

Evolution of Human Mate Choice

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This article provides a review of evolutionary theory and empirical research on mate choices in non-human species and used as a frame for understanding the how and why of human mate choices. The basic principle is that the preferred mate choices and attendant social cognitions and behaviors of both women and men, and those of other species, have evolved to focus on and exploit the reproductive potential and reproductive investment of members of the opposite sex. Reproductive potential is defined as the genetic, material, and (or) social resources an individual can invest in offspring, and reproductive investment is the actual use of these resources to enhance the physical and social well being of offspring. Similarities and differences in the mate preferences and choices of women and men are reviewed, and can be understood in terms of similarities and differences in the form reproductive potential that women and men have to offer and their tendency to use this potential for the well-being of children.

The study of human sexual behavior and human sex differences has been approached from many vantage points (Davidson & Moore, 2001; McGillicuddy-De Lisi & De Lisi, 2002) and in recent years has been viewed through the lens of evolutionary theory (Buss, 1994; Campbell, 2002; Geary, 1998; Low, 2000; Symons, 1979). However, many psychologists, social scientists, and social critics are reluctant and sometimes vigorously opposed to understanding human behavior in general and human sexuality in particular from an evolutionary perspective (Segerstrale, 2000), or at the very least argue that social influences are predominant (Wood & Eagly, 2002). Our goal is not to address the attendant philosophical or social issues, but rather to provide an introduction to the theory and empirical research generated from the evolutionary perspective. In particular, we focus on women's and men's preferences and choices of mates and marriage partners, and invite the reader to judge for himself or herself the utility of this approach.

In the first section, we provide an introduction to the theoretical and empirical literatures on mate choices in other species (Andersson, 1994; Darwin, 1871) and the framework for appreciating the advantages of this approach for understanding human mate choices. In the second and third respective sections, we provide overviews of evolutionary research on women's and men's mate choices. In the final section, we describe how human mate choices are moderated by social and ecological conditions.

MATE CHOICE IN NONHUMAN SPECIES

Darwin and Wallace (1858) independently discovered the primary mechanisms ---natural selection--- that drive evolutionary change within species and result in the origin of new species. Darwin also discovered another group of

mechanisms that operate within species and are principle factors in the evolution of sex differences (Darwin, 1871). These mechanisms are called *sexual selection* and involve competition with members of the same sex over mates (*intrasexual competition*) and discriminative choice of mating partners (*intersexual choice*). The most common mating dynamic involves male-male competition over access to mates and female choice of mating partners (Andersson, 1994). In the first section, we describe why this dynamic is so common and when exceptions (e.g., male choice) are predicted to evolve. In the second section, we describe intersexual choice in nonhuman species.

Compete or Choose?

Darwin (1871) defined sexual selection, but did not determine why males tend to compete over mates and why females are the choosier of the sexes (see Cronin, 1991). About 100 years later, Williams (1966) and Trivers (1972) determined that any sex difference in the tendency to compete or choose largely but not exclusively turns on the degree of each sexes' investment in parenting. The sex that provides more than his or her share of parental investment becomes, in effect, an important reproductive resource for members of the opposite sex (Dawkins, 1989; Trivers, 1972). One result is competition among members of the lower investing sex (typically males) over the parental investment of members of the higher investing sex (typically females). Members of the higher investing sex are thus in demand, and can be choosy when it comes to mates. Clutton-Brock and Vincent (1991) determined that any sex difference in the tendency to parent is linked to a sex difference in the potential rate of reproduction. As we describe in the next sections, the potential rate of reproduction interacts with social conditions, in particular the operational sex ratio (OSR), to create mating dynamics.

Sex Differences in Rate of Reproduction

The basic issue is the biological limit on how many offspring

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males and females can potentially produce in their lifetime. The upper limit is determined by how fast the individual can potentially reproduce (Clutton-Brock & Vincent, 1991). The biological limit for female mammals is determined by gestation time and length of postpartum suckling. The limit for male mammals, in contrast, is determined by the number of females to which they gain sexual access. In any given breeding season, females will typically have one offspring, whereas males who successfully compete for access to females will have many offspring.

The predicted result of the sex difference in rate of reproduction is an evolved bias of mammalian females toward high levels of parental investment (which includes gestation and suckling) and mammalian males toward competition for mates and no parental investment. This pattern is found in more than 95% of mammalian species (Clutton-Brock, 1989). The corresponding behavioral biases are a male preference for multiple mates and more variability in reproductive outcomes across males than females. Some males sire many offspring, and many males sire no offspring, a dynamic that intensifies male-male competition.

Operational Sex Ratio

The OSR is the ratio of sexually active males to sexually active females in a given breeding population and is related to the rate of reproduction (Emlen & Oring, 1977). In a population where there are as many sexually mature females as males---an actual sex ratio of 1:1---any sex difference in the rate of reproduction will skew the OSR. As noted, male mammals have a faster potential rate of reproduction than female mammals and thus there are typically many more sexually receptive males than females in most populations. The resulting bias leads to intense male-male competition over access to a limited number of sexually receptive females. Male-male competition, in turn, creates the conditions under which female choosiness can evolve (Andersson, 1994). For species in which females have a faster rate of reproduction (e.g., when males incubate eggs), females compete and males choose (Amundsen, 2000; Reynolds & Szekely, 1997).

In some situations, the sex with the higher potential rate of reproduction is better off investing in parenting than in competing for mates. One example is provided by callitrichid monkeys. Here, shared territorial defense, concealed ovulation, female-on-female aggression, twinning, and perhaps other yet unknown factors functionally negate the sex difference in the potential rate of reproduction and result in a more balanced OSR, monogamy, and high levels of male parenting (Dunbar, 1995). Generally, paternal investment occurs in species in which males are reproductively more successful when they parent than when they compete, although a mix of competing and parenting is evident in some species, including humans (see Geary, 2000).

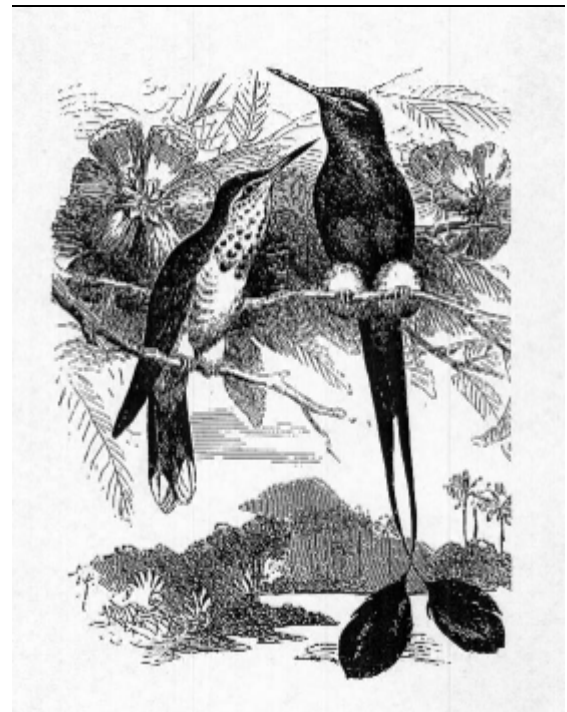
Mate Choice

One of the principal correlates of parental investment is choosiness when it comes to mates. Because females tend

to invest more in parenting than males, female choice is more common than male choice (Andersson, 1994; Darwin, 1871; Trivers, 1972) and has been demonstrated across species of bird, insect, fish, reptile, and mammal (Andersson, 1994; Sargent, Rush, Wisenden, & Yan, 1998). One result of female choice is the evolution of exaggerated male traits. An example is shown in Figure 1, where hummingbird females choose mates in part based on the length of the males' tail feathers. Traits such as those shown in Figure 1 are typically an indicator of the physical or genetic health of the male or serve as an indicator of his ability (e.g., vigor in searching for food) to provide parental investment (Andersson, 1994; Zahavi, 1975).

The physical and genetic health of males is related, in part, to immunocompetence---that is, the ability to resist infection by parasites in the local ecology (Folstad & Karter, 1992; Hamilton & Zuk, 1982). It appears that immunocompetence is heritable and thus the offspring of males with exaggerated traits survive in greater numbers than do the offspring of other males (Saino, Møller, & Bolzern, 1995; Saino, Primmer, Ellegren, & Møller, 1997). Thus, male ornaments are barometers that are strongly affected by the condition of the male, and female mate choices reflect the evolution of females' ability to read these barometers. Although the research in this area is less extensive, there is

Figure 1. Female (left) and male (right) humming birds (*Spathura underwoodi*). From *The descent of man, and selection in relation to sex* (Vol. II, p. 77), by C. Darwin, 1871, London: John Murray. Copyright by John Murray. Reprinted with permission



evidence that similar mechanisms may operate in species in which males parent or females vary greatly in their reproductive success. In these species, males tend to be choosy when it comes to mates and females often have exaggerated traits (Roulin, 1999; Roulin, Jungi, Pfister, & Dijkstra, 2000; Szykman et al., 2001).

MATE CHOICE IN HUMANS

As with other mammals, most women invest heavily in parenting and are choosy when it comes to mating and marriage partners (Buss, 1994). Men also express the basic mammalian pattern: That is, they compete intensely for access to preferred and oftentimes multiple mates, but in addition many men invest in the well-being of their children (Geary, 2000; Geary & Flinn, 2001). Men's parenting complicates the dynamics of sexual selection. In addition to male-male competition and female choice, female-female competition and male choice are also common. Discussion of the interrelatedness of intrasexual competition and intersexual choice, the dynamics of marriage systems, and constraints on mate choice are beyond the scope of this paper, as are the specifics of male-male competition and female-female competition (see Buss, 1994; Campbell, 2002; Daly & Wilson, 1983; Flinn & Low, 1986; Geary, 1998, 2002; Symons, 1979).

Our goals are more modest: specifically, to review theory and research on women's mate choices in the first section and men's mate choices in the second. The reviewed studies largely reflect preferences that are unrestricted by demands of kin, the marriage system, or wider ecological conditions (Flinn & Low, 1986). Thus, the descriptions are primarily of psychological preferences, which are not always realized in actual mate choices. The gist is that the preferred mate choices and attendant social cognitions and behaviors of both women and men are predicted to have evolved to focus on and exploit the reproductive potential and reproductive investment of members of the opposite sex. Reproductive potential is the individual's ability to invest in the growth, development, and later social and reproductive competencies of offspring and/or the potential genetic benefits a mate would confer on offspring (Alexander, 1987; Geary, 2002). *Reproductive investment* is the expenditure of this potential on offspring.

In most mammals, sexual relationships are short-term. Men's paternal investment extends the potential length of these relationships such that many are long-term. One consequence is that human sexual relationships can vary from very brief to decades. Table 1 and Table 2 provide a corresponding organizational framework for considering the potential costs and benefits of short-term and long-term sexual relationships for men and women (Table 1), and levels of choosiness in mate choice decisions and parameters that should influence these choices (Table 2). The most fundamental difference is that the costs of reproduction are higher for women than for men, and therefore women are predicted to be choosy in their mate choices for both short-term and long-term relationships. In fact,

women on average are predicted to largely avoid short-term relationships, given that the potential costs outweigh the potential benefits. The opposite pattern is evident for men, given that potential benefits of short-term relationships outweigh the potential costs. When men do commit to a long-term relationship, the costs increase and thus the level of choosiness is predicted to increase accordingly. Note that most people are not consciously aware of these patterns, but they are predicted to respond (e.g., preference for casual sex) in ways that are consistent with them.

Women's Mate Choices

Evolutionary logic indicates that the best situation for a woman is a long-term partner with good genes who has reproductive potential and the willingness to invest this potential in her and her children. Men's reproductive potential is determined by the ability to parent and the ability to invest social and material resources in children. One way to conceptualize men's resources is in terms of their cultural success (Irons, 1979): that is, their social status and their control of material resources. We describe women's preference for culturally successful men in the first section. In the second and third sections respectively, we describe the behavioral and physical traits that women prefer in prospective partners. We present a brief discussion of alternative mating strategies in the final section.

Culturally Successful Men

In primate species in which long-term relationships develop, females generally prefer dominant males as mates. In comparison to other males, dominant males provide greater protection from conspecifics (i.e., members of the same species) and often provide better access to high-quality foods (Smuts, 1985). Similarly, the social status of men is an important consideration in women's choices of and

Table 1. Examples of Costs and Benefits of Short-Term and Long-Term Sexual Relationships

| Costs | Benefits |
|-----------------------------------|-------------------------------------|
| Women's short-term mating | |
| Risk of STD | Some resources from mate |
| Risk of pregnancy | Good genes from mate |
| Reduced value as a long-term mate | |
| Women's long-term mating | |
| Restricted sexual opportunity | Significant resources from mate |
| Sexual obligation to mate | Paternal investment |
| Men's short-term mating | |
| Risk of STD | Potential to reproduce |
| Some resource investment | No parental investment ^a |
| Men's long-term mating | |
| Restricted sexual opportunity | Increased reproductive certainty |
| Heavy parental investment | Higher quality children |
| Heavy relationship investment | Sexual and social companionship |

Note. STD = sexually transmitted disease.

^aLow paternal investment may result in lower quality children, but this is not a cost to the man because it does not lower his ability to invest in other relationships.

Table 2. Predicted Levels and Parameters of Mate Choosiness in Sexual Relationships

| <u>Short-term</u> | | <u>Long-term</u> | |
|-------------------|---|------------------|---|
| Choosiness | Parameters | Choosiness | Parameters |
| Women | | | |
| High | Indicators of good genes ^a | High | Status Resources Indicators of good genes ^a Family orientation Social compatibility ² |
| Men | | | |
| Low | Fertility cues ^a Sexual opportunity | High | Fertility cues ^a Parenting ability Social compatibility ² |

^aFertility cues and indicators of good genes include physical traits that members of the opposite sex find attractive. ²This applies largely to Western culture, where husband-wife relationships are more intimate than in many other cultures (Geary, 1998)

preferences for marriage partners (Buss, 1994). Although the markers of social status can vary somewhat from one culture to the next (Irons, 1979, 1983), the basic relation is the same: Culturally successful men are preferred as mating and marriage partners. These men wield social influence and have control over resources that women can use for themselves and their children. In short, culturally successful men have more reproductive potential than other men, and women's mating and marriage preferences suggest that they are motivated to capture and use this potential for their own reproductive ends.

The reason for this is clear: In all cultures so studied, the children of culturally successful men have lower mortality rates than the children of other men (see Geary, 2000). Even in cultures in which mortality rates are low, children of culturally successful men benefit in terms of psychological and physical health and in terms of longevity in adulthood (Adler et al., 1994). These are exactly the conditions that would result in the evolution of women's preference for socially dominant and culturally successful marriage partners.

Actual choices. In many cultures, women's mate choices are complicated by the influence and often-times competing interests of their kin (Daly & Wilson, 1983; Flinn, 1988b). The marriage patterns of the Kipsigis, a pastoral group in Kenya, provide an example (Borgerhoff Mulder, 1988, 1990). Choice of marriage partners is technically made by the young woman's kin, but in most cases the parents' decision is influenced by their daughters' preferences. These joint decisions are strongly influenced by the amount of land made available to her and her future children.

In this society, land and cattle are controlled by men, and gaining access to these resources has important reproductive consequences for women. "Land access is correlated with women's reproductive success, and may be an important causal factor contributing to reproductive differentials, given the greater availability of food in the homes

of 'richer' women and the lower incidence of illness among them and their offspring" (Borgerhoff Mulder, 1990, p. 256). Because this land is divided among her sons, who eventually use the land to attract wives, women who gain access to large land plots (through marriage) have more surviving grandchildren than do women with small land plots (Borgerhoff Mulder, 2000). Given this relation, it is not surprising that across an 18-year period, Borgerhoff Mulder (1990) found that the two men offering the most land were chosen as husbands by 13 of 29 brides and their families, and either one or both of these men got married in 11 of the 15 years in which one or more marriages occurred. The two lowest ranking men were chosen as husbands in only 1 of these 15 years.

Thus, culturally successful Kipsigis men are preferred marriage partners because they provide the resources women need to keep their children alive and healthy. A preference for culturally successful marriage partners is, in fact, found throughout the world, at least in societies in which material resources can be accumulated or where men provide a high-quality but perishable resource, such as meat obtained through hunting (Buss, 1996; Irons, 1983; Symons, 1979). A woman's decision to stay married or not is also influenced by the quantity and quality of resources provided by her husband (Betzig, 1989; Buckle, Gallup, & Rodd, 1996; Campbell, 2002). In the most extensive cross-cultural study of the pattern of marital dissolution ever conducted, Betzig found that "inadequate support is reported as cause for divorce in 21 societies and ascribed exclusively to the husband in all but one unspecified case" (Betzig, 1989, p. 664).

When material resources are not readily accumulated, women's preferences are still influenced by the social status of prospective marriage partners, as exemplified by the Yanomamö Indians of Venezuela (Chagnon, 1997). The Yanomamö are characterized by frequent raiding between different villages (Chagnon, 1988). Under these conditions, men who are skilled at political negotiations or are fierce warriors enjoy a higher social status than do other men, although they do not differ from other men in material wealth (Hames, 1996). These high-status men have more wives than other men, but receive food tributes from other families in their village (Hames, 1996). The net result is that women and their children who marry these men do not suffer nutritionally (in comparison to monogamously married women) and appear to be better treated by other group members as a consequence of their marriages (Hames, 1992, 1996). Of course, many of these women might prefer to be monogamously married to these high-status men but are not able to achieve this end due to the competing reproductive interests of their husbands.

Preferred choices. A woman's preferred marriage partner and her actual marriage partner are not always the same, due to competition from other women and men's mate choice preferences. Social psychological studies of explicit preferences for marriage partners are thus an important adjunct to research on actual marriage choices. These preferences

appear to more clearly capture the processes associated with evolved social and psychological mechanisms that guide reproductive behaviors (Buss, 1996; Geary, 1998; Kenrick, Sadalla, Groth, & Trost, 1990).

Research conducted throughout the world strongly supports the position that women prefer marriage partners who are culturally successful or have the potential to become culturally successful. The most extensive of these studies included 10,000 people in 37 cultures across six continents and five islands (Buss, 1989). On the mate choice survey, women rated "good financial prospect" higher than did men in all cultures. In 29 samples, the "ambition and industriousness" of a prospective mate were more important for women than for men, presumably because these traits are indicators of his reproductive potential--that is, his ability to eventually achieve cultural success. Hatfield and Sprecher (1995) found the same pattern for college students in the United States, Japan, and Russia. In each culture, women valued a prospective mate's potential for success, earnings, status, and social position more highly than did men.

A meta-analysis of research published from 1965 to 1986 revealed the same sex difference (Feingold, 1992). Across studies, 3 out of 4 women rated socioeconomic status as more important in a prospective marriage partner than did the average man. Studies conducted prior to 1965 showed the same pattern (e.g., R. Hill, 1945) as did a more recent survey of a nationally representative sample of unmarried adults in the United States (Sprecher, Sullivan, & Hatfield, 1994). Across age, ethnic status, and socioeconomic status, women preferred husbands who were better educated than they were and who earned more money than they did. Buunk and colleagues found the same pattern for women ranging in age from their 20s to their 60s (Buunk, Dijkstra, Fetchenhauer, & Kenrick, 2002). This preference is highlighted when women make cost-benefit trade-offs between a marriage partner's cultural success and other important traits, such as his physical attractiveness (Li, Bailey, Kenrick, & Linsenmeier, 2002; Waynforth, 2001). When women are forced to make such trade-offs, a prospective marriage partner's cultural success is rated as a necessity and other characteristics as a luxury.

Women's preference for culturally successful men is also found in studies of singles ads and popular fiction novels. In a study of 1,000 "lonely hearts" ads, Greenlees and McGrew (1994) found that British women were 3 times more likely than British men to seek financial security in a prospective partner. Oda (2001) found that Japanese women were 31 times more likely than Japanese men to seek financial security and social status in a prospective long-term partner; 9.4% of Japanese women explicitly sought these traits, compared to 0.3% of men. Whissell (1996) found the same themes across 25 contemporary romance novels and six classic novels that have traditionally appealed to women more than men, including two stories from the Old Testament written about 3,000 years ago. In these stories, the male protagonist is almost

always an older, socially dominant, and wealthy man who ultimately marries the woman.

Finally, Bereczkei's and Csanaky's (1996) study of more than 1,800 Hungarian men and women who were 35 years of age or older (and thus not likely to have more children) found that women who had married older and better educated men on average had more children, were less likely to get divorced, and reported higher levels of marital satisfaction than did women who married younger and/or less educated men. In short, marrying a culturally successful man provides the woman with social, psychological, and reproductive benefits (Geary, 2000; Low, 2000).

Personal and Behavioral Attributes

A preference for a culturally successful marriage partner is not enough, in and of itself, to constitute the most successful reproductive strategy for women. Culturally successful men are often arrogant, self-serving, and better able to pursue their preferred reproductive interests than are other men. As described later, these preferences often involve pursuing multiple mating partners rather than investing in a single woman and her children (Betzig, 1986; Pérusse, 1993; Pratto, 1996). As a result, the personal and behavioral characteristics of men are an important consideration in the choice of a marriage partner. These characteristics provide information on the ability and willingness of the man to make a long-term investment in the woman and her children (Buss, 1994). The bottom line is that women want culturally successful marriage partners and they want some level of influence over the behavior of these men.

With the exception of age and physical attractiveness, women are more selective in their choice of marriage partners than are men (Feingold, 1992; Hatfield & Sprecher, 1995; Hill & Hurtado, 1996; Kenrick et al., 1990). In addition to ambition, industriousness, and social dominance, women tend to rate the emotional stability and the family orientation of prospective marriage partners more highly than do men (e.g., Oda, 2001; Waynforth, 2001). Buss (1989) found that women rated a prospective husband who was kind, understanding, and intelligent more highly than a prospective husband who was none of these but had the potential to become culturally successful. These patterns indicate that women prefer husbands who have resources and have the personal and social attributes that suggest they will, in fact, invest these resources in a family. Women also seem to prefer men with whom they feel physically safe and who are physically capable of protecting them from other men should the need arise (Geary & Flinn, 2001; Hill & Hurtado, 1996; Surbey & Conohan, 2000).

Finally, many women prefer men with whom they can develop an intimate and emotionally satisfying relationship (Buss, 1994; MacDonald, 1992), although this appears to be more of a luxury than a necessity (Li et al., 2002). In keeping with the distinction between luxury and necessity, the preference for this type of relationship is more common in middle-class and upper-middle-class Western cultures than in many other cultures (Hewlett, 1992) or in the work-

ing-class of Western societies (Argyle, 1994). We are not saying that the development of an intimate pair-bond is not important or not preferred by women in non-Western cultures. Rather, it is not as high a priority in mate choice decisions as it is for many women in Western culture (MacDonald, 1992). In many non-Western contexts, women are more focused on keeping their children alive than on developing intimacy with their husbands.

Physical Attractiveness and Good Genes

In classical literature and in romance novels, the male protagonist is almost always socially dominant, wealthy, and handsome (Whissell, 1996). Indeed, a preference for an attractive mate makes biological sense (Fink & Penton-Voak, 2002; Gangestad, 1993; Gangestad & Buss, 1993). Not only are handsome husbands more likely to sire children who are attractive and thus sought out as mating and marriage partners in adulthood, but these men and their children also appear to be physically healthier than other men and their children (Gangestad, Thornhill, & Yeo, 1994; Grammer & Thornhill, 1994; Singh, 1995a; Thornhill & Gangestad, 1993, 1994). In other words, the physical attributes that women find attractive in men are indicators of the man's physical and genetic health (Gangestad & Simpson, 2000), just as the long tail feathers of the hummingbird shown in Figure 1 are an indicator of his genetic and physical quality.

Women prefer men who are somewhat taller than average, and have an athletic (but not too muscular) and symmetric body shape, including a 0.9 waist-to-hip ratio (WHR), and shoulders that are somewhat wider than their hips (Barber, 1995; Beck, Ward-Hull, & McClear, 1976; Cunningham, Barbee, & Pike, 1990; Gangestad et al., 1994; Hatfield & Sprecher, 1995; Oda, 2001; Pierce, 1996; Singh, 1995a). The facial features that women rate as attractive include somewhat larger than average eyes, a large smile area, and prominent cheek bones and chin (Barber, 1995; Cunningham et al., 1990; Scheib, Gangestad, & Thornhill, 1999). These physical traits appear to be good indicators of genetic variability (which is important for disease resistance), a lack of illness during development, and current physical health (Barber, 1995; Thornhill & Gangestad, 1993). For instance, the development of prominent cheek bones and a masculine chin is related to androgen levels and androgen/estrogen ratios during puberty (Fink & Penton-Voak, 2002; Tanner, 1990). Chronic illness during this time can suppress androgen secretion, which would result in the development of less prominent cheekbones, a more feminine-looking chin, and, as a result, lower rated physical attractiveness (Thornhill & Gangestad, 1993).

Shackelford and Larsen (1997) found that men with less symmetric facial features were less physically active, manifested more symptoms of depression and anxiety, and reported more minor physical problems (e.g., colds, headaches) than their peers with more symmetric faces. Men with asymmetric faces and body features also have higher basal metabolic rates, somewhat lower IQs, and

fewer sexual partners than their more symmetric peers (Furlow, Armijo-Prewitt, Gangestad, & Thornhill, 1997; Gangestad & Simpson, 2000; Gangestad & Thornhill, 1997; Manning, Koukourakis, & Brodie, 1997). Confirming that women's stated preferences are often put into practice, Phillips et al. (2001) and Nettle (2002) found that physically smaller and less-robust men are less likely to be chosen as marriage partners than are taller and more-robust men.

There is also evidence that women's mate and marriage choices are influenced by men's immune-system genes (Wedekind, Seebeck, Bettens, & Paepke, 1995), just as the mate choices of females of at least some other species are influenced by indicators of the males' immunocompetence (Hamilton & Zuk, 1982). Women, of course, are not directly aware of these genetic differences. Immune-system genes are signaled through pheromones and women are sensitive to and respond to these scents, especially during the second week of their menstrual cycle when they are most fertile (Gangestad & Thornhill, 1998). Furthermore, women show a preference for the scents of men with the above-noted features (such as facial symmetry), suggesting that high-quality men exhibit a variety of correlated physical and pheromonal traits that distinguish them from other men and that serve as cues that influence female choice (Thornhill & Gangestad, 1999).

It is not simply the quality (i.e., presumed resistance to disease) of the man's immune-system genes but also how these genes match up with those of the woman that influence women's mate preferences. In terms of disease resistance, the best outcome for offspring occurs when there is high variability in immune-system genes (Hamilton, Axelrod, & Tanese, 1990). In addition to mutations (Nei & Hughes, 1991), variability results when parents have different versions of these genes. Wedekind et al. (1995) found that women who are not taking oral contraceptives---these change sensitivity to pheromones---rated the scents of men with dissimilar immune-system genes as more pleasant and sexy than the scents of men with similar immune-system genes. In a 5-year prospective study of fertility, Ober and her colleagues found couples with dissimilar immune-system genes conceived more quickly (2 vs. 5 months) and had fewer spontaneous abortions than did couples with more similar genes (Ober, Elias, Kostyu, & Hauck, 1992; Ober et al., 1997).

The evidence supports the view that women's mate and marriage choices are influenced by indicators of the physical and perhaps genetic health of men, as reflected, in part, in the man's physical attractiveness and scent (Thornhill & Gangestad, 1993). However, a series of studies by Graziano and his colleagues qualifies this pattern (Graziano, Jensen-Campbell, Shebilske, & Lundgren, 1993). Women's ratings of the physical attractiveness of men were moderated by the ratings of the women's peers, especially if the peer ratings were negative. Other studies suggest that women's ratings of the physical attractiveness of men are also influenced by the men's perceived social

dominance (e.g., Townsend, Kline, & Wasserman, 1995) and by the age of the women's fathers when they were children (Perrett et al., 2002).

Still other studies show that women's preference for physically attractive men varies across the menstrual cycle (Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999) and with her physical attractiveness (Little, Burt, Penton-Voak, & Perrett, 2001). Penton-Voak and colleagues demonstrated that women preferred men with masculine facial features (e.g., prominent chin) around the time of ovulation and men with more feminine facial features at other times in their cycle; implications are discussed in the "Extra-pair sex" section. Little et al. (2001) found that physically attractive women rated masculine-looking men as more attractive long-term partners than did other women, presumably because attractive women are better able to divert (e.g., through threats of abandonment) the activities of these attractive men from mating effort to parental effort.

In sum, women's ratings of the attractiveness of men are complex and vary across their menstrual cycle. They generally prefer men with physical traits that appear to be indicators of the man's genetic quality (e.g., immunocompetence), although these same physical traits also are an indication of the man's ability to protect her and her offspring from other men. In any case, women's ratings of men's physical attractiveness are influenced by social comparisons and other social processes, including their own attractiveness and thus value as a mate, above and beyond his actual physical traits.

Alternative Mating Strategies

Despite the costs noted in Table 2, women can sometimes benefit by engaging in short-term sexual relationships or a sexual relationship with a man other than her social or marital partner, or by engaging in serial relationships or practicing polyandry. These various alternatives to the monogamous high-investment relationships that many women prefer are described in the respective sections below. As noted in Table 1, the gist is that these relationships allow women to (a) secure additional material resources for themselves and their children, or (b) mate with physically attractive men and thus secure better genes for their children.

Short-term mates. Due to the costs of pregnancy, women are on average more sexually cautious than men (Buss & Schmidt, 1993; Oliver & Hyde, 1993), but they sometimes engage in short-term sexual relationships (Gangestad & Simpson, 2000). It appears that some women use their reproductive potential, that is, their sexuality, to initiate relationships with men who would not otherwise invest in them. Stated somewhat differently, men's preference for short-term mates and sexual variety (described later) creates a demand that some women use for financial or other material gains (Brewer et al., 2000). Many other women appear to engage in short-term sexual relationships when they perceive the potential for the

development of a longer term relationship (Surbey & Conohan, 2000), suggesting that women sometimes use sexuality as a means to initiate a relationship with a potential marriage partner.

In contexts in which most men are unable or unwilling to make a long-term investment in women and their children, or in contexts in which investment in children comes largely from the woman's resources and those of her kin, women's sexual and reproductive options may be largely based on choice of short-term mates. Women's choices in these contexts have not been systematically studied, but are predicted to be strongly influenced by the physical and pheromonal traits of men (Gangestad & Simpson, 2000) for reasons described earlier (e.g., immunocompetence).

Extra-pair sex. Extra-pair sex is common even in socially monogamous species. Extra-pair copulations (EPC) and cuckoldry of the social partner (the male providing parental care to the offspring of another male) is in fact much more common than once believed. Birkhead and Møller (1996; see also Jennions & Petrie, 2000) estimated that for bird species in which male provisioning improved offspring survival rates but was not absolutely essential, about 15% of nestlings were sired by extra-pair males. In these species, female mate choice involves a trade-off between obtaining higher quality genes for offspring and thus lower mortality rates versus the risk of being abandoned by their social partner if an EPC is detected.

A definitive study of human cuckoldry rates has not been conducted, although it clearly happens (Potthoff & Whittinghill, 1965). Essock-Vitale and McGuire (1988) found that about 20% of American women reported engaging in at least one extra-marital affair and that some of these relationships resulted in pregnancy. Bellis and Baker (1990) found that when women initiated an infidelity it often occurred around the time of ovulation. For this sample, 7% of the copulations during the time of ovulation were with an extra-pair man, and these relationships were less likely to involve the use of contraceptives than were copulations with their social partner. Although definitive conclusions cannot be reached at this time, it appears that men are deceived by their partners into raising the children of another man, that is, cuckolded, about 10% of the time (Bellis & Baker, 1990; Flinn, 1988a; Gaulin, McBurney, & Brakeman-Wartell, 1997; McBurney, Simon, Gaulin, & Geliebter, 2002). The issues are complex, however, as the rate varies significantly across cultural settings and socioeconomic status. Sasse, Muller, Chakraborty, and Ott (1994) reported that nonpaternity rates were 1 % in Switzerland, but others have reported rates greater than 20% in low socioeconomic settings (Cerdeira-Flores, Barton, Marty-Gonzalez, Rivas, & Chakraborty, 1999; Potthoff & Whittinghill, 1965). It is also possible that some of these men are aware of the nonpaternity of the children they are raising and thus have not been technically cuckolded.

The dynamics of women's EPCs appear to be influenced by hormonal fluctuations. In particular, women as a group show systematic changes in sexual fantasy and

attractiveness to extra-pair men, among other sex-related traits, around the time of ovulation (Bellis & Baker, 1990; Gangestad & Thornhill 1998; Gangestad, Thornhill, & Garver, 2002; Geary, DeSoto, Hoard, Sheldon, & Cooper, 2001; Macrae, Alnwick, Milne, & Schloerscheidt, 2002; Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999; Thornhill & Gangestad, 1999). Women are not only more likely to fantasize about (Gangestad et al., 2002) and sometimes engage in an affair during this time (Bellis & Baker, 1990), but they are also more sensitive to and attracted by male pheromones. Gangestad and Thornhill (1998; Thornhill & Gangestad, 1999) found that the scent of facially symmetric men was rated as more attractive and sexy than was the scent of less symmetric men but only during this fertile time frame. Penton-Voak and colleagues found that women rated masculine faces---those with a more prominent jaw---as especially attractive around the time of ovulation (Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999). As noted above, scent, facial symmetry, and a masculine jaw bone may be proximate cues to a man's genetic fitness (Shackelford & Larsen, 1997).

The emerging picture is one in which women appear to have an evolved sensitivity to the proximate cues of men's fitness, a sensitivity that peaks around the time women ovulate and are thus most likely to conceive. The pattern also suggests that women's sexuality can involve a mixed social and reproductive strategy (Gangestad & Simpson, 2000). The occasional result is the cuckoldry of the woman's social partner (Bellis & Baker, 1990; Gangestad & Thornhill, 1998; Geary, 1998). The mixed strategy may be most effective if women are psychologically and socially attentive to the relationship with their primary partner and thus maintain his investment (Geary, 2000) and only become sensitive to the cues of more physically attractive men at the time of ovulation. Many of these women never engage in an EPC, and those who do seem to prefer an extra-pair partner with whom they have level of emotional intimacy as contrasted with a stranger (Banfield & McCabe, 2001). In any case, when extra-pair relations do occur, they are typically initiated by the woman around the time of ovulation.

Serial monogamy and polyandry. For many women, marriage to a socially dominant, wealthy, and physically attractive man who is devoted to her and her children is not achievable. This is especially true in contexts where most men do not have the material or social resources to support a family. To adjust to this circumstance, some women develop a successive series of relationships with a number of men or several simultaneously, each of whom provides some investment during the course of the relationship (Campbell, 2002; Buss & Schmitt, 1993). These women are practicing serial monogamy and sometimes polyandry. In recounting a study conducted in the Dominican Republic, Lancaster noted that in comparison to women monogamously married to men with low incomes,

women who excluded males from the domestic unit and maintained multiple liaisons were more fecund, had healthier children with fewer pre- and post-natal mishaps, were able to raise more children over the age of five, had better nourished children (as measured by protein per capita), and had better psychological adjustment (as measured by self-report and lower maternal blood pressure). (Lancaster, 1989, pp. 68-69)

In several South American Indian societies, such as the Ache and Bari, women will engage in sexual relations with men who are not their social partners, especially after becoming pregnant (Beckerman et al., 1998; Hill & Hurtado, 1996). By tradition, these men are called secondary fathers and are socially obligated to provide material resources and social protection to the woman's child, although not all of them do so. The result seems to be a confusion of paternity such that both primary and secondary fathers invest in the child. The mortality rate of Ache children with one secondary father is about one half that of children with no secondary father or two or more secondary fathers (Hill & Hurtado, 1996). With more than one secondary father paternity is too uncertain, and thus these men do not invest in the child. The benefit of a secondary father cannot be attributed to qualities of the mother, as Beckerman et al. (1998) found that 80% of Bari children with a secondary father survived to adulthood compared to 61 % of their siblings without a secondary father.

Men's Mate Choices

As noted in Table 1 and Table 2, men's mate choices are predicted to vary with the anticipated length of the relationship and thus their anticipated level of parental investment should a pregnancy occur. Given relatively low levels of investment in the relationship and no anticipated investment in any resulting children, men should have low standards for short-term sexual relationships. The one area in which men's preferences may not change significantly is for fertility cues---that is, women's physical attractiveness. As with women, and males and females of other species, men's choosiness is predicted to increase with increases in their level of parental investment (Trivers, 1972). Men's mate choice criteria are thereby predicted to be similar to women's criteria when choosing a marriage partner, although given the costs of pregnancy women are still predicted to be the choosier of the sexes.

On the basis of the sex differences in the costs and benefits of short-term relationships (see Table 1 and Table 2), men are predicted to express a greater desire for a variety of casual sexual partners and devote more effort to finding these partners, as we describe in the following section. In the second section we present a description of the personal and behavioral attributes that men prefer in marriage partners. In the third section, we describe the physical attributes of women whom men find attractive and why men find these attributes attractive.

Short-Term Mating Strategies

Women will often pursue short-term sexual relationships,

most typically as a means to secure material or other resources for themselves or their children. Men, in contrast, are predicted to pursue short-term sexual relationships as ends in themselves (Buss & Schmitt, 1993; Symons, 1979). The prediction follows from the general mammalian reproductive pattern (Clutton-Brock, 1989) and from the accompanying sex differences in the costs (higher for women) and benefits (higher for men) of any resulting children, in which many of these men will not invest (see Table 1 and Table 2). There are, of course, individual differences within men. Men who are culturally successful (Perusse, 1993), have the physical traits that women find attractive (Gangestad, Bennett, & Thornhill, 2001), or are would-be alpha males---young men who are driven to achieve cultural success (Pratto & Hegarty, 2000)---are more likely to succeed in attracting short-term mates than are other men. These short-term relationships are likely to be with women looking for long-term mates or those who are engaged in an extra-pair relationship.

In any case, in the two respective sections we describe sex differences in sexual fantasies and in use of prostitutes. Research described in both sections clearly supports the prediction that men, on average, prefer some number of short-term casual sexual relationships and a variety of sexual partners.

Sexual attitudes and fantasy. In a meta-analysis of sexual attitudes and sexual behavior, Oliver and Hyde (1993) found large sex differences in attitudes toward casual sex and the frequency of masturbation; the latter reflects, in part, a disparity between sexual appetite and the number of sexual partners. About 4 out of 5 men were more enthusiastic about the prospect of casual sex than was the average woman, and about 6 out of 7 men reported masturbating more frequently than the average woman. Women, in contrast, more strongly endorsed the double standard (i.e., premarital sex is less acceptable for women than men) and reported more anxiety and guilt over sex than did men, although these differences were not large.

The sex difference in attitudes toward casual sex did not differ for studies conducted in the 1960s, '70s, or '80s, suggesting that this is a relatively stable difference (see also Symons, 1979). Other aspects of sexual behavior and sexual attitudes did change across decades, indicating that many aspects of sexuality are influenced by cultural mores. The largest change was found in attitudes toward sexual relationships for couples who are engaged to be married, with women more likely to endorse this type of relationship in the 1980s than in the 1960s. Thus, as social prohibitions against women's sexuality lessened in the United States, the attitudes of women towards sexual relationships showed only selective changes. The general preference to avoid casual sexual relationships remained unchanged, but women's willingness to engage in a sexual relationship with a man committed to a long-term relationship increased greatly.

Men's attitudes toward casual sex are put into practice, if the opportunity arises (Buss & Schmitt, 1993). In a set

of studies in which undergraduates approached attractive but unfamiliar members of the opposite sex and asked them for dates, to go to their apartments, or to engage in casual sex (i.e., an EPC), Clark and Hatfield (1989) found that one half of the men and one half of the women accepted the date. When asked to engage in casual sex, 3 out of 4 men agreed, but none of the women agreed. Indeed, Banfield and McCabe (2001) found that fewer than 2% of the women they surveyed had ever engaged in a purely sexual EPC, but 12% reported an EPC with romantic attachment to the extra-pair man.

There are also differences in the quantity and nature of the sexual fantasies of men and women (Ellis & Symons, 1990; Wilson, 1997). Wilson found that men were 2.5 times more likely to fantasize about group sex than were women. Ellis and Symons found that men were twice as likely as women to report having sexual fantasies at least once a day and were 4 times as likely to report having fantasized about sex with more than 1,000 different people (8% of women vs. 32% of men). Although there were no sex differences in feelings of guilt over sexual fantasies, men and women differed considerably in the content of their fantasies. Women were 2.5 times as likely to report thinking about the personal and emotional characteristics of their partners, whereas men were nearly 4 times as likely to report focusing on the physical characteristics of their partners. Moreover, women were twice as likely to report fantasizing about someone with whom they are currently romantically involved with or had been involved with, whereas men were 3 times as likely to fantasize about having sex with someone they were not involved with and had no intention of becoming involved with.

Prostitution. If there is a sex difference in the preference for short-term mating partners, then this difference should and clearly does manifest itself in the use of prostitutes. The demand for prostitutes is almost entirely male-driven. Although the focus of this demand can be other men (i.e., male prostitutes), it is predominantly women (Brewer et al., 2000; Turner et al., 1998). Across two national (United States) surveys of 9,066 adults between the ages of 18 and 59 years, Brewer et al. found that on average men reported between 1.5 and 2.5 times as many sexual partners during the past year and 5 years, respectively, than did the average woman. On the basis of prostitution arrest and rearrest records, surveys, interviews, and other techniques, they further estimated that a typical female prostitute in the United States will have 700 male sexual partners a year. This number was then combined with the estimated prevalence rate of 22 prostitutes per 100,000 adults, and used to determine if the sex difference in the reported number of sexual partners might be due to use of prostitutes. Indeed, once the estimated use of prostitutes was controlled, there was no sex difference in the number of sexual partners.

It is difficult to estimate the number of men who have resorted to prostitution as a means to secure short-term mates, because men are reluctant to admit to this behavior (Brewer et al., 2000). In a survey of 1,729 males between

the ages of 15 and 19, 2.5% reported having had sex at least once with a prostitute (Turner et al., 1998). Given the age range in this sample, the percentage of men who resort to prostitution at some point in their lifetimes must be considerably higher than 2.5%. Indeed, for a random sample of 852 Danish and Swedish adults between the ages of 23 and 87, 16% of the men but none of the women reported having visited a prostitute at least once (Bonnerup et al., 2000).

Personal and Behavioral Attributes

In addition to casual relationships, most men want a long-term marriage partner, and many men only want a long-term partner (Miller, Putcha-Bhagavatula, & Pedersen, 2002). These are reproductive relationships in which men have committed to investing in children. As noted in Table 2, men are predicted to be nearly as choosy as women and show both similarities and differences in the criteria used to choose long-term mates.

In long-term relationships, men, like women, prefer intelligent marriage partners and partners with whom a compatible and cooperative relationship can be developed (Buss, 1989; Li et al., 2002). Kenrick et al. (1990), for instance, found that men rated the personality, friendliness, and sense of humor of a potential marriage partner very highly, and just as highly or more highly than her physical attractiveness (see also Kenrick, Groth, Trost, & Sadalla, 1993). Across cultures, Buss found that men rated the intelligence, kindness, and understanding of a prospective mate as important attributes, and for many men these traits were more important than her physical attractiveness.

One area in which men and women differ is the importance of their partner's sexual fidelity. Men's concern for their partner's sexual fidelity is an evolutionarily coupled feature of the earlier-described cuckoldry risks and the costs associated with investing in the child of another man. Sagarin and colleagues, for instance, found that men were distressed by the prospect of their partner having an EPC with another man and thus risking pregnancy, but were not distressed by the prospect of their partner having an EPC with a woman and thus not risking pregnancy (Sagarin, Becker, Guadagno, Nicastle, & Millevoi, 2003). The social and psychological manifestation is sexual jealousy, which has a near universal influence on the dynamics of men's and women's relationships, including male-on-female aggression and men's attempts to control the social and sexual behavior of their partners (Daly & Wilson, 1988; Daly, Wilson, & Weghorst, 1982; Dickemann, 1981; Buss, Larsen, Westen, & Semmelroth, 1992; Flinn, 1988a; Geary, Rumsey, Bow-Thomas, & Hoard, 1995). Although the associated sexual proprietary behavior of men and the more general sex differences in jealousy patterns have been questioned (e.g., Harris, 2000), men's actual behavior and their behavior as reported by their partners is consistent with the evolutionary model, and may be especially pronounced in men who strive for social dominance (Pratto & Hegarty, 2000).

The dynamics of men's sexual jealousy are illustrated by Flinn's observational study of mate guarding in a rural

Trinidadian village. In this village, "13 of 79 (16.4%) offspring born ... during the period 1970-1980 were putatively fathered by males other than the mother's coresident mate. Clearly, mate guarding could have significant effects on fitness" (Flinn, 1988a, p. 10). Indeed, mate guarding by men but not women was found to be a common feature of long-term relationships, although the guarding varied with the pregnancy risks of the man's partner. Men monitored the activities less diligently and had fewer conflicts with pregnant and older wives than they did with younger and nonpregnant wives. In a related study, women reported that their partners engaged in more mate guarding during the week when the women were most likely to ovulate, the time frame when these same women reported an increase in sexual fantasy and interest in an extra-pair man (Gangestad et al., 2002).

Sexual jealousy is also implicated in the dissolution of many relationships. Betzig (1989) found that, with the exception of sterility, adultery was the most common cause of marital dissolution across cultures. "In 25 societies, divorce follows from adultery by either partner; in 54 it follows only from adultery on the wife's part and in 2 only from adultery on the husband's. If marriage qualifies as near universal, so must the double standard" (Betzig, 1989, p. 658). More seriously, Daly's and Wilson's (1988) seminal study of homicide indicates that a common motive for a man killing his wife is her sexual infidelity, her suspected sexual infidelity, or her desertion of him.

Physical Attributes and Fertility

Both women and men prefer sexually attractive partners, but this preference is consistently found to be more important---a necessity and not a luxury---for men than for women (Buss, 1989; Feingold, 1990; Hatfield & Sprecher, 1995; Li et al., 2002; Oda, 2001). Men's ratings of women's physical attractiveness are related to several specific physical traits, including a waist-to-hip ratio (WHR) of 0.7, facial features that signal a combination of sexual maturity but relative youth, body and facial symmetry, and age (Cunningham, 1986; Jones, 1995; Jones & Hill, 1993; Kenrick & Keefe, 1992; Møller, Soler, & Thornhill, 1995; Singh, 1993a, 1993b, 1995b). Body mass index (BMI), a measure of leanness to obesity independent of height, is also associated with rated attractiveness. Hume and Montgomerie (2001) found a negative relation between BMI and the rated attractiveness of women (but not men), such that leaner women were rated more attractive than heavier women.

The combination of all of these traits (e.g., WHR, age) provides cues to women's fertility, as noted in Table 2 and predicted from the evolutionary perspective. As an example, women's fertility is low in the teen years, peaks at about age 25, and then gradually declines to near zero by age 45 (Menken, Trussell, & Larsen, 1986). Teenage mothers experience more complications during pregnancy (e.g., ectopic pregnancy, stillbirth) than do women in their 20s (Andersen, Wohlfahrt, Christens, Olsen, & Melbye,

2000). Risks begin to increase in the 30s and increase sharply after age 35. Spontaneous abortion is the most common cause of fetal loss, with the risk of loss at 9% for a 22-year-old woman, 20% for a 35-year-old, 40% for a 40-year-old, and 84% for a 48-year-old. Given this, men's mate preferences would almost certainly evolve to be sensitive to indications of women's age.

Buss' (1989) earlier described 37-culture study as well as other studies support this prediction (e.g., Buckle et al., 1996; Buss & Shackelford, 1997; Kenrick & Keefe, 1992; Kenrick, Keefe, Gabrielidis, & Cornelius, 1996; Sprecher et al., 1994). Across all 37 cultures, men preferred marriage partners who were younger than themselves. Marriage patterns in these cultures indicated that these preferences were put into practice: Brides were, on average, 3 years younger than their grooms. Kenrick and Keefe (1992) demonstrated this same pattern across samples from the United States, Germany, Holland, and India. Marriage patterns in the 20th century in the United States and in Poro, a small Philippine island, revealed the same pattern. The patterns also revealed that as men aged, they tended to marry younger and younger women (Buckle et al., 1996; Kenrick & Keefe, 1992). For instance, in 1923 the typical American man in his 20s married a woman who was about 3 years younger than himself, as did the typical Filipino man between 1913 and 1939. The typical man in his 60s married a woman who was about 15 years younger than himself in the United States and 20 years younger in Poro. These patterns cannot be attributed to a social norm that men should marry younger women and women should marry older men. Kenrick et al. (1996) found that the most attractive dating partner for teenage males was a woman about 5 years older than themselves, that is, a woman with higher fertility than females of the same age or younger than these adolescent males.

As we noted, women's WHR also influences men's assessment of their physical attractiveness. Across age and ethnic and racial status, men rate women of average weight and with a WHR of 0.7 as more attractive than thinner and heavier women with a 0.7 ratio and women of any weight with ratios different from 0.7 (Singh, 1993a, 1993b, Singh & Luis, 1995); the attractiveness of the relative thinness of women varies across cultures but the preferred WHR appears to be invariant. The WHR, in turn, appears to be an honest indicator of women's health and fertility. Women with ratios greater than 0.85 are at risk for a number of physiological disorders and appear to have greater difficulty conceiving than women with lower ratios (Singh, 1993a; Zaadstra et al., 1993). Manson et al. (1995) found that as WHR increased in middle-aged women, the risk of death due to coronary heart disease increased exponentially. Overall, however, BMI was a better predictor of premature death than was WHR.

Facial and body symmetry also influence men's ratings of women's physical attractiveness, although symmetry appears to be relatively more important for the rated attractiveness of men than women (e.g., Shackelford & Larsen,

1997). One possible exception is breast symmetry. The breasts of nonsuckling women are relatively larger than those found in other primates, suggesting that breast size is a sexually selected and exaggerated trait in women (Barber, 1995; Diamond, 1992). Singh (1995b) found that women with asymmetric breasts were rated by men as less attractive than women with symmetric breasts. Scutt and Manning (1996) found that these and many other physical traits show greater symmetry due to soft tissue changes at the time of ovulation relative to other points in the cycle. The increase in symmetry would increase women's attractiveness, men's sexual interest, and therefore women's ability to influence the behavior of men. Møller et al. (1995) found that breast asymmetry was negatively related to fertility in samples of women from Spain and the United States; women with large breast asymmetries had fewer children, on average, than other women. Manning, Scutt, Whitehouse, and Leinster (1997) found the same pattern for women in England.

Although the results are not conclusive, it appears that women are not only more symmetric during the time of ovulation but that they may also produce olfactory cues that signal ovulation (Singh & Bronstad, 2001; but see Thornhill & Gangestad, 1999). In the better controlled of these studies, Singh and Bronstad asked women to wear t-shirts during the time of ovulation and during a nonovulatory phase of their menstrual cycles. Men then rated the t-shirt odors in terms of pleasantness, sexiness, and intensity. Shirts worn during the ovulatory phase were rated as more pleasant and sexy than shirts worn by the same women during the nonovulatory phase. There were, in contrast, no phase differences for rated intensity. Men may thus be sensitive to cycle-related fertility cues.

Cultural and Historical Variation in Mate Choices

It should be clear that there is not one reproductive strategy for women and another for men, as the strategies adopted by both sexes often vary across contexts, historical periods, and characteristics of the individual. Regarding the latter, people with traits that are desired by the opposite sex, such as cultural success or physical attractiveness, are in higher demand than are other members of their sex and thus exert more influence in their intersexual relationships (Pratto & Hegarty, 2000; Perusse, 1993). Important wider social and ecological influences on mate choices and reproductive dynamics include the OSR, cultural mores, and resource availability (Flinn & Low, 1986; Guttentag & Secord, 1983; McGraw, 2002; Pedersen, 1991), as we briefly overview in the following sections.

Operational Sex Ratio

The OSR or operation sex ratio is the ratio of marriage-age men to marriage-age women in the local population, and imbalances in the ratio influence the reproductive strategies adopted by both sexes. In industrial societies, growth rate can skew the OSR such that expanding populations yield an "oversupply" of women. The oversupply results

from the preference of women for older marriage partners and of men for younger marriage partners. With an expanding population, the younger generation of women will be selecting marriage partners from a smaller cohort of older men. The resulting imbalance in the OSR can have a profound influence on a number of general social patterns, including divorce rates, sexual mores, and levels of paternal investment, among others (Guttentag & Secord, 1983; Pedersen, 1991). "Sex ratios by themselves do not bring about societal effects, but rather that they combine with a variety of other social, economic, and political conditions to produce the consequent effects on the roles of men and women and the relationships between them" (Guttentag & Secord, 1983, p. 137).

In the United States, the most recent substantive imbalance in the OSR occurred from 1965 through the 1970s. During this time, there were more women than men looking for marriage partners, which enabled men to better pursue their reproductive preferences. In comparison to other historical periods, these skewed OSRs are characterized by liberal sexual mores (i.e., many short-term mates for both sexes); high divorce rates; increases in the number of out-of-wedlock births and the number of families headed by single women; an increase in women's participation in the workforce; and lower levels of paternal investment (Guttentag & Secord, 1983). During these periods, men are better able to express their preference for a variety of sexual partners and relatively low levels of paternal investment (Pedersen, 1991). A very different pattern emerges when there is an oversupply of men (Guttentag & Secord, 1983). Here, women are better able to enforce their preferences than are men. As a result, these periods are characterized by an increase in the level of commitment of men to marriage, as indexed by declining divorce rates and greater levels of paternal investment (Pedersen, 1991).

Cultural Mores and Resource Availability

Wider social mores also influence the dynamics of sexual selection. One of the most important of these mores is the prohibition against polygynous marriages (Alexander, 1979; MacDonald, 1995; White & Burton, 1988). In societies in which polygyny is not constrained, culturally successful men (about 10-15% of men) will typically marry several women (Murdock, 1981). One crucial consequence is an increase in the reproductive variability among men (but not women); that is, some men sire many children and many men sire no children. The result is an increase in male-on-male aggression and other changes in reproductive dynamics (Geary, 1998).

Western culture has a history of monogamous marriages, but polygynous matings by culturally successful men. These men typically have a single wife with whom heirs are sired as well as sexual access to many other women (Betzig, 1986, 1992, 1995). In Western Europe, cultural prohibitions emerged slowly during the Middle Ages such that the ability of dominant men to mate polygynously was gradually reduced (Betzig, 1995; MacDonald, 1995). The

result is a system of socially imposed monogamy (Flinn & Low, 1986) in which nearly all men have the potential to reproduce. One prediction is that culturally successful men will be especially selective when it comes to marriage partners, as they are constrained to invest their resources in a single woman and her children. The intensity of female-female competition to marry these men is predicted and appears to increase accordingly (Campbell, 2002; Geary, 1998).

These days, polygyny is achieved in Western culture through serial monogamy. Serial monogamy has important reproductive consequences for men but not women. In an extensive study of more than 900 Swedish women and men over the age of 40, Forsberg and Tullberg (1995) found that men but not women who engaged in serial monogamy had more children than their peers who stayed monogamously married.

The resources needed to raise a family and the availability of these resources in the local ecology also influence mate choice criteria. In ecologies where resources are scarce and it takes the efforts of both parents to keep children alive, the ability of a prospective mate to secure resources becomes crucial in the mate choice decisions of both men and women. In these contexts, polygyny is rare and monogamy and high levels of paternal investment are the norm (Flinn & Low, 1986). A similar pattern is evident even in wealthy societies. McGraw (2002) found that women's criteria for marriage partners varied with the cost of living in cities in the United States. In cities with a high cost of living, women placed a greater emphasis on the man's earning potential than did women living in other cities. In Spain, women with economic resources appear to place less emphasis on men's socioeconomic status than do women with fewer resources (Gil-Burmann, Peláez, & Sánchez, 2002).

SUMMARY AND CONCLUSION

The evidence we have presented supports the view that human mate preferences and choices are a product of our evolutionary history, and reflect many of the same mechanisms (i.e., sexual selection) that influenced the evolution and proximate expression of mate choices in other species (Darwin, 1871; Geary, 1998). The bottom line is that the preferred mate choices and attendant cognitions and behaviors of both sexes evolved to focus on and exploit the reproductive potential and reproductive investment of the opposite sex. Reproductive potential is the genetic or other resources (e.g., ability to have children) an individual can potentially invest in children, whereas reproductive investment is the actual use of these resources to promote the well-being of children. The combination defines the individual's mate value (Symons, 1979) and drives the dynamics of male-male and female-female competition for the best mates. For most people, competition creates a gap between preferred and actual mate choices and allows individuals with high reproductive potential to better achieve their preferences than other individuals.

Although the details of how success is achieved can vary from one setting to the next, culturally successful men have high reproductive potential and high reproductive success (Irons, 1979; Low, 2000). These are men who wield greater social influence than other members of the community and control the resources---money, land, cattle, and so forth---that women would prefer to have invested in themselves and their children. When men invest these material and social resources in parenting, children's mortality rates decline and their reproductive potential in adulthood is enhanced (Geary, 2000; Geary & Flinn, 2001). Women are thus predicted to prefer these men as monogamous marriage partners. This prediction is supported by social-psychological studies, "lonely heart" ads, and other measures (Buss, 1994; Oda, 2001; Whissell, 1996). In short, most women prefer monogamous marriages to wealthy, socially dominant, and physically attractive men, and want these men to be devoted to them and their children. For most women, this preference is not achieved. Some women attempt to achieve a compromise of sorts through relationships with several men. The implicit goal appears to be to get the best material investment from one man and the best genetic investment from another (Bellis & Baker, 1990; Gangestad et al., 2002).

In most mammalian species, males compete for access to mates and invest nothing in parenting. The best reproductive outcome is achieved by the males that sire the most offspring (Andersson, 1994; Clutton-Brock, 1989). Men's parental investment complicates reproductive dynamics. Specifically, men are predicted to show a more mixed reproductive strategy, preferring multiple casual sexual partners and a single (or serial) long-term partner. In the latter relationships, men are predicted to be and are similar to women in many of their mate choice criteria (Geary, 2000; Kenrick et al., 1990). The primary differences are that men are more focused on the physical traits of a long-term mate and less concerned about her cultural success or her potential for cultural success (Buss, 1989; Li et al., 2000). In theory, men should have evolved to focus on those physical attributes of women that are predictive of their reproductive potential, specifically their ability to conceive, carry, and birth healthy children. These traits include age, body mass index, waist-to-hip ratio, and breast symmetry, among others (Andersen et al., 2000; Singh, 1993a; Møller et al., 1995; Zaadstra et al., 1993). As predicted, men do indeed focus on these traits when judging the attractiveness of women as potential short-term and long-term mates (Kenrick & Keefe, 1992).

Although there is still much to be learned, it has become clear that the evolutionary perspective adds to our understanding of human mate choices and other reproductive and sexual behaviors. It is important to understand that this perspective does not mean there is a single strategy for women and another for men. Rather, how men and women use their reproductive potential is predicted to vary with resource availability, social dynamics (e.g., the OSR), cultural mores, and characteristics of the individual (Flinn &

Low, 1986; Pratto & Hegarty, 2000). The goal should not be to debate the utility of evolutionary versus cultural and experiential influences on human sexuality, but rather to study how our evolutionary history interacts with current and developmental circumstances to produce observable mate choice patterns and other aspects of human sexual behavior.

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