidelity or departure from a mateship (Shackelford, Goetz, & Buss, 2005). These tactics may include *vigilance* regarding a mate's whereabouts (e.g., calling to check-up on a partner), *mate-guarding* (e.g., monopolizing a mate's time, keeping a mate from interacting with same-sex rivals), *emotional manipulation* (e.g., self-abasement, threats of self-harm), or *verbal and physical violence* (e.g., threatening a rival or mate, physically attacking a rival or mate). On average, both men and women exhibit these behaviors, although the cues that elicit such behaviors and the kind of behaviors themselves differ by sex (Buss, 2003b).

For example, contemporary evolutionary research on sexual jealousy suggests that it may be a mechanism aimed at mate-retention and that, contrary to societal beliefs, sexual jealousy is not sex-biased toward men (Buunk, Angleitner, Oubaid, & Buss, 1996). Rather, men and women equally exhibit jealous behaviors; however, the cues that spark such behavior are different and adaptively relevant for each sex (Buss, Larsen, Westen, & Semmelroth, 1992). Given the specter of cuckoldry, men tend to focus on cues that suggest a mate's infidelity, while women focus on signals that suggest their partner's emotional involvement with someone else, which may signal resource channeling. In the short, across numerous studies, research has found that both men and women report being jealous; however, the manner in which this jealousy plays-out and the contexts that trigger such jealousy vary (see Buss 2003a, for review). Men more than women report distress in relation to a partner's sexual infidelity, whereas women more than men report distress in relation to a partner's emotional infidelity. It warrants repeating that these are mean differences; it is not the case that *all* men or *all* women follow this pattern.

Several contexts seem to influence the use and severity of mate retention tactics. Women partnered to higher income (resource rich), status-striving men report engaging in more vigilance, violence, appearance-enhancement, possessive ornamentation, submission, and self-abasement than do women partnered to lower income men (Buss & Shackelford, 1997b). Men with young, attractive (high reproductive value) wives report using more mate-guarding, greater resource display, and more violence than do men with less attractive wives. Additionally, men who perceive a high likelihood of their partner's infidelity report more mate-retention efforts than do women (Buss & Shackelford, 1997a).

SUMMARY

Contemporary EP offers a biological perspective on heterosexual human mating behavior that goes beyond the normal sociocultural perspectives that permeate the social sciences. By connecting the basics of reproductive and behavioral biology and by examining the effect of relevant ecological contexts on psychological processes, a deeper understanding of what it is to be human has emerged. In the past decade, the application of sexual selection theories (e.g., fitness indicator and signaling theories) has shifted the focus of human mating psychology from that of remarkable confusion to fascinating explanation. Until recently, the main focus of EP has been the exploration of sex differences in the mating psychologies of men and women. This perspective has emphasized the mean differences in female versus male preferences, while ignoring individual variation within each sex. However, as we have attempted to show, sex differences are not dichotomized, as is suggested by popular notions of *Venus* and *Mars.* Several lines of evidence clearly demonstrate there is much overlap between the sexes in mating preferences, as well as variation within each sex for traits desired in a sexual partner.

One group of factors that seem to account for a large proportion of sex and individual differences is the ecological context. Humans, like all animals, are intimately tied to their environment, both from an evolutionary-historical perspective, as well as from an ontogenetic-lifetime perspective. Therefore, it is not surprising that mating behaviors (patterns, preferences, strategies) vary with environmental factors, such as resource availability, pathogen load, sex-ratio, etc. Whether it is a long-term socially monogamous couple from a high predation environment who invest only in each other and their offspring, or mating preferences for resources, “good genes,” fertility, or simply beauty, or a short-term mating strategy focused on “gene-capture raids,” each behavior (or suite of behaviors) is an evolutionarily derived reaction to a signal within the greater ecological context.

ISSUES FOR FUTURE CONSIDERATION

In this paper, we have attempted to offer a coherent account of human mating behavior from the perspective of Evolutionary Psychology. A main goal of this chapter was to fill gaps that we believe exist in the majority of evolutionary discussions about human mating. Namely, EP has often times focused its efforts on explaining sex differences in mating preferences (i.e., women want resources, and men want physically attractive women). For a fuller account of human mating to evolve, future research needs to move beyond this simplistic view and incorporate the study of within-sex variation (individual differences). Research needs to examine women’s preferences for fertility markers in male partners, as well as men’s preferences for resources and particular personality traits in female partners. While EP’s focus on adaptive benefits of mating preferences makes theoretical sense, signaling theories suggests that many non-adaptive preferences are also relevant. Further, as several researchers (e.g., Hrdy, 1999; Gangestad & Simpson, 2000) have shown, the hard-lined distinction between a woman’s focus on long-term mating and a man’s focus on short-term mating needs to be re-evaluated.

As with most areas of psychological research, the majority of studies have examined undergraduate college students. For several reasons, results drawn from this evolutionarily novel population may have limited applicability to other human populations. College students are experiencing novel stimuli (e.g., large-groups of same-sex and other sex-peers, little familial supervision and support) in contexts that may not have existed during the majority of human evolution. It is likely that college students are just figuring out which preferences and mating strategies work best for them. To alleviate these difficulties and create a more coherent account of mating psychology, research needs to examine adults of various ages, cultures, and populations.

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NOTES

1. The actual statement from Plato's *Symposium* (Benardete, 2001) is: "human nature was originally one and we were a whole, and the desire and pursuit of the whole is called love."
2. A haplogroup is a large grouping of haplotypes—a series of alleles at specific loci on the chromosome. Of interest here are the non-recombining portions of the Y-chromosome (NRY) haplogroups, which trace patrilineal descent and can be used to define genetic populations. Currently, there are 19 major NRY haplogroups that encompass all known Y-chromosome polymorphisms, suggesting that only 19 main male lineages span the globe.

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