

Sexual Selection and the Evolution of Human Sex Differences

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Abstract

Darwin's (1871) theory of sexual selection and the associated mechanisms of intrasexual competition (e.g., male-male competition) and intersexual choice (e.g., female choice of mates) have guided the scientific study of sex differences in hundreds of non-human species. These mechanisms and several recent advances in our understanding of the evolution and expression of sex differences in non-human species are described. The usefulness of this theory for approaching the study human sex differences is illustrated with discussion of patterns of women's mate preferences and choices and with discussion of men's one-on-one and coalitional competition. A comparison of these aspects of intersexual choice and intrasexual competition in humans and non-human species is provided, as is discussion of cultural variation in the expression of these behaviors.

Psychologists and other social scientists have been studying human sex differences for 100 years (Acher, 1910; Woolley, 1910, 1914), and in recent decades demonstrated that many of the differences that emerge in Western cultures are found in every other culture in which they have been studied (Best & Williams, 1993; La Freniere, Strayer & Gauthier, 1984; Maccoby, 1988, 1990, 1998; Whiting & Edwards, 1988). The origin of these sex differences, however, was and remains a matter of debate. When consistent sex differences were found in the early 20th century, the proposal was their origin rested with socialization and cultural influences (e.g., Woolley, 1910). In 1914, Woolley explicitly rejected the possibility that human sex differences might be related to evolutionary and biological factors, specifically, Darwin's (1871) sexual selection (described below). By the 1970s, there was acknowledgement that biological influences, especially sex hormones (e.g., testosterone) could influence the expression of some human sex differences, but most sex differences were still thought to be due to social and cultural influences (Maccoby & Jacklin, 1974).

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There was little, if any, consideration that human sex differences might be related to human evolutionary history until the 1980s, with the emergence of evolutionary psychology (Buss, 1989; Daly & Wilson, 1983, 1988; Symons, 1979). Even with the application of evolutionary principles in psychology and the demonstration that observed behavior and its development often result from an interaction between the genotype and experience (Caspi, McClay, Moffitt, Mill, Martin, Craig, *et al.*, 2002), the prevailing models of the origin of human sex differences continue to emphasize socialization and cultural influences (e.g., Wood & Eagly, 2002). With this article, I will outline the logic of Darwin's (1871) sexual selection and illustrate how these processes result in the evolution and proximate – here and now – expression of sex differences in nonhuman species. I then use these basic patterns as a means to illustrate how some human sex differences have evolved (see also Geary, 1998).

Sexual Selection in Nonhuman Species

Darwin and Wallace (Darwin, 1859; Darwin & 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 the 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). Although both intrasexual competition and intersexual choice can be found for both sexes, as is the case with humans, the most common mating dynamics across species involve male-male competition over access to mates and female choice of mating partners (Andersson, 1994). In the first section, I describe why this pattern is so common, and when variation from this pattern (i.e., male choice and female-female competition) is predicted to evolve. In the second and third respective sections, I provide a brief overview and a few examples of intersexual choice and intrasexual competition in nonhuman species. In the final section, I briefly discuss sex hormones as related to the evolution and proximate expression of sex differences.

Compete or Choose?

Darwin (1871) defined and described sexual selection, but was not able to determine why males tend to compete over mates and why females are choosy. Nearly 100 years later, Williams (1966) and Trivers (1972) put the pieces together and discovered that the tendency to compete or choose is tightly linked to parenting. The tendency to be choosy increases with increases in parental

investment, and the tendency to compete is associated with less and sometimes no parental investment, even among females of some species (i.e., little or no postnatal investment). In other words, any sex difference in the tendency to compete or choose largely, but not exclusively, turns on the degree to which females and males invest in parenting. Sex differences emerge when one sex invests more in parenting than the other sex. The sex that provides more than his or her share of parental investment then becomes an important reproductive resource for members of the opposite sex (Trivers, 1972). The 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 investment sex are thus in demand, and as a result can be choosy when it comes to mates.

Clutton-Brock and Vincent (1991) discovered that sex differences in the potential rate of reproduction create biases in the reproductive benefits of competing for mates or investing in parenting, and thus the underlying reason why males tend to compete for mates and females tend to invest in offspring. As described in the next sections, the potential rate of reproduction interacts with social conditions, in particular the operational sex ratio (OSR), to create the observable dynamics of competing and choosing.

Rate of Reproduction

Across species, the sex with the higher potential rate of reproduction tends to invest more in competing for mates than in parenting, and the sex with the lower rate of reproduction tends to invest more in parenting than in competing (Clutton-Brock & Vincent, 1991). The pattern emerges because members of the sex with the higher potential rate of reproduction can rejoin the mating pool more quickly than can members of the opposite sex and it is often in their reproductive best interest to do so (Parker & Simmons, 1996). Individuals of the lower-investing sex typically have more offspring if they compete for mates than if they parent, whereas members of the higher-investing sex show the opposite pattern, and benefit more from being choosy than do members of the lower-investing sex.

For mammals, internal gestation and obligatory postpartum female care, as with suckling, create a very large sex difference in the potential rate of reproduction (Clutton-Brock, 1991). These biological factors result in a strong female bias toward parental investment, and an important sex difference in the benefits of seeking additional mates (Trivers, 1972). Males can benefit from seeking and obtaining additional mates, whereas females cannot. Thus, the sex difference in reproductive rate, combined with offspring that can be effectively raised by the female, creates the potential for large female-male differences in the mix of parenting and competing, and this difference is found in 95 to 97% of mammalian species (Clutton-Brock, 1989). Basically, female care of offspring frees males to

compete for mates, and successful males have many offspring each breeding season and most other males never reproduce.

Operational Sex Ratio

The OSR is the ratio of sexually active males to sexually active females in a given breeding population at a given point in time, and is related to the rate of reproduction (Emlen & Oring, 1977). An actual sex ratio of 1:1 represents a population in which there are as many sexually mature females as males, but any sex difference in the rate of reproduction will skew the OSR. Because mammalian males have a faster potential rate of reproduction than mammalian females, there are typically many more sexually receptive males than sexually receptive females in most populations. The resulting bias in the OSR creates the conditions that lead to intense male-male competition over access to a limited number of sexually-receptive females. Male-male competition, in turn, creates the conditions in which female choosiness can evolve.

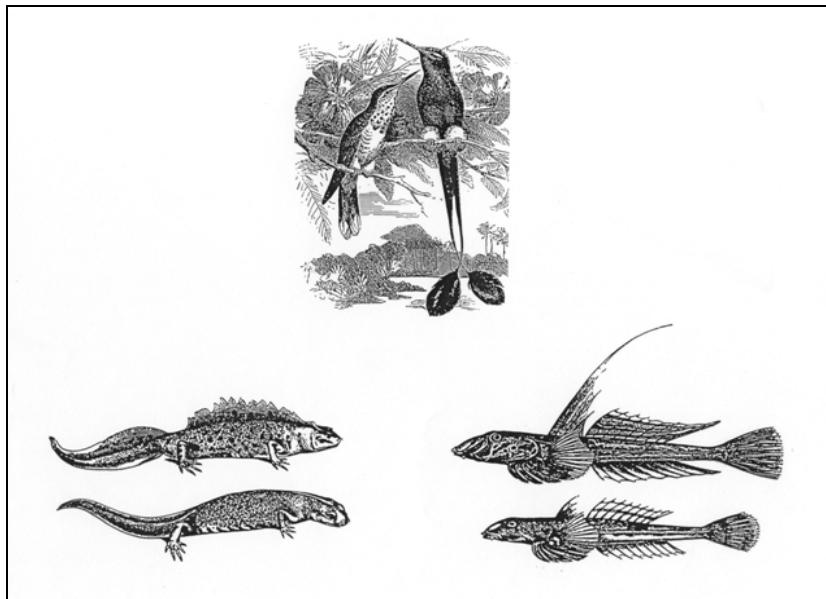
Although these patterns are most evident in mammals, they are also found in many species of bird, fish and reptile (Andersson, 1994), and are not limited to males. Critically, the predicted reversal of sex differences is found for species in which females have a faster rate of reproduction, as in species in which males incubate eggs. Females in these polyandrous species have the potential to reproduce in each breeding season with more than one mate and males mate monogamously. As predicted, females of these species are typically larger, more colorful, and more pugnacious than males and males tend to be choosy (Amundsen, 2000; Berglund, Rosenqvist & Bernet, 1997; Eens & Pinxten, 2000; Jones & Avise, 2001; Reynolds & Székely, 1997).

In addition to the biology of internal fertilization and gestation, other factors sometimes influence the OSR. In some situations, the sex with the higher potential rate of reproduction is better off by investing in parenting than in competing for mates. For instance, social monogamy and high levels of male parenting are common in canids (e.g., coyotes, *Canis latrans*), who tend to have large litters (Asa & Valdespino, 1998; Mock & Fujioka, 1990). Large litter sizes, prolonged offspring dependency, and the ability of the male to provide food during this dependency result in canid males being able to sire more offspring with a monogamous, high- parenting reproductive strategy than with a polygynous high-competition reproductive strategy. The result is a more balanced OSR. Generally, it appears that 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, 2005a).

Intersexual Choice

Because female investment in parenting makes them a valuable reproductive resource for males, female choice is more common than male choice (Andersson, 1994; Darwin, 1871; Trivers, 1972). For species in which males parent and species in which there are large individual differences in females' ability to successfully rear offspring, male choice is predicted to evolve, although this prediction has not been as thoroughly tested as female choice (Amundsen, 2000). In any case, female choice has been studied extensively in birds, and is also evident in many species of fish, insect reptile, and mammal (Andersson, 1994; Sargent, Rush, Wisenden & Yan, 1998). One evolutionary result of female choice is an exaggeration of the male traits on which females base their mate choices. Several examples are shown in Figure 1, where females choose mates, in part, based on traits such as the length and symmetry of the males' tail feathers, dorsal fin, or coloration.

Figure 1. Indicators of Male Fitness Shaped by Female Choice for Selected Species of Fish, Amphibian, and Bird



At the top are female (left) and male (right) humming birds (*Spathura underwoodi*) from *The descent of man, and selection in relation to sex*, Vol. II, by C. Darwin, 1871, London, John Murray, (p. 77); to the bottom right are the male (top) and female (bottom) *Callionymus lyra* from *The Descent of Man, and Selection in Relation to Sex* (Part II, p. 8), by C. Darwin, 1871, London: John Murray; to the bottom left are male (top) and female (bottom) *Triton palmipes* from *The Descent of Man, and Selection in Relation to Sex* (Part II, p. 24), by C. Darwin, 1871, London: John Murray.

In many species, traits such as those shown in Figure 1 are an indicator of the physical or genetic health of the male, or serve as an indicator his ability (e.g., vigor in searching for food) to provide parental investment (Andersson, 1994; Zahavi, 1975). Male birds with a colorful plumage or more complex songs are chosen as mating partners more often than their duller peers, because these traits provide females with information on males' immunocompetence and physical health (Hamilton & Zuk, 1982); immunocompetence has a heritable component and thus offspring sired by healthy males have lower mortality (Saino, Møller, & Bolzern, 1995), as do grand-offspring in at least one species (Reid, Arcese, Cassidy, Hiebert, Smith, & Stoddard *et al.*, 2005). These traits provide females with information on male health because testosterone can suppresses functioning of the immune system and thus males with a healthy immune system are better able to tolerate the high levels of testosterone needed to develop these elaborate traits (Folstad & Karter, 1992).

In short, it appears that male ornaments, such as the long tail features of the male hummingbird shown in Figure 1, are barometers that are strongly affected by the condition of the male, and female mate choice reflects the evolution of the female's ability to read these barometers. Females have evolved to be sensitive to these barometers and males to develop them if they can, because they advertise the reproductive benefits the female will accrue if she mates with the male. Although the research is less extensive and therefore less conclusive, there is 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 (Amundsen, 2000). Roulin and colleagues found male barn swallows (*Tyto alba*) preferred colorful females as mates and that the offspring of highly ornamented females showed greater resistance to infection than did offspring of other females, suggesting that at least in this species ornamentation is indeed an indicator of female quality (Roulin, 1999; Roulin, Jungi, Pfister, & Dijkstra, 2000).

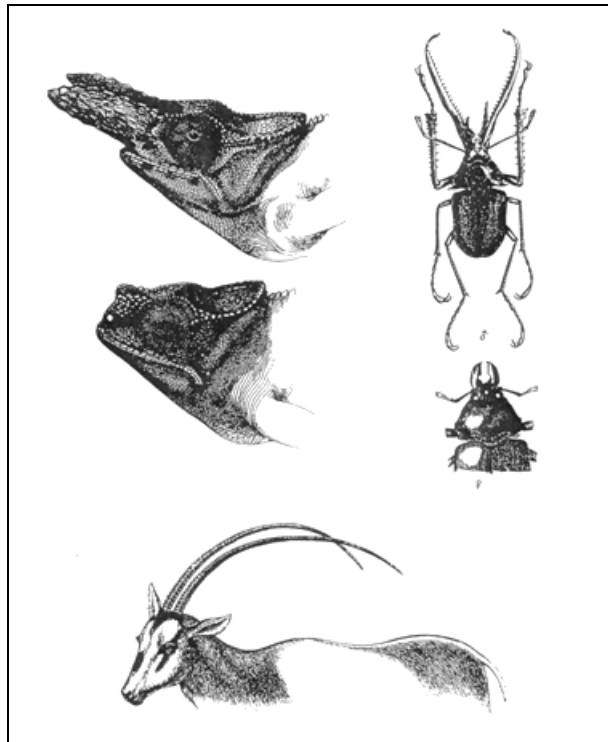
Intrasexual Competition

For males, one of the more common expressions of intrasexual competition involves physical threats and fights over access to females or for control of the territory or resources that females need to raise offspring (e.g., nesting spots). For most species, male-male competition is one-on-one but in some species also involves coalitions.

One-on-One Competition

Physical one-on-one male-male competition is common across species of insect, fish, reptile, and mammal and results in the evolution of sex differences in the physical traits that support this competition (Andersson, 1994). The typical result is that physically larger, healthier, and more aggressive males monopolize the reproductive potential of the majority of conspecific (same species) females. The accompanying individual differences in reproductive success – some individuals have many offspring, others few or none – result in the selection for and evolution of sex differences in physical size, armament and weaponry, as well as aggressiveness (Darwin, 1871). Several examples of such male traits are shown in Figure 2.

Figure 2. Sexually Selected Characteristics Used in Physical Male-Male Competition



To the upper left are the male (top) and female (bottom) of the *Chamaeleon bifurcus*; to the upper right are the male and female of the beetle *Chiasognathus grantii*; at the bottom is a male *Oryx leucoryx*, a species of antelope. From “The descent of man, and selection in relation to sex,” by C. Darwin, 1871, London, John Murray, p. 35, Vol. II; p. 377, Vol. I; and, p. 251, Vol. II, respectively.

The traits that facilitate intrasexual competition are not always physical. Sexual selection will operate on brain and cognitive traits in the same manner as physical traits, if the associated abilities and behavioral biases provide reproductive benefits. One well studied example involves comparison of related species of voles (*Microtus*; Gaulin, 1992). In the polygynous meadow vole (*Microtus pennsylvanicus*), males compete by searching for and attempting to mate with females dispersed throughout the habitat. The males of monogamous prairie (*Microtus ochrogaster*) and pine voles (*Microtus pinetorum*), in contrast, do not search for additional mates, once paired. For meadow voles, intrasexual competition favors males that court the most females, which is possible only through expansion of the home range. This form of male-male competition should result in larger home ranges for male than female meadow voles but no such sex difference for prairie or pine voles. Indeed, field studies indicate male meadow voles have home ranges that cover 4 to 5 times the area of females' home ranges, but only during the breeding season. As predicted, the home ranges of male and female prairie and pine voles do not differ in size. Variation in size of the home range leads to the prediction of better developed spatial abilities in male than female meadow voles, and no sex difference in monogamous prairie and pine voles. A series of laboratory and field studies confirmed these predictions (Gaulin & Fitzgerald, 1986).

Coalitional Competition

In some species, male-male competition involves of combination of competition between coalitions of males and one-on-one competition for dominance within each coalition (Wrangham, 1999). As an example, male lions (*Panthera leo*) form alliances with other males, and these "coalitions must compete successfully against other coalitions in order to gain and retain residence in prides. ... Larger coalitions oust smaller ones from prides and chase nomadic coalitions from their prides' ranges" (Packer, Herbst, Pusey, Bygott, Hanby, Cairns & Mulder, 1988, pp. 371-372). The bias to form competitive coalitions can be understood as evolving in lions, because individuals that form coalitions are more likely to gain access to prides than are lone individuals. The primary cost is that sexual access to females must be shared among coalitional males, with a corresponding decline in the number of offspring sired by each male. The reproductive cost of coalition formation is, however, reduced if coalition members are related, as two offspring sired by a brother is genetically equivalent to one offspring sired by the individual (Hamilton, 1964). This leads to a very specific prediction regarding the evolution of coalitional behavior in lions and in other species: Selection should favor individuals that tend to form coalitions with brothers or other kin, and this is indeed the case, at least for lions (see Packer, Gilbert, Pusey & O'Brien, 1991).

The chimpanzee (*Pan troglodytes*), one of our closest living relatives, provides a more complex example of coalitional behavior than that seen in the lion (Goodall, 1986; de Waal, 1982; Mitani & Watts, 2001; Watts & Mitani, 2001). Chimpanzee communities are defined by coalitions of related males that defend a territory. Situated within this territory are sub-groups of females and their offspring (Wrangham, 1986). Within these communities, small coalitions of males cooperate to achieve social dominance over other male coalitions (Mitani, Merriwether & Zhang, 2000). Successful coalitions gain some level of control over the social and sexual behavior of other community members, and as especially related to attempts to monopolize sexual access to estrous females (Goodall, 1986). The finding that coalitions are sometimes formed between distantly related males (Mitani *et al.*, 2000), suggests very strong reproductive benefits to coalitional behavior in male chimpanzees.

At other times, smaller coalitions combine and cooperate to patrol the community's border and to make incursions into the territory of neighboring communities (Goodall, Bandora, Bergmann, Busse, Matama, Mpongo, *et al.*, 1979; Watts & Mitani, 2001). "A patrol is typified by cautious, silent travel during which the members of the party tend to move in a compact group. There are many pauses as the chimpanzees gaze around and listen. Sometimes they climb tall trees and sit quietly for an hour or more, gazing out over the "unsafe" area of a neighboring community" (Goodall, 1986, p. 490). When members of such patrols encounter individuals from another community, the typical response is pant-hooting (a vocal call) and physical displays on both sides, with the smaller group eventually withdrawing (Wilson, Hauser & Wrangham, 2001). On some occasions, patrols from one group will ambush and kill individual males of neighboring communities. Goodall (1986) describes a series of such attacks by one community of chimpanzees on their southern neighbor. Over a four-year period, males of the southern group were eliminated, one individual at a time, by males of the northern community. The southern territory and many of the southern females were then incorporated into the territory and social group of the northern males.

For the male chimpanzee, the development and maintenance of coalitions is a complex social endeavor that requires a balance of cooperative and competitive motivational dispositions and behavioral strategies (de Waal, 2000). Coalitions need to be large enough to be competitive but not too large, given the reproductive cost of shared mating. Because competitiveness is determined by the coalitional behavior of other males, and because males will often shift alliances, there is no fixed optimal coalition size. Rather, the optimal size is constantly changing, depending on the dynamics of male relationships. To further complicate the issue, males form dominance hierarchies within their coalitions (Goodall, 1986). Dominant males have preferential mating access but also appear to organize the social behavior of other males, that is, these dominance hierarchies are not simply related to preferential mating, they may also facilitate the coordinated activities needed for successful coalitional competition.

Sex Hormones

The evolution and proximate expression of all of the above described sex differences and many others will be influenced by prenatal and postnatal exposure to sex hormones, especially androgens (male hormones; Arnold & Gorski, 1984; Morris, Jordan & Breedlove, 2004). Androgens typically influence sex differences in cognition and behavioral biases through early prenatal organization of associated brain areas, through activation of these areas with postnatal exposure to androgens, or some combination. The influences of sex hormones on brain, cognition, and behavior, however, are complex and sometimes very subtle, often interacting reciprocally with genetic sex, physical health, as well as social and ecological context (Arnold, Xu, Grisham, Chen, Kin, Itoh, *et al.*, 2004; McEwen, Biron, Brunson, Bulloch, Chambers, Dhabhar, *et al.*, 1997; Sapolsky, 1991). As noted below, these reciprocal relations are important for understanding how testosterone is related to male health, social context (e.g., mate choices), and how it relates to the evolution of sex differences, such as the colorful plumage of the males of many species of bird (Hamilton & Zuk, 1982).

For adult meadow voles, testosterone increases significantly during the breeding season and is associated with the increased activity levels associated with home range expansion (Perrot-Sinal, Innes, Kavaliers & Ossenkopp, 1998; Turner, Iverson & Sevenson, 1983); castration prevents these changes (Rowsemitt, 1986). For sexually-selected behaviors that require an extended period of learning to reach competitive levels of skill, pre- and postnatal testosterone may act to increase behavioral engagement in these behaviors during development but does not in and of itself result in adult-level competencies. As an example, bower birds compete and females choose based on the size and quality of the bower built by the male (Borgia, 1985); an example is shown in Figure 3. For satin bower birds (*Ptilonorhynchus violaceus*), skill at constructing and maintaining high quality bowers is related to age, social learning, social dominance, sex hormones, and the frequency of bower destruction by competitors (Collis & Borgia, 1992). During the roughly ten year maturational period, young males visit the bowers of mature males and imitate their displays and bower building. Borgia and Wingfield (1991) found that testosterone levels were strongly related to the quantity of bower decorations, for example number of sticks in the bower, but not to bower quality, such as symmetry. Male sex hormones thus appear to influence the energetic features of bower building (i.e., gathering materials) but experience, which comes from age and practice, influences the overall quality of the construction. Sex hormones are also related to which males are able to construct and maintain a bower and which are not; bower holding males have higher testosterone levels than males who do not hold bowers and tend to be socially dominant over other males.

Figure 3. Bower Building and Behavioral Male-Male Competition in the Bowerbird (*Chlamydera maculata*)



From *The Descent of Man, and Selection in Relation to Sex* (Part II, p. 70), by C. Darwin, 1871, London: John Murray.

Sexual Selection and Human Sex Differences

Given that sex differences are common across species and the evolution and proximate expression of these differences can be understood in terms of sexual selection and the action of sex hormones, respectively, it is only logical that these same mechanisms can be used to understand many human sex differences. As I noted in the introduction, there is nonetheless considerable resistance among social scientists to acknowledging these influences. Most generally and on the basis of cross-species patterns (Andersson, 1994; Plavcan & van Schaik, 1997), the some of the best evidence that sexual selection has operated during human evolution includes sex differences in physical size, upper-body musculature, rate and pattern of physical development, and hormonal and other physiological responses to stressors and competition (Tanner, 1990). These sex differences strongly support the proposal that physical male-male competition was important during human evolution.

Human reproductive dynamics, including male-male competition, are complicated by men's investment in their children (Geary, 2000). This investment results in female-female competition over investing males and male choice of long-

term mates, in addition to male-male competition and female choice. Moreover, the combination of within-sex differences in reproductive strategy (e.g., level of paternal investment; Gangestad & Simpson, 2000) and hormonal and experiential mechanisms that result in continuous rather than categorical differences in these strategies lead to a prediction of between-sex overlap in the traits that have been shaped by sexual selection. A full discussion of these many differences is beyond the scope of this article, but I illustrate the usefulness of sexual selection for approaching the study of human sex differences through discussion of some aspects of female choice and male-male competition.

Female Choice

At the most basic level, female choice in all species is based on the reproductive benefits they will receive from males. These benefits may be genetic, assistance with provisioning, social support, direct parenting, or some combination. Women are predicted to show the same basic pattern, which for humans is predicted to emerge as a preference to marry men in good physical health, who control culturally-important resources, have social influence, and are willing to invest these in the women and their children. This combination of male traits would result in healthy children, and an increase in women's access to culturally-important resources and enhanced social influence. I describe women's preference for culturally successful men in the first section. In the second and third respective sections, I describe the behavioral and physical traits that women prefer in prospective partners.

Culturally Successful Men

The social status of men is predicted to be an important consideration in women's choices of and preferences for marriage partners, because these men have the resources that women can use for their own benefit and to successfully raise their children (Buss, 1994). Although indicators of social status can vary across cultures (Irons, 1979), the basic relation is the same – culturally successful men are preferred as mating and marriage partners. The reason for this is clear: In all of cultures in which it has been studied, the children of culturally successful men have lower mortality rates than the children of other men (see Geary, 2000, 2005a). 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, Boyce, Chesney, Cohen, Folkman, Kahn & Syme, 1994). These are exactly the conditions that would result in the evolution of women's preference for socially dominant and culturally successful marriage partners. Preferred and actual mate choices are not always the same, however, because of competition from

other women, men's mate choices, and trade-offs involved when a potential mate has one preferred trait (e.g., attractive) but not another (e.g., resources).

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, 1988). The marriage patterns of the Kipsigis, a pastoral group in Kenya, provide an example (Borgerhoff Mulder, 1988, 1990, 2000). 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 were 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 partner 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 across-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 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 marriage (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 their husbands' reproductive interests.

Preferred Choices

As noted, 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 preferences. Social psychological studies of explicit preferences for marriage partners are thus an important addition to research on actual marriage choices. These preferences appear to more clearly capture the processes associated with evolved social and psychological mechanisms that influence reproductive behaviors (Buss, 1996; Geary, 1998; Kenrick, Sadalla, Groth & Trost, 1990). Research conducted throughout the world indicates that women prefer culturally successful marriage partners or partners who 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). In all cultures, women rated "good financial prospect" higher than did men. 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 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 mates' potential for success, earnings, status, and social position more highly than did men. A meta-analysis of research published from 1965 to 1986 confirmed this pattern (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 60s (Buunk, Dijkstra, Fetchenhauer & Kenrick,

2002). This preference is highlighted when women make cost-benefit trade-offs between a marriage partner's cultural success versus 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 three 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. Whissell (1996) found the same themes across 25 Western contemporary romance novels and six classic novels that have traditionally appealed to women more than men, including two stories 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.

Bereczkei's and Csanaky's (1996) study of more than 1,800 Hungarian men and women who were 35 years of age or older found that women who had married older and better educated men had, on average, 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 partners is not enough, in and of itself, to constitute the a successful reproductive strategy for women. Culturally successful men are often arrogant, self-serving, and are better able to pursue their preference for multiple mates than are other men (Betzig, 1986; Pérusse, 1993; Pratto, 1996). As a result, the personal and behavioral characteristics of men are an important consideration in women's choice of a marriage partner. These characteristics provide information on the ability and the 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.

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 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)

Many women also 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 culture than in many other cultures (Hewlett, 1992). It is not that the development of a 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 husband. Even in Western cultures, the pattern of women's mate choices is influenced by local circumstances and opportunity (Argyle, 1994). In economically depressed areas, where very few men are culturally successful, some women favor personnel attributes of a long-term mate, such as commitment and kindness, over his wealth, whereas other women seem to adapt a multiple mates strategy (Vigil, Geary & Byrd-Craven, 2006). These latter women want commitment from their long-term partner, but also indicate that they would choose short-term partners for monetary gain or based on his physical attractiveness (see below).

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). A preference for an attractive mate may make 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, these men and their children may be physically healthier than other men (Gangestad, Thornhill & Yeo, 1994; Grammer & Thornhill, 1994; Singh, 1995; Thornhill & Gangestad, 1993, 1994), although the relation between attractiveness and health in men is not always straightforward, especially in Western contexts where most individuals are generally healthy (see Geary, 2005b; Grammer, Fink, Møller & Manning, 2005; Weeden & Sabini, 2005). Nonetheless, the physical attributes that women find attractive in men may be 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 wider than their hips (Barber, 1995; Beck, Ward-Hull & McClear, 1976; Cunningham, Barbee & Pike, 1990; 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; Scheib, Gangestad & Thornhill, 1999; Cunningham *et al.*, 1990). These physical traits appear to be good indicators of genetic variability (which can be important for disease resistance), a lack of illness during development, and current physical health (Barber, 1995; Thornhill & Gangestad, 1993). 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, Philips, Handelsman, Eriksson, Forsén, Osmond and Barker (2001) as well as 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, that is, 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; it is how these genes match up with those of the woman. 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, 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 five-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, Weitkamp, Cox, Dytch, Kostyu & Elias, 1997).

The evidence supports the view that women's mate and marriage choices are influenced by indicators of the physical, and perhaps, the 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 their peers, especially if the rating was negative. Other studies suggest that women's ratings of the physical attractiveness of men are also influenced by his perceived social dominance (e.g., Townsend, Kline & Wasserman, 1995), and by the age of the women's father when she was a child (Perrett, Penton-Voak, Little, Tiddeman, Burt, Schmidt *et al.*, 2002).

Male-Male Competition

As I described earlier, male-on-male physical competition for social dominance thus access to mates or control of the resources females need to reproduce is common across species (Andersson, 1994; Darwin, 1871). A typical result is the evolution of larger males than females and the evolution of associated behavioral sex differences, as in aggressiveness. The consideration of male-male competition during human evolution is complicated by male parenting (which provides males with different ways to attract a mate), coalitional competition, and cultural influences on the expression of this competition (Geary, 1998). A complete overview of associated predictions and empirical findings is beyond the scope of this article. Rather, in the following sections I provide illustrations of the usefulness of sexual selection and male-male competition for understanding physical sex differences, forms of competition, and cultural variation in the expression of many of these differences.

Physical Sex Differences

There are many human sex differences that are consistent with an evolutionary history of physical male-male competition (Geary, 1998). As noted earlier, among these traits are a male advantage in physical size, musculature, cardiovascular capacity, bone density, and a host of other physical and physiological sex differences (Tanner, 1990). There is, in fact, evidence of a male advantage in physical size and some sex differences in bone architecture for all species of hominid (i.e., bipedal ape), which must then include the ancestors of modern humans. As an illustration, studies of one of the more extensively evaluated hominid species, *Australopithecus afarensis*, suggest males were somewhere between 50% heavier (McHenry, 1991) and 100% heavier than females (Frayer & Wolpoff, 1985). Recent studies suggest the same sexual dimorphism in the predecessor of *A. afarensis*, that is, *A. anamensis* (Leakey, Feibel, McDougall & Walker, 1995; Leakey, Feibel, McDougall, Ward & Walker, 1998). The fossil record and currently found physical sex differences suggest at least a four million year evolutionary history of physical male-male competition in hominids.

A sex difference in physical size and an evolutionary history of male-male competition does not mean that females were not physically aggressive. Comparative studies of primate species indicate that female-on-female physical aggression is in fact just as common as male-on-male physical aggression (Silk, 1987, 1993). However, female aggression is typically over control of food or territory that contains food sources (e.g., fruit trees), whereas male aggression is typically over control of females or the territory females need to reproduce (Wrangham, 1980). In a review of sex differences in aggression, Smuts (1987) found that male-on-male aggression resulted in more severe wounds (e.g., open gashes) than female-on-female aggression in all 16 primate species for which information on intrasexual aggression was available for both sexes. If these patterns were also common in early hominids, then the sex difference in physical size simply means that male-male competition was more intense and resulted in greater individual differences in reproductive outcomes among males than among females. In short, the physical dimorphism does not imply that female hominids were not physically aggressive.

Reproductive Benefits of Competition

As with other species in which it is found, human male-on-male aggression is often related to the establishment and maintenance of social dominance, the acquisition of the resources needed to support reproduction (e.g., stealing cattle to pay bride-price), or the direct capture of women (Chagnon, 1979; Daly & Wilson, 1983; Trivers, 1972). This competition can be one-on-one, coalitional, or some combination. Often one-on-one competition is related to the establishment of

within-group dominance, and coalitional competition is often between groups. Whatever form it takes, the reproductive benefits for successful males can be considerable. It is these benefits that resulted in the evolution of the physical and behavioral traits that facilitate male-male competition and that maintain this competition in many societies.

One example of the reproductive benefits gained by men who are successful in male-male competition is provided by the Yanomamö. In this population, the single most reproductively successful man, Shinbone, had 43 children, as compared to 14 children for the single most successful woman. Shinbone's father "had 14 children, 143 grandchildren, 335 great grandchildren and ... 401 great-great grandchildren" (Chagnon, 1979, p. 380). At the same time, other Yanomamö men have had few or no children (see also Jaffe, Urribarri, Chacon, Diaz, Torres & Herzog, 1993). The Yanomamö are not unique among traditional societies.

In fact, one-on-one and coalitional male-on-male aggression is a common feature of hunter-gatherer, horticultural, pastoral, and agricultural societies. Ambushes, raids, and occasional larger-scale battles between male kin groups from neighboring villages or bands are common features of social life in about 90% of these societies (Ember, 1978; Keeley, 1996); many of the remaining societies are relatively isolated or politically subjugated to larger groups (Keeley, 1996). In more than ½ of these societies, intergroup conflict occurs more or less continuously, that is, at least once a year, and ultimately results in the death of about 30% of the group's young men, on average (Chagnon, 1988; Keeley, 1996; White & Burton, 1988). Across societies, motives for these conflicts include "blood revenge" (i.e., retaliation for the killing of a member of the kin group), economic gain (i.e., land, booty, and slaves), the capture of women, and personal prestige. The latter typically involves the accumulation of culturally-important trophies, such as the heads of competitors, that influence the man's reputation and social status within the community, which will, in turn, influences his desirability as a marriage partner, as described earlier.

The pattern of intergroup aggression cannot be attributed to interference from modern societies, as warfare is typically less frequent after contact with modern societies (Keeley, 1996). Nor can this pattern be considered a relatively recent phenomenon, as archaeological evidence suggests frequent intergroup aggression over at least the past 20 to 30 thousand years (see Keeley, 1996). Betzig as argued that in every one of the first six civilizations – ancient Mesopotamia, Egypt, Aztec (Mexico), Inca (Peru) and imperial India and China – "powerful men mate with hundreds of women, pass their power on to a son by one legitimate wife, and take the lives of men who get in their way" (Betzig, 1993, p. 37; see also Betzig, 1986). The same is true, although on a much smaller scale, in many regions of world today. In the Yanomamö, about 2 out of 5 men have participated in at least one murder and those who have killed have a higher social status than men who have not killed, along with two to three times as many wives and about three times as many children, on average (Chagnon,

1988). In the hunter-gatherer Ache (South America), about 1 out of 5 men have participated in at least one murder and these men have more surviving children than men who have not murdered (Hill & Hurtado, 1996).

Population Genetics

Population genetic studies are recent additions our understanding of human social dynamics and provide support for a pattern of coalitional male-male competition, at least during recent human evolutionary history. The basic finding is that one group of related males often reproductively displaces another group. One of the more extreme results was reported by Carvajal-Carmona and colleagues (Carvajal-Carmona, Soto, Pineda, Ortíz-Barrientos, Duque, Ospina-Duque *et al.*, 2000). Here, mtDNA- (inherited only from mother) and Y-chromosome (inherited only from father) patterns were assessed for a Columbian (South America) population that was established in the 16th-17th centuries. The results revealed that the maternal ancestry of this population was largely (> 90%) Amerindian (i.e., native South American), whereas the paternal ancestry was largely (94%) European. When combined with historical records, these genetic patterns paint a picture of male-male competition in which European men displaced Amerindian men to the reproductive benefit of the former and at a large cost to the latter.

Zerjal and colleagues analyzed the Y-chromosome genes of 2,123 men from regions throughout Asia (Zerjal, Xue, Bertorelle, Wells, Bao, Zhu *et al.*, 2003). They found that 8% of the men in this part of the world have a single common ancestor who emerged from Mongolia and lived about 1,000 years ago. The geographic distribution of these genes fit well with the historic boundaries of the empire of Genghis Khan (c. 1162-1227), who was known to have had hundreds of wives and many, many children. They estimated that Genghis Khan and his close male relatives are the direct ancestors of 16 million men in Asia, ranging from northeast China to Uzbekistan, and the ancestors of about 0.5% of the world's total population. Related studies have found similar though less extreme patterns in other South American and North American populations (Bortolini, Silva Junior, Castro de Guerra, Remonato, Mirandola, Hutz, Weimer, *et al.*, 1999; Merriwether, Huston, Iyengar, Hamman, Norris, Shetterly, *et al.*, 1997). A related analysis of Y-chromosome genes from 1,062 men from various parts of the world suggest a repeating pattern of one population of men replacing another population of men in Africa, Europe, and Asia (Underhill, Shen, Lin, Jin, Passarino, Yang *et al.*, 2000).

Philopatry

An important frame for understanding the social ecology of human evolution, and the evolution of male coalitional competition, is philopatry, or the tendency of members of one sex to stay in the birth group and members of the other sex to migrate to another group. Male-biased philopatry in chimpanzees, bonobos (*Pan paniscus*), and humans in traditional societies suggest that the modal social ecology during human evolution was male philopatry (Foley & Lee, 1989; Ghiglieri, 1987; Goodall, 1986). There is, of course, variability in migration patterns across chimpanzee, bonobo, and human communities, but the prototypical pattern is for females to migrate and males to stay in the birth group (Geary & Flinn, 2001; Pasternak, Ember & Ember, 1997; Seielstad, Minch & Cavalli-Sforza, 1998). In traditional settings, 67% of societies are patrilocal, that is, the woman migrates to the community of her husband, and 15% of societies are matrilineal, that is, the man migrates to the community of his wife (Pasternak *et al.*, 1997). Even when the man migrates, he typically lives near (often in the same village) his male kin and remains socially and politically engaged with these kin, whereas many women who migrate cannot easily maintain strong ties to her kin. This does not mean that women do not have an evolved motivational disposition to maintain ties with kin, they do (MacDonald, 1992). In fact, the motivation may be stronger in women than in men, because it may have occurred with little effort for men throughout human evolution, but only with considerable effort for women.

In any case, additional evidence for male-biased philopatry comes from genetic studies of human populations. Most of these studies reveal that men in most local communities are more closely related to one another than are women, but women have more kin ties to other communities in the region (e.g., Seielstad *et al.*, 1998; Wells, Yuldasheva, Ruzibakiev, Underhill, Evseeva, Blue-Smith, Jin *et al.*, 2001; Wilson, Weiss, Richards, Thomas, Bradman & Goldstein, 2001). The genetic and historical records also suggest that more distant migrations are typically male-biased (e.g., Hammer, Karafet, Redd, Jarjanazi, Santachiara-Benerecetti, Soodyall & Zegura, 2001; Semino, Passarino, Oefner, Lin, Arbuzova, Beckman *et al.*, 2000). In these situations, a coalition of men from the local community leaves, often temporarily, but not to marry women from another community. Rather, they are exploring in search of additional trade routes, or in search of other ways to gain additional material and reproductive resources.

Male biased philopatry is important for understanding the evolution male-male competition, because it provides a social ecology in which male kin-based groups can form. As with lion coalitions, coalitions among related men can be larger and more stable (i.e., less within group conflict) than other groups and this provides a context in which men can evolve a bias to form large competition-related coalitions.

Cultural Variation in Male-Male Competition

A contrast of the above patterns with patterns that emerge in Western industrial societies provides an illustration of cultural variation in the form of male-male competition and illustration of historical changes in this competition within a society. In relation to the pattern found in many traditional societies, the level of male-male physical violence is relatively low in industrial societies (Daly & Wilson, 1988; Ember, 1978; Keeley, 1996). When male-on-male aggression does escalate to homicide in industrial societies, the precipitating events are often centered on sexual jealousy or male status competition, as in traditional societies (Daly & Wilson, 1988). Nonetheless, in industrial societies with socially-imposed monogamy, that is, where polygynous marriage is illegal, male-male competition is most generally focused on the acquisition of social and material indicators of cultural success. Or stated otherwise, in modern society, middle- and upper-middle-class men typically compete to acquire those social and material resources (e.g., income) that influence female choice of mating and marriage partners.

Prior to wide-scale industrialization, it appears that the relation between cultural success and reproductive success was the same in modern nations as is currently found in traditional societies (Betzig, 1995). Based on extensive parish and government birth, marriage, and death records between 1760 and 1810, Klindworth and Voland (1995) were able to reconstruct the relation between social status and long-term reproductive outcomes for Krummhörn men in Germany. Tax records indicated large differences in the wealth (e.g., land, cattle ownership) held by different families. In comparison to other men, the wealthiest Krummhörn men sired more children, primarily because they married younger wives, and had more children survive to adulthood. In comparison to higher status men, lower status men were four times more likely to experience an extinction of their lineage, that is, reach a point where there were no surviving direct descendants.

However, in industrial nations today there is little or sometimes a negative relation between cultural success (i.e., income, occupation, education) and reproductive success (Kaplan, Lancaster, Bock & Johnson, 1995). Men with higher earnings and all the trappings of cultural success, such as a college education and a professional occupation, do not sire more children than their less successful peers. This pattern has led some investigators to argue that any evolved tendencies associated with male-male competition are no longer relevant in technologically advanced societies (Vining, 1986). Pérusse (1993, 1994), in contrast, argued that the combination of socially-imposed monogamy and contraception obscures the relation between cultural success and mating success in these societies. A study of the relation between socioeconomic status (SES) and the sexual behavior of more than 400 men from Québec supported this position (Pérusse, 1993, 1994). Here, cultural success was defined in terms of income, educational level, and occupational status and sexual behavior in terms of the number of reported sexual partners and the overall frequency of sex. The combination of the number of sexual

partners and frequency of sex was used to derive an estimate of the likelihood of paternity, in the absence of birth control. For unmarried men 30 years of age and older, SES was strongly and positively related to individual differences in the likelihood of paternity, explaining as much as 63% of the individual differences on this measure. This relationship was somewhat lower, but still positive, in younger unmarried men, as might be expected, given the length of time needed to acquire indicators of cultural success in modern societies (e.g., higher education).

Thus, men in industrial societies compete in terms of the indicators of success in these cultures, just as men in other societies compete in terms of the dimensions of cultural success in their societies (e.g., control of cattle or having murdered). Similarly, across societies, a man's cultural success influences his ability to attract and retain mates (Irons, 1993). It appears that in terms of male-male competition, the primary difference between industrial societies and other societies is that the combination of socially-imposed monogamy and birth control in the former eliminates the relation between cultural success and reproductive success in industrial societies (Townsend *et al.*, 1995). In addition, there are legal controls that suppress on male-male violence, which has greatly reduced male-on-male homicide and physical injury in these societies, although such violence still occurs to some degree (Daly & Wilson, 1988). When these legal controls are weakened or the central government is unable to contain conflict, men often revert to the patterns described in traditional societies. They often form competition related coalitions, often around male kinship, and often engage in deadly intergroup (e.g., based on ethnic background) conflict for control of economic and other resources, such as land (Horowitz, 2001).

DISCUSSION

Sexual selection is now a firmly established and well supported area of study within the wider field of evolutionary biology (Andersson, 1994). The associated mechanisms of intrasexual competition (male-male, female-female) and intersexual choice (female choice, male choice) and proximate hormonal and social (e.g., OSR) influences on how these behaviors are expressed have been studied in hundreds of non-human species. Thus, this theory and research provides a solid foundation for the theoretical and empirical study of human sex differences (Geary, 1998), despite continued resistance to this approach from many social and behavioral scientists (Wood & Eagly, 2002). I have used this approach to study many aspects of human sex differences, and have illustrated its usefulness in this article with consideration of women's mate choices and the dynamics of men's intrasexual competition.

As with other species, women's mate preferences and their actual choices are focused on the resources a prospective mate has to offer to them and their children (Buss, 1994). The resources can vary from one context to another, but typically involve some combination of social influence, control of culturally-important

physical (e.g., land) and biological (e.g., food) resources, and sometimes indicators of physical and genetic health as reflected in the man's physical attractiveness (Irons, 1979; Gangestad & Buss, 1993). Men who possess these resources and attributes are culturally successful and marriage to these men provides women the resources they can use to improve the health and later social influence of their children (Geary & Flinn, 2001). Male-male competition in humans is also similar to that found in other species, although in humans, as in a few other species (e.g., chimpanzee), this involves coalitional competition as well as the more common one-on-one competition. In traditional societies, groups of related men cooperate in order to compete with other men for control of resource-rich ecologies and control of other important resources (Chagnon, 1988, 1997; Geary & Flinn, 2001). Within these groups, men compete for dominance and political influence. Dominant men of successful coalitions have more wives and children than do other men, as predicted by the theory of sexual selection (Betzig, 1986). Laws, cultural mores, and other factors can influence the details of how this competition is expressed, but the underlying motives and behavioral biases remain the same (e.g., Geary, Byrd-Craven, Hoard, Vigil & Numtee, 2003).

There is no real mystery to these findings, as they all follow logically from the predictions of the theory of sexual selection and from the patterns found in many other species (Andersson, 1994; Darwin, 1871). This does not mean that cultural and social influences are not important, they clearly are, as I illustrated with the cross-cultural and historical variation in the form of male-male competition. We will better understand cultural and social influences on the expression of human sex differences, once we acknowledge and come to better understand how biases that have evolved through sexual selection interact with experiences during development and in adulthood to influence the ways in which sex differences are expressed.

REFERENCES

- Acher, R.A. (1910). Spontaneous constructions and primitive activities of children analogous to those of primitive man. *American Journal of Psychology*, 21, 114-150.
- Adler, N.E., Boyce, T., Chesney, M.A., Cohen, S., Folkman, S., Kahn, R.L., & Syme, S.L. (1994). Socioeconomic status and health: The challenge of the gradient. *American Psychologist*, 49, 15-24.
- Amundsen, T. (2000). Why are female birds ornamented? *Trends in Ecology and Evolution*, 15, 149-155.
- Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.
- Arnold, A.P., & Gorski, R.A. (1984). Gonadal steroid induction of structural sex differences in the central nervous system. *Annual Review of Neuroscience*, 7, 413-442.

- Arnold, A.P., Xu, J., Grisham, W., Chen, X., Kin, Y.-H., & Itoh, Y. (2004). Sex chromosomes and brain sexual differentiation. *Endocrinology*, *145*, 1057-1062.
- Argyle, M. (1994). *The psychology of social class*. New York: Routledge.
- Asa, C.S., & Valdespino, C. (1998). Canid reproductive biology: An integration of proximate mechanisms and ultimate causes. *American Zoologist*, *38*, 251-259.
- Barber, N. (1995). The evolutionary psychology of physical attractiveness: Sexual selection and human morphology. *Ethology and Sociobiology*, *16*, 395-424.
- Beck, S.P., Ward-Hull, C.I., & McClearn, P.M. (1976). Variables related to women's somatic preferences of the male and female body. *Journal of Personality and Social Psychology*, *34*, 1200-1210.
- Berezkei, T., & Csanaky, A. (1996). Mate choice, marital success, and reproduction in a modern society. *Ethology and Sociobiology*, *17*, 17-35.
- Berglund, A., Rosenqvist, G., Bernet, P. (1997). Ornamentation predicts reproductive success in female pipefish. *Behavioral Ecology and Sociobiology*, *40*, 145-150.
- Best, D.L., & Williams, J.E. (1993). A cross-cultural viewpoint. In A.E. Beall & R.J. Sternberg (Eds.), *The psychology of gender* (pp. 215-248). New York: Guilford Press.
- Betzig, L.L. (1986). *Despotism and differential reproduction: A Darwinian view of history*. New York: Aldine Publishing Company.
- Betzig, L. (1989). Causes of conjugal dissolution: A cross-cultural study. *Current Anthropology*, *30*, 654-676.
- Betzig, L. (1993). Sex, succession, and stratification in the first six civilizations: How powerful men reproduced, passed power on to their sons, and used power to defend their wealth, women, and children. In L. Ellis (Ed.), *Social stratification and socioeconomic inequality, Volume 1: A comparative biosocial analysis* (pp. 37-74). Westport, CT: Praeger.
- Betzig, L. (1995). Medieval monogamy. *Journal of Family History*, *20*, 181-216.
- Borgerhoff Mulder, M. (1990). Kipsigis women's preferences for wealthy men: Evidence for female choice in mammals? *Behavioral Ecology and Sociobiology*, *27*, 255-264.
- Borgerhoff Mulder, M. (2000). Optimizing offspring: The quantity-quality tradeoff in agropastoral Kipsigis. *Evolution and Human Behavior*, *21*, 391-410.
- Borgia, G. (1985). Bower destruction and sexual competition in the satin bower bird (*Ptilonorhynchus violaceus*). *Behavioral Ecology and Sociobiology*, *18*, 91-100.
- Borgia, G., & Wingfield, J.C. (1991). Hormonal correlates of bower decoration and sexual display in the satin bowerbird (*Ptilonorhynchus violaceus*). *Condor*, *93*, 935-942.
- Bortolini, M.C., Silva Junior, W.A.D., Castro de Guerra, D., Remonato, G., Mirandola, R., Hutz, M.H., Weimer, T.A., Silva, M.C.B.O., Zago, M.A., & Salzano, F.M. (1999). African-derived South American populations: A history of symmetrical and asymmetrical matings according to sex revealed by bi- and uni-parental genetic markers. *American Journal of Human Biology*, *11*, 551-563.

- Buckle, L., Gallup, G.G., Jr., & Rodd, Z.A. (1996). Marriage as a reproductive contract: Patterns of marriage, divorce, and remarriage. *Ethology and Sociobiology*, 17, 363-377.
- Buunk, B.P., Dijkstra, P., Fetchenhauer, D., & Kenrick, D.T. (2002). Age and gender differences in mate selection criteria for various involvement levels. *Personal Relationships*, 9, 271-278.
- Buss, D.M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral & Brain Sciences*, 12, 1-49.
- Buss, D.M. (1994). *The evolution of desire: Strategies of human mating*. New York: Basic Books.
- Buss, D.M. (1996). The evolutionary psychology of human social strategies. In E.T. Higgins & A.E. Kruglanski (Eds.), *Social psychology: Handbook of basic principles* (pp. 3-38). New York: The Guilford Press.
- Campbell, A. (2002). *A mind of her own: The evolutionary psychology of women*. New York: Oxford University Press.
- Carvajal-Carmona, L.G., Soto, I.D., Pineda, N., Ortíz-Barrientos, D., Duque, C., Ospina-Duque, J., McCarthy, M., Montoya, P., Alvarez, V.M., Bedoya, G., & Ruiz-Linares, A. (2000). Strong Amerind/White sex bias and a possible Sephardic contribution among the founders of a population in northwest Columbia. *American Journal of Human Genetics*, 67, 1287-1295.
- Caspi, A., McClay, J., Moffitt, T. E., Mill, J., Martin, J., Craig, I. W., Taylor, A. & Poulton, R. (2002). Role of genotype in the cycle of violence in maltreated children. *Science*, 297, 851-854.
- Chagnon, N.A. (1979). Is reproductive success equal in egalitarian societies? In N.A. Chagnon & W. Irons (Eds.), *Evolutionary biology and human social behavior: An anthropological perspective* (pp. 374-401). North Scituate, MA: Duxbury Press.
- Chagnon, N.A. (1988). Life histories, blood revenge, and warfare in a tribal population. *Science*, 239, 985-992.
- Chagnon, N.A. (1997). *Yanomamö (fifth edition)*. Fort Worth, TX: Harcourt.
- Clutton-Brock, T.H. (1989). Mammalian mating systems. *Proceedings of the Royal Society of London B*, 236, 339-372.
- Clutton-Brock, T.H. (1991). *The evolution of parental care*. Princeton, NJ: Princeton University Press.
- Clutton-Brock, T.H., & Vincent, A.C.J. (1991). Sexual selection and the potential reproductive rates of males and females. *Nature*, 351, 58-60.
- Collis, K., & Borgia, G. (1992). Age-related effects of testosterone, plumage, and experience on aggression and social dominance in juvenile male satin bowerbirds (*Ptilonorhynchus violaceus*). *Auk*, 109, 422-434.
- Cunningham, M.R., Barbee, A.P., & Pike, C.L. (1990). What do women want? Facialmetric assessment of multiple motives in the perception of male facial physical attractiveness. *Journal of Personality and Social Psychology*, 59, 61-72.

- Daly, M., & Wilson, M. (1983). *Sex, evolution and behavior* (2nd. ed.). Boston, MA: Willard Grant.
- Daly, M., & Wilson, M. (1988). *Homicide*. New York: Aldine de Gruyter.
- Darwin, C. (1859). *The origin of species by means of natural selection*. London: John Murray.
- Darwin, C. (1871). *The descent of man, and selection in relation to sex*. London: John Murray.
- Darwin, C., & Wallace, A. (1858). On the tendency of species to form varieties, and on the perpetuation of varieties and species by natural means of selection. *Journal of the Linnean Society of London, Zoology*, 3, 45-62.
- de Waal, F.B.M. (1982). *Chimpanzee politics: Power and sex among apes*. New York: Harper & Row.
- de Waal, F.B.M. (2000). Primates: A natural heritage of conflict resolution. *Science*, 289, 586-590.
- Eens, M., & Pinxten, R. (2000). Sex-role reversal in vertebrates: Behavioural and endocrinological accounts. *Behavioural Processes*, 51, 135-147.
- Ember, C.R. (1978). Myths about hunter-gatherers. *Ethnology*, 17, 439-448.
- Emlen, S.T., & Oring, L.W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, 197, 215-223.
- Feingold, A. (1992). Gender differences in mate selection preferences: A test of the parental investment model. *Psychological Bulletin*, 112, 125-139.
- Fink, B., & Penton-Voak, I. (2002). Evolutionary psychology of facial attractiveness. *Current Directions in Psychological Sciences*, 11, 154-158.
- Flinn, M.V. (1988). Parent-offspring interactions in a Caribbean village: Daughter guarding. In L. Betzig, M. Borgerhoff Mulder, & P. Turke (Eds.), *Human reproductive behaviour: A Darwinian perspective* (pp. 189-200). Cambridge, England: Cambridge University Press.
- Foley, R.A., & Lee, P.C. (1989). Finite social space, evolutionary pathways, and reconstructing hominid behavior. *Science*, 243, 901-906.
- Folstad, I., & Karter, A.J. (1992). Parasites, bright males, and the immunocompetence handicap. *American Naturalist*, 139, 603-622.
- Frayser, D.W., & Wolpoff, M.H. (1985). Sexual dimorphism. *Annual Review of Anthropology*, 14, 429-473.
- Furlow, F.B., Armijo-Prewitt, T., Gangestad, S.W., & Thornhill, R. (1997). Fluctuating asymmetry and psychometric intelligence. *Proceedings of the Royal Society of London B*, 264, 823-829.
- Gangestad, S.W. (1993). Sexual selection and physical attractiveness. *Human Nature*, 4, 205-235.

- Gangestad, S.W., & Buss, D.M. (1993). Pathogen prevalence and human mate preferences. *Ethology and Sociobiology*, *14*, 89-96.
- Gangestad, S.W., & Simpson, J.A. (2000). The evolution of human mating: Trade-offs and strategic pluralism. *Behavioral and Brain Sciences*, *23*, 573-644.
- Gangestad, S.W., & Thornhill, R. (1997). The evolutionary psychology of extrapair sex: The role of fluctuating asymmetry. *Evolution and Human Behavior*, *18*, 69-88.
- Gangestad, S.W., & Thornhill, R. (1998). Menstrual cycle variation in women's preferences for the scent of symmetrical men. *Proceedings of the Royal Society of London B*, *265*, 927-933.
- Gangestad, S.W., Thornhill, R., & Yeo, R.A. (1994). Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology*, *15*, 73-85.
- Gaulin, S.J.C. (1992). Evolution of sex differences in spatial ability. *Yearbook of Physical Anthropology*, *35*, 125-151.
- Gaulin, S.J.C., & Fitzgerald, R.W. (1986). Sex differences in spatial ability: An evolutionary hypothesis and test. *American Naturalist*, *127*, 74-88.
- Geary, D.C. (1998). *Male, female: The evolution of human sex differences*. Washington, DC: American Psychological Association.
- Geary, D.C. (2000). Evolution and proximate expression of human paternal investment. *Psychological Bulletin*, *126*, 55-77.
- Geary, D.C. (2005a). Evolution of paternal investment. In D.M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 483-505). Hoboken, NJ: John Wiley & Sons.
- Geary, D.C. (2005b). Evolution of life history trade-offs in mate attractiveness and health: Comment on Weeden and Sabini (2005). *Psychological Bulletin*, *131*, 654-657.
- Geary, D.C., Byrd-Craven, J., Hoard, M.K., Vigil, J., & Numtee, C. (2003). Evolution and development of boys' social behavior. *Developmental Review*, *23*, 444-470.
- Geary, D.C., & Flinn, M.V. (2001). Evolution of human parental behavior and the human family. *Parenting: Science and Practice*, *1*, 5-61.
- Ghiglieri, M.P. (1987). Sociobiology of the great apes and the hominid ancestor. *Journal of Human Evolution*, *16*, 319-357.
- Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA: The Belknap Press.
- Goodall, J., Bandora, A., Bergmann, E., Busse, C., Matama, H., Mpongo, E., Pierce, A. & Riss, D. (1979). Inter-community interactions in the chimpanzee population of the Gombe National Park. In D.A. Hamburg, & E.R. McCown (Eds.), *The great apes* (pp. 13-53). Menlo Park, CA: The Benjamin/Cummings Publishing Company.
- Grammer, K., Fink, B., Möller, A.P., & Manning, J.T. (2005). Physical attractiveness and health: Comment on Weeden and Sabini (2005). *Psychological Bulletin*, *131*, 658-661.

- Grammer, K., & Thornhill, R. (1994). Human (*Homo sapiens*) facial attractiveness and sexual selection: The role of symmetry and averageness. *Journal of Comparative Psychology*, *108*, 233-242.
- Graziano, W.G., Jensen-Campbell, L.A., Shebilske, L.J., & Lundgren, S.R. (1993). Social influence, sex differences, and judgments of beauty: Putting the interpersonal back in interpersonal attraction. *Journal of Personality and Social Psychology*, *65*, 522-531.
- Greenlees, I.A., & McGrew, W.C. (1994). Sex and age differences in preferences and tactics of mate attraction: Analysis of published advertisements. *Ethology and Sociobiology*, *15*, 59-72.
- Hames, R. (1992). Variation in paternal care among the Yanomamö. In B.S. Hewlett (Ed.), *Father-child relations: Cultural and biosocial contexts* (pp. 85-110). New York: Aldine de Gruyter.
- Hames, R. (1996). Costs and benefits of monogamy and polygyny for Yanomamö women. *Ethology and Sociobiology*, *17*, 181-199.
- Hamilton, W.D., Axelrod, R., & Tanese, R. (1990). Sexual reproduction as an adaptation to resist parasites (A review). *Proceedings of the National Academy of Sciences, USA*, *87*, 3566-3573.
- Hamilton, W.D., & Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites? *Science*, *218*, 384-387.
- Hammer, M.F., Karafet, T.M., Redd, A.J., Jarjanazi, H., Santachiara-Benerecetti, S., Soodyall, H., & Zegura, S.L. (2001). Hierarchical patterns of global human Y-chromosome diversity. *Molecular Biology and Evolution*, *18*, 1189-1203.
- Hatfield, E., & Sprecher, S. (1995). Men's and women's preferences in marital partners in the United States, Russia, and Japan. *Journal of Cross-Cultural Psychology*, *26*, 728-750.
- Hewlett, B.S. (1992). Husband-wife reciprocity and the father-infant relationship among Aka pygmies. In B.S. Hewlett (Ed.), *Father-child relations: Cultural and biosocial contexts* (pp. 153-176). New York: Aldine de Gruyter.
- Hill, K., & Hurtado, A.M. (1996). *Ache life history: The ecology and demography of a foraging people*. New York: Aldine de Gruyter.
- Hill, R. (1945). Campus values in mate selection. *Journal of Home Economics*, *37*, 554-558.
- Horowitz, D.L. (2001). *The deadly ethnic riot*. Berkeley, CA: University of California Press.
- Irons, W. (1979). Cultural and biological success. In N.A. Chagnon & W. Irons (Eds.), *Natural selection and social behavior* (pp. 257-272). North Scituate, MA: Duxbury Press.
- Irons, W. (1983). Human female reproductive strategies. In S. Wasser & M. Waterhouse (Eds.), *Social behavior of female vertebrates* (pp. 169-213). New York: Academic Press.
- Irons, W. (1993). Monogamy, contraception and the cultural and reproductive success hypothesis. *Behavioral and Brain Sciences*, *16*, 295-296.

- Jaffe, K., Urribarri, D., Chacon, G.C., Diaz, G., Torres, A., & Herzog, G. (1993). Sex-linked strategies of human reproductive behavior. *Social Biology*, 40, 61-73.
- Jones, A.G., & Avise, J.C. (2001). Mating systems and sexual selection in male-pregnant pipefishes and seahorses: Insights from microsatellite-based studies of maternity. *Journal of Heredity*, 92, 150-158.
- Kaplan, H.S., Lancaster, J.B., Bock, J.A., & Johnson, S.E. (1995). Does observed fertility maximize fitness among New Mexican men? A test of an optimality model and a new theory of parental investment in the embodied capital of offspring. *Human Nature*, 6, 325-360.
- Keeley, L.H. (1996). *War before civilization: The myth of the peaceful savage*. New York: Oxford University Press.
- Kenrick, D.T., Keefe, R.C., Gabrielidis, C., & Cornelius, J.S. (1996). Adolescents' age preferences for dating partners: Support for an evolutionary model of life-history strategies. *Child Development*, 67, 1499-1511.
- Klindworth, H., & Voland, E. (1995). How did the Krummhörn elite males achieve above-average reproductive success? *Human Nature*, 6, 221-240.
- La Freniere, P., Strayer, F.F., & Gauthier, R. (1984). The emergence of same-sex affiliative preferences among preschool peers: A developmental/ethological perspective. *Child Development*, 55, 1958-1965.
- Leakey, M.G., Feibel, C.S., McDougall, I., & Walker, A. (1995). New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature*, 376, 565-571.
- Leakey, M.G., Feibel, C.S., McDougall, I., Ward, C., & Walker, A. (1998). New specimens and confirmation of an early age for *Australopithecus anamensis*. *Nature*, 393, 62-66.
- Li, N.P., Bailey, J.M., Kenrick, D.T., & Linsenmeier, J.A.W. (2002). The necessities and luxuries of mate preferences: Testing the tradeoffs. *Journal of Personality and Social Psychology*, 82, 947-955.
- Low, B.S. (2000). *Why sex matters: A Darwinian look at human behavior*. Princeton, NJ: Princeton University Press.
- Maccoby, E.E. (1988). Gender as a social category. *Developmental Psychology*, 24, 755-765.
- Maccoby, E.E. (1990). Gender and relationships: A developmental account. *American Psychologist*, 45, 513-520.
- Maccoby, E.E. (1998). *The two sexes: Growing up apart, coming together*. Cambridge, MA: Belknap Press.
- Maccoby, E.E., & Jacklin, C.N. (1974). *The psychology of sex differences*. Stanford, CA: Stanford University Press.
- MacDonald, K. (1992). Warmth as a developmental construct: An evolutionary analysis. *Child Development*, 63, 753-773.

- Manning, J.T., Koukourakis, K., & Brodie, D.A. (1997). Fluctuating asymmetry, metabolic rate and sexual selection in human males. *Evolution and Human Behavior*, 18, 15-21.
- McEwen, B.S., Biron, C.A., Brunson, K.W., Bulloch, K., Chambers, W.H., Dhabhar, F.S., Goldfarb, R.H., Kitson, R.P., Miller, A.H., Spencer, R.L. & Weiss, J.M. (1997). The role of adrenocorticoids as modulators of immune function in health and disease: Neural, endocrine and immune interactions. *Brain Research Reviews*, 23, 79-133.
- McHenry, H.M. (1991). Sexual dimorphism in *Australopithecus afarensis*. *Journal of Human Evolution*, 20, 21-32.
- Merriwether, D.A., Huston, S., Iyengar, S., Hamman, R., Norris, J.M., Shetterly, S.M., Kamboh, M.I., & Ferrell, R.E. (1997). Mitochondrial versus nuclear admixture estimates demonstrate a past history of directional mating. *American Journal of Physical Anthropology*, 102, 153-159.
- Mitani, J.C., Merriwether, D.A., & Zhang, C. (2000). Male affiliation, cooperation and kinship in wild chimpanzees. *Animal Behaviour*, 59, 885-893.
- Mitani, J.C., & Watts, D.P. (2001). Why do chimpanzees hunt and share meat? *Animal Behaviour*, 61, 915-924.
- Mock, D.W., & Fujioka, M. (1990). Monogamy and long-term pair bonding in vertebrates. *Trends in Ecology & Evolution*, 5, 39-43.
- Morris, J.A., Jordan, C.L., & Breedlove, S.M. (2004). Sexual differentiation of the vertebrate nervous system. *Nature Neuroscience*, 7, 1034-1039.
- Nettle, D. (2002). Height and reproductive success in a cohort of British men. *Human Nature*, 13, 473-491.
- Ober, C., Elias, S., Kostyu, D.D., & Hauck, W.W. (1992). Decreased fecundability in Hutterite couples sharing HLA-DR. *American Journal of Human Genetics*, 50, 6-14.
- Ober, C., Weitkamp, L.R., Cox, N., Dytch, H., Kostyu, D., & Elias, S. (1997). HLA and mate choice in humans. *American Journal of Human Genetics*, 61, 497-504.
- Oda, R. (2001). Sexual dimorphic mate preference in Japan: An analysis of lonely hearts advertisements. *Human Nature*, 12, 191-206.
- Packer, C., Gilbert, D.A., Pusey, A.E., & O'Brien, S.J. (1991). A molecular genetic analysis of kinship and cooperation in African lions. *Nature*, 351, 562-565.
- Packer, C., Herbst, L., Pusey, A.E., Bygott, J.D., Hanby, J.P., Cairns, S.J., & Mulder, M.B. (1988). Reproductive success of lions. In T.H. Clutton-Brock (Ed.), *Reproductive success: Studies of individual variation in contrasting breeding systems* (pp. 363-383). Chicago, IL: University of Chicago Press.
- Parker, G.A., & Simmons, L.W. (1996). Parental investment and the control of selection: Predicting the direction of sexual competition. *Proceedings of the Royal Society of London B*, 263, 315-321.
- Pasternak, B., Ember, C.R., & Ember, M. (1997). *Sex, gender, and kinship: A cross-cultural perspective*. Upper Saddle River, NJ: Prentice-Hall.

- Perrett, D.I., Penton-Voak, I.S., Little, A.C., Tiddeman, B.P., Burt, D.M., Schmidt, N., Oxley, R., Kinloch, N., & Barrett, L. (2002). Facial attractiveness judgements reflect learning of parental age characteristics. *Proceedings of the Royal Society of London B*, 269, 873-880.
- Perrot-Sinal, T.S., Innes, D., Kavaliers, M., & Ossenkopp, K.-P. (1998). Plasma testosterone levels are related to various aspects of locomotor activity in wild-caught male meadow voles (*Microtus pennsylvanicus*). *Physiology & Behavior*, 64, 31-36.
- Pérusse, D. (1993). Cultural and reproductive success in industrialized societies: Testing the relationship at the proximate and ultimate levels. *Behavioral and Brain Sciences*, 16, 267-322.
- Pérusse, D. (1994). Mate choice in modern societies: Testing evolutionary hypotheses with behavioral data. *Human Nature*, 5, 255-278.
- Phillips, D.I.W., Handelsman, D.J., Eriksson, J.G., Forsén, T., Osmond, C., & Barker, D.J.P. (2001). Prenatal growth and subsequent marital status: Longitudinal study. *British Medical Journal*, 322, 771.
- Pierce, C.A. (1996). Body height and romantic attraction: A meta-analytic test of the male-taller norm. *Social Behavior and Personality*, 24, 143-150.
- Plavcan, J.M., & van Schaik, C.P. (1997). Intrasexual competition and body weight dimorphism in anthropoid primates. *American Journal of Physical Anthropology*, 103, 37-68.
- Pratto, F. (1996). Sexual politics: The gender gap in the bedroom, the cupboard, and the cabinet. In D.M. Buss & N.M. Malamuth (Eds.), *Sex, power, conflict: Evolutionary and feminist perspectives* (pp. 179-230). New York: Oxford University Press.
- Reid, J.M., Arcese, P., Cassidy, A.L.E.V., Hiebert, S.M., Smith, J.N.M., Stoddard, P.K., Marr, A.B., & Keller, L.F. (2005). Fitness correlates of song repertoire in free-living song sparrows (*Melospiza melodia*). *American Naturalist*, 165, 299-310.
- Reynolds, J.D., & Székely, T. (1997). The evolution of parental care in shorebirds: Life histories, ecology, and sexual selection. *Behavioral Ecology*, 8, 126-134.
- Roulin, A. (1999). Nonrandom pairing by male barn owls (*Tyto alba*) with respect to a female plumage trait. *Behavioral Ecology*, 10, 688-695.
- Roulin, A., Jungi, T.W., Pfister, H., & Dijkstra, C. (2000). Female barn swallows (*Tyto alba*) advertise good genes. *Proceedings of the Royal Society of London B*, 267, 937-941.
- Rowsemitt, C.N. (1986). Seasonal variation in activity rhythms of male voles: Mediation by gonadal hormones. *Physiology & Behavior*, 37, 797-803.
- Saino, N., Møller, A.P., & Bolzern, A.M. (1995). Testosterone effects on the immune system and parasite infestations in the barn swallow (*Hirundo rustica*): An experimental test of the immunocompetence hypothesis. *Behavioral Ecology*, 6, 397-404.

- Sapolsky, R.M. (1991). Testicular function, social rank and personality among wild baboons. *Psychoneuroendocrinology*, *16*, 281-293.
- Sargent, R.C., Rush, V.N., Wisenden, B.D., & Yan, H.Y. (1998). Courtship and mate choice in fishes: Integrating behavioral and sensory ecology. *American Zoologist*, *38*, 82-96.
- Scheib, J.E., Gangestad, S.W., & Thornhill, R. (1999). Facial attractiveness, symmetry and cues of good genes. *Proceedings of the Royal Society of London B*, *266*, 1913-1917.
- Seielstad, M.T., Minch, E., & Cavalli-Sforza, L.L. (1998). Genetic evidence for a higher female migration rate in humans. *Nature Genetics*, *20*, 278-280.
- Semino, O., Passarino, G., Oefner, P.J., Lin, A.A., Arbuzova, S., Beckman, L.E., De Benedictis, G., Francalacci, P., Kouvatsi, A., Limborska, S., Marcikiae, M., Mika, A., Mika, B., Primorac, D., Santachiara-Benerecetti, A.S., Cavalli-Sforza, L.L., & Underhill, P.A. (2000). The genetic legacy of Paleolithic *Homo sapiens* in extant Europeans: A Y chromosome perspective. *Science*, *290*, 1155-1159.
- Silk, J.B. (1987). Social behavior in evolutionary perspective. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, & T.T. Struhsaker (Eds.), *Primate societies* (pp. 318-329). Chicago, IL: The University of Chicago Press.
- Silk, J.B. (1993). The evolution of social conflict among female primates. In W.A. Mason & S.P. Mendoza (Eds.), *Primate social conflict* (pp. 49-83). Albany, NY: State University of New York Press.
- Singh, D. (1995). Female judgment of male attractiveness and desirability for relationships: Role of waist-to-hip ratio and financial status. *Journal of Personality and Social Psychology*, *69*, 1089-1101.
- Shackelford, T.K., & Larsen, R.J. (1997). Facial asymmetry as an indicator of psychological, emotional, and physiological distress. *Journal of Personality and Social Psychology*, *72*, 456-466.
- Smuts, B.B. (1987). Sexual competition and mate choice. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, & T.T. Struhsaker (Eds.), *Primate societies* (pp. 385-399). Chicago, IL: The University of Chicago Press.
- Sprecher, S., Sullivan, Q., & Hatfield, E. (1994). Mate selection preferences: Gender differences examined in a national sample. *Journal of Personality and Social Psychology*, *66*, 1074-1080.
- Surbey, M.K., & Conohan, C.D. (2000). Willingness to engage in casual sex: The role of parental qualities and perceived risk of aggression. *Human Nature*, *11*, 367-386.
- Symons, D. (1979). *The evolution of human sexuality*. New York: Oxford University Press.
- Tanner, J.M. (1990). *Foetus into man: Physical growth from conception to maturity*. Cambridge, MA: Harvard University Press.
- Thornhill, R., & Gangestad, S.W. (1993). Human facial beauty: Averageness, symmetry, and parasite resistance. *Human Nature*, *4*, 237-269.
- Thornhill, R., & Gangestad, S.W. (1994). Human fluctuating asymmetry and sexual behavior. *Psychological Science*, *5*, 297-302.

- Thornhill, R., & Gangestad, S.W. (1999). The scent of symmetry: A human sex pheromone that signals fitness? *Evolution and Human Behavior*, 20, 175-201.
- Townsend, J.M., Kline, J., & Wasserman, T.H. (1995). Low-investment copulation: Sex differences in motivations and emotional reactions. *Ethology and Sociobiology*, 16, 25-51.
- Trivers, R.L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man 1871-1971* (pp. 136-179). Chicago, IL: Aldine Publishing.
- Turner, B.N., Iverson, S.L., & Severson, K.L. (1983). Seasonal changes in open-field behavior in wild male meadow voles (*Microtus pennsylvanicus*). *Behavioral and Neural Biology*, 39, 60-77.
- Underhill, P.A., Shen, P., Lin, A.A., Jin, L., Passarino, G., Yang, W.H., Kauffman, E., Bonn -Tamir, B., Bertranpetit, J., Francalacci, P., Ibrahim, M., Jenkins, T., Kidd, J.R., Mehdi, S.Q., Seielstad, M.T., Wells, R.S., Piazza, A., Davis, R.W., Feldman, M.W., Cavalli-Sforza, L.L., & Oefner, P.J. (2000). Y chromosome sequence variation and the history of human populations. *Nature Genetics*, 26, 358-361.
- Vigil, J.M., Geary, D.C., & Byrd-Craven, J. (2006). Trade-offs in low income women's preferences for long-term and short-term mates: Within-sex differences in reproductive strategy. *Human Nature*, 17.
- Vining, D.R., Jr. (1986). Social versus reproductive success: The central theoretical problem of human sociobiology. *Behavioral and Brain Sciences*, 9, 167-216.
- Watts, D.P., & Mitani, J.C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, 138, 299-327.
- Waynforth, D. (2001). Mate choice trade-offs and women's preference for physically attractive men. *Human Nature*, 12, 207-219.
- Wedekind, C., Seebeck, T., Bettens, F., & Paepke, A.J. (1995). MHC-dependent mate preferences in humans. *Proceedings of the Royal Society of London B*, 260, 245-249.
- Wells, R.S., Yuldasheva, N., Ruzibakiev, R., Underhill, P.A., Evseeva, I., Blue-Smith, J., Jin, L., Su, B., Pitchappan, R., Shanmugalakshmi, S., Balakrishnan, K., Read, M., Pearson, N.M., Zerjal, T., Webster, M.T., Zholoshvili, I., Jamarjashvili, E., Gambarov, S., Nikbin, B., Dostiev, A., Aknazarov, O., Zalloua, P., Tsoy, I., Kitaev, M., Mirrakhimov, M., Chariev, A., & Bodmer, W.F. (2001). The Eurasian heartland: A continental perspective on Y-chromosome diversity. *Proceedings of the National Academy of Sciences USA*, 98, 10244-10249.
- Whissell, C. (1996). Mate selection in popular women's fiction. *Human Nature*, 7, 427-447.
- White, D.R., & Burton, M.L. (1988). Causes of polygyny: Ecology, economy, kinship, and warfare. *American Anthropologist*, 90, 871-887.
- Whiting, B.B., & Edwards, C.P. (1988). *Children of different worlds: The formation of social behavior*. Cambridge, MA: Harvard University Press.

- Williams, G.C. (1966). *Adaptation and natural selection: A critique of some current evolutionary thought*. Princeton, NJ: Princeton University Press.
- Wilson, J.F., Weiss, D.A., Richards, M., Thomas, M.G., Bradman, N., & Goldstein, D.B. (2001). Genetic evidence for different male and female roles during cultural transitions in the British isles. *Proceedings of the National Academy of Sciences USA*, 98, 5078-5083.
- Wilson, M.L., Hauser, M.D., & Wrangham, R.W. (2001). Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? *Animal Behaviour*, 61, 1203-1216.
- Weeden, J., & Sabini, J. (2005). Physical attractiveness and health in Western societies: A review. *Psychological Bulletin*, 131, 635-653.
- Wood, W., & Eagly, A.H. (2002). A cross-cultural analysis of the behavior of women and men: Implications for the origins of sex differences. *Psychological Bulletin*, 128, 699-727.
- Woolley, H.T. (1910). A review of the recent literature on the psychology of sex. *Psychological Bulletin*, 7, 335-342.
- Woolley, H.T. (1914). The psychology of sex. *Psychological Bulletin*, 11, 353-379.
- Wrangham, R.W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, 75, 262-300.
- Wrangham, R.W. (1999). Evolution of coalitionary killing. *Yearbook of Physical Anthropology*, 42, 1-30.
- Zahavi, A. (1975). Mate selection: A selection for a handicap. *Journal of Theoretical Biology*, 53, 205-214.
- Zerjal, T., Xue, Y., Bertorelle, G., Wells, R.S., Bao, W., Zhu, S., Qamar, R., Ayub, Q., Mohyuddin, A., Fu, S., Li, P., Yuldasheva, N., Ruzibakiev, R., Xu, J., Shu, Q., Du, R., Yang, H., Hurles, M.E., Robinson, E., Gerelsaikhan, T., Dashnyam, B., Mehdi, Q., & Tyler-Smith, C. (2003). The genetic legacy of the Mongols. *American Journal of Human Genetics*, 72, 717-721.

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