Review Article

Beauty and the beast: mechanisms of sexual selection in humans

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Abstract

Literature in evolutionary psychology suggests that mate choice has been the primary mechanism of sexual selection in humans, but this conclusion conforms neither to theoretical predictions nor available evidence. Contests override other mechanisms of sexual selection; that is, when individuals can exclude their competitors by force or threat of force, mate choice, sperm competition, and other mechanisms are impossible. Mates are easier to monopolize in two dimensional mating environments, such as land, than in three-dimensional environments, such as air, water, and trees. Thus, two-dimensional mating environments may tend to favor the evolution of contests. The two-dimensionality of the human mating environment, along with phylogeny, the spatial and temporal clustering of mates and competitors, and anatomical considerations, predict that contest competition should have been the primary mechanism of sexual selection in men. A functional analysis supports this prediction. Men's traits are better designed for contest competition than for other sexual selection mechanisms; size, muscularity, strength, aggression, and the manufacture and use of weapons probably helped ancestral males win contests directly, and deep voices and facial hair signal dominance more effectively than they increase attractiveness. However, male monopolization of females was imperfect, and female mate choice, sperm competition, and sexual coercion also likely shaped men's traits. In contrast, male mate choice was probably central in women's mating competition because ancestral females could not constrain the choices of larger and more aggressive males through force, and attractive women could obtain greater male investment. Neotenous female features and body fat deposition on the breasts and hips appear to have been shaped by male mate choice.
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1. Introduction

Viewing human mating in a developed nation, one surmises that success in heterosexual competition for mates entails attracting members of the opposite sex. Beauty, fashion, and physical fitness are so important in places like the United States that they have become multi-billion dollar industries. Men and women have virtual autonomy to choose their mates. These conditions are so pervasive that it is tempting to think that they have characterized our evolution —that humans evolved in a context where, in the mating arena, the preferences of the opposite sex were the primary forces shaping our phenotypes.

With notable exceptions (e.g., Apostolou, 2007; Archer, 2009; Buss & Dedden, 1990; Buss & Duntley, 2006; Buss & Shackelford 1997; Daly & Wilson, 1988; Lassek & Gaulin, 2009; Sell et al., 2009), the recent literature in

evolutionary psychology reinforces this impression. The vast majority of research on sexual selection in *Homo sapiens* focuses on mate choice. Of papers on human sexual selection, more than 75% (55 of 73) published from 1997 to 2007 in the journals *Evolution and Human Behavior* and *Human Nature* mainly concern mate choice (categorized by the present author and a trained research assistant into "mate choice," "dominance and status competition," and "other," according to the hypotheses tested in the paper). According to an influential researcher, in sexual species, "all genes must propagate through the gateway of sex, and mate choice is the guardian of that gateway. For this reason, sexual courtship was probably central in human evolution and remains central in modern human life" (Miller, 1998, p. 119). According to another leading researcher, "the desires of one sex establish the critical dimensions along which members of the opposite sex compete" (Buss, 1996, p. 307). The extensive evidence leaves little doubt that the preferences of each sex have been important selection pressures on the other.

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But has mate choice been the primary mechanism of human sexual selection, as the literature might suggest? I argue here that it has not. Rather, contest competition—in which force or threats of force are used to exclude same-sex rivals from mating opportunities—has been the main form of mating competition in men, whereas male mate choice has predominated as a mechanism of sexual selection operating on women. This argument will be built on theory developed from cross-species comparison and subsequently tested by examining evidence of apparent design in humans.

2. Sexual selection

Darwin (1859; 1871) proposed sexual selection to explain traits that seemed harmful to survival—the hooked jaw of the male salmon, the stag's antlers, the cock's spurs, and the "gorgeous plumage" and "strange antics" (1859, p. 137) of the male rock-thrush and bird of paradise, for example. Although these traits might impair survival, Darwin postulated that they could nevertheless promote their own passage into the next generation by helping their bearers win mating opportunities: They could be favored under sexual selection. In the intervening years, a massive literature has validated this postulate and elaborated on the modes of sexual selection and the traits that each mode favors. Same-sex contests favor size, strength, weapons, and aggression, for example, whereas mate choice favors sexual ornaments and displays. (The term ornament is used here to refer to a trait that contributes to fitness primarily through a preference for this trait in the opposite sex.) Sperm competition favors the production of large ejaculates, motile sperm, and frequent copulation, scramble competition favors sensory and locomotory organs for swift mate location (Andersson, 1994, Table 1.1.1), and sexual coercion favors size, strength, and other traits that facilitate harassment, punishment, and forced copulation (Savalli, 2001).

We have also made considerable headway in understanding why one sex, usually males, often exhibits more elaborate ornamentation, mating displays, aggression, weaponry, and so forth. Clearly, the sex whose reproduction is more reliant on access to mates will experience stronger sexual selection. This depends on the operational sex ratio, the ratio of fertilizable females to sexually active males at a given time (Emlen, 1976). A scarcity of available mates forces the commoner sex into competition for them. The operational sex ratio, in turn, depends on the relative reproductive rates of males and females (Clutton-Brock & Vincent, 1991), and these rates typically depend on relative parental investment (Bateman, 1948; Trivers, 1972; Williams, 1966). In general, the sex that invests less in producing and rearing offspring finishes each reproductive venture sooner and re-enters the mating pool to find a shortage of the more-investing, slower-reproducing sex. Because males usually invest less than females do, males usually more competitive for mates.

2.1. Mechanisms of sexual selection

Despite such advances toward our understanding of sexual selection, one question has attracted surprisingly little attention: *What mechanisms of sexual selection will operate in a given species?* That is, can we predict whether mating competition will take the form of ornaments and displays for attracting mates, weapons and aggression for excluding competitors by force, traits for winning fertilizations in sperm competition, another mechanism of sexual selection, or some combination of these (Fig. 1)?

2.1.1. Constraints on contest competition

We can begin with the premise that same-sex contests can override other mechanisms of sexual selection. If contest outcomes are decisive, with winners excluding losers from proximity to potential mates, there will be no opportunity for choice (thus no need for coercion) and no sperm competition. Other mechanisms can occur only to the extent that the competing sex (for brevity, males, unless noted otherwise) cannot exclude competitors from potential mates by force or threat. Logically, the next step is to determine what might limit contest competition across species, affecting males' ability to monopolize females by force.

One limiting factor is the spatial and temporal clustering of females (Emlen & Oring, 1977). Resource distribution
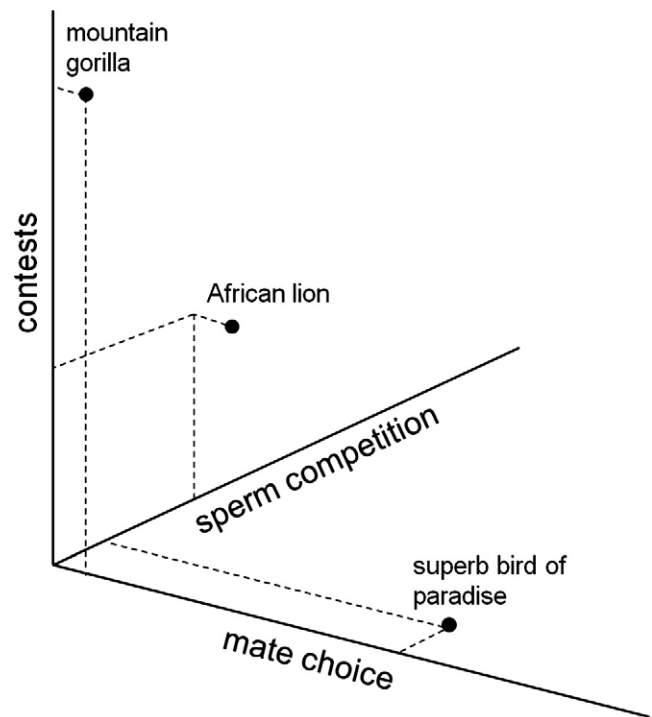

Fig. 1. Different mechanisms of sexual selection are theoretically distinct avenues by which mates can be obtained. Mechanisms vary in importance to fitness across species. Distance along an axis represents the correlation between success in that form of mating competition and mating success. (Examples are approximations.)

and predator risk determine the distribution of females, which determines the distribution of males (Leutenegger & Kelly, 1977; Lindenfors, Froberg, & Nunn, 2004). If females form groups or are solitary but closely dispersed, they may be collectively defensible by a single male. This can lead to intense male contests for control of multiple females (Emlen & Oring, 1977). However, if groups of females are large, a single male cannot exclude competitors, leading to multi-male, multi-female groups, thus reducing the importance of contests (Leutenegger & Kelly, 1977). For example, males have reduced canines and are smaller overall in relation to females among multi-male group-living primates, compared to those that exhibit single-male polygyny (Clutton-Brock & Harvey, 1984). However, testes are larger relative to body weight in multi-male groups (Harcourt, Harvey, Larson, & Short, 1981), indicating more sperm competition. This suggests that multi-male and single-male primates differ in the mechanism, but not necessarily the strength, of sexual selection. Temporal clustering due to breeding synchrony can also make multiple fertile females difficult for a single male to defend, especially if the females are widely distributed spatially (Emlen & Oring, 1977).

A second constraint on contests may be ecological costs. Flight (Caizergues & Lambrechts, 1999; Tobalske & Dial, 2000) and arboreality (Crook, 1972) should limit the evolution of the large bodies that would otherwise be useful for winning contests. Contests are relatively rare among birds (Emlen & Oring, 1977) and most intense among largely terrestrial birds in which males compete on land for display territories (Payne, 1984). Arboreal primates also exhibit less body size dimorphism than terrestrial ones (Clutton-Brock, Harvey, & Rudder, 1977; Plavcan & van Schaik, 1997).

Third, anatomical characteristics determine the benefits of contests. Gaulin and Sailer (1984) pointed out that the force generated by a blow increases with mass (a cubic function of length), whereas the ability to resist the blow increases at most as a square function (e.g., cross-sectional surface area of bone). Consequently, larger animals should be able to inflict more damaging blows. Males of larger species might therefore be more successful in excluding competitors by force or threat, and contests might be likelier to evolve.

Although the above variables may affect males' ability to monopolize mates, none is satisfactory as a general explanation. Intense contests occur across all social structures, including multi-male groups (e.g., yellow baboons), single-male groups (e.g., gorillas and red deer), and solitary species (e.g., beetles and orangutans). Moreover, ecological constraints on body size explain neither the rarity of contests in aquatic environments (Andersson, 1994), which impose few size limitations (consider blue whales), nor the frequency of contests in small-bodied animals, such as arthropods. Finally, contests require only the physical monopolization of mates, not the ability to injure competitors. Thus, contests may be intense in small animals, such as beetles (Eberhard, 1979).

2.1.2. The dimensionality hypothesis

An ecological variable that has apparently escaped notice in this context is the dimensionality of the environment in which mating competition takes place. To succeed in contests, males must exclude same-sex competitors from mates or the resources necessary to attract them (Emlen & Oring, 1977). This may be feasible in the essentially one-dimensional environments of burrows and tunnels, and in two-dimensional environments such as dry land, but impossible in three dimensions (air, water, or trees), where there are too many in-routes for competitors. For example, the three-dimensional aquatic environment of bottlenose dolphins hinders individual males from monopolizing females, resulting in a promiscuous mating system (Connor, Richards, Smolker, & Mann, 1996), and presumably sperm competition.

Fig. 2 illustrates differences in the relative size and dimensionality of the region that must be defended when mating competition takes place in (a) a one-dimensional environment (e.g., dung beetles competing for mates in a tunnel), (b) a two-dimensional environment (e.g., fur seals competing for mates on land), (c) a three-dimensional environment bounded by a territory (e.g., blue-headed wrasses guarding coral reefs), and (d) an open three-dimensional environment (e.g., bottlenose dolphins competing for mates in the open ocean). Whereas the difficulty of defense increases linearly with the radius of the defense region in two dimensions, it increases with the square of this radius in three-dimensional environments.

2.1.3. Evidence for the dimensionality hypothesis

Qualitative comparative evidence suggests that the dimensionality of the mating environment explains substantial interspecific variation in contest competition, and
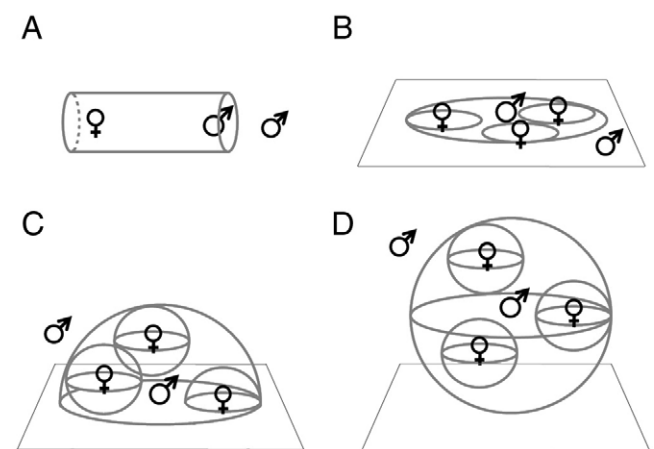

Fig. 2. Small discs, hemispheres and spheres represent females' movement in relation to each other. Cylinder and large disc, hemisphere and sphere represent the regions that a male must defend in order to monopolize the females depicted. Defense regions increase in size and decrease in defensibility from left to right and top to bottom and represent (A) one-dimensional, (B) two-dimensional, (C) three-dimensional hemispheric, and (D) three-dimensional spherical regions.

consequently, other mechanisms of sexual selection. For example, contests are more extreme in arthropods that compete for mates on land (e.g., beetles, pseudoscorpions, and spiders: Eberhard, 1979; Watson, 1990; Zeh, 1987) and the floors of bodies of water (e.g., crabs and crayfish: Christy & Salmon, 1991; Crane, 1975; Snedden, 1990; Sneddon, Huntingford, & Taylor, 1997), than in those that fly, such as butterflies, katydids, and locusts (Andersson, 1994). Contests are especially intense among arthropods, such as some dung beetles, that compete for mates in the essentially one-dimensional environments of burrows or tunnels (Emlen, 2008; Emlen & Philips, 2006).

Contests are rare in the three-dimensional aquatic environments of fish (Andersson, 1994), whereas mate choice (Noble, 1938) and sperm competition (e.g., Fuller, 1998) are more common. However, contests occur in species such as bluegills (Gross & MacMillan, 1981), wrasses (Robertson & Hoffman, 1977), and pufferfish (Gladstone, 1987), where males guard territories on lake, stream, or sea floors (Turner, 1993) and mating environments are thus reduced in volume. In sockeye salmon, mating competition occurs in the shallow, effectively two-dimensional head-waters of streams (Quinn, Hendry, & Buck, 2001), and males use body size and specialized hooked jaws to fight for females (Quinn, Adkison, & Ward, 1996).

Mate choice is the predominant mechanism of sexual selection across bird species (Andersson, 1994; Emlen & Oring, 1977), which because of flight tend to compete for mates in three dimensions. Terrestriality is a derived trait in birds, evolving independently at least four times in Galliformes, Struthioniformes, Casuariiformes, and Rheiformes. Each of these incidences of evolution toward a more two-dimensional mating environment is associated with a movement away from social monogamy and an increase in contest competition (Andersson, 1994; Emlen & Oring, 1977).

Scrambles may be the primary sexual selection mechanism in aquatically-mating pinnipeds. Female Weddell seals are larger than males, and males obtain copulations underwater via speed and agility (Andersson, 1994). However, in terrestrially-breeding pinnipeds, such as sea lions, elephant seals, and fur seals, males are several times the size of females, and male contests are intense and bloody (Boyd, 1989; Le Boeuf, 1974; Lindenfors, Tullberg, & Biuw, 2002). Thus, among pinnipeds, male contests and large body size have evolved in two-dimensional mating environments despite the ecological costs of carrying a large body on land.

Contests are also common among terrestrial primates, which exhibit greater body and canine size sexual dimorphism than arboreal and arboreal/terrestrial species (Clutton-Brock et al., 1977; Leutenegger & Cheverud, 1982; Plavcan & van Schaik, 1997). Differences in body size dimorphism might reflect mass limitations of arboreality (Clutton-Brock et al., 1977). However, arboreality imposes no clear constraints on canine size, and selection in terrestrial species favoring larger canines for predator defense (Leutenegger & Kelly, 1977) should affect both sexes. Reduced contest competition in three-dimensional arboreal environments may have decreased body and canine size dimorphism and increased the importance of mate choice. Female preferences for brightly-colored males have been demonstrated in arboreal primates (Cooper & Hosey, 2003), which apparently exhibit greater sexual dichromatism than terrestrial primates (Crockett, 1987).

The dimensionality of the mating environment thus helps explain why contests occur in some taxa and not others. Having developed a theoretical framework for predicting the mechanisms and relative intensity of sexual selection, we return our attention to humans.

3. Sexual selection in humans

Women invest more in offspring than men do through gestation and nursing for up to several years in foraging societies (Eibl-Eibesfeldt, 1989) and through providing more parental care on average in all known societies (Hewlett, 1992). Greater investment slows women's reproductive rates, skewing the operational sex ratio so that there are more males than females available for mating. Across species, these conditions foster mating competition in the more rapidly-reproducing sex. Evidence suggests that men have indeed experienced stronger sexual selection. Compared to women, men have higher reproductive variance (e.g., Brown, Laland, & Borgerhoff Mulder, 2009; Howell, 1979), are larger, more muscular, mature later, and senesce and die sooner—all correlates of an effectively polygynous mating system (Daly & Wilson, 1983). However, men invest heavily in offspring compared with males of most animal species and virtually all mammals. This investment constitutes a basis for female competition. Evidence (below) suggests that sexual selection has influenced women's phenotypes as well.

The variables proposed to predict sexual selection mechanisms are nearly unanimous: contests should be the dominant mode of sexual selection in men (Table 1). More precisely, ancestral men's mating success should have correlated more strongly with success in male contests than with success in other modes of sexual selection. [See Schwagmeyer and Woontner (1986) for a similar comparison of contests and scrambles in ground squirrels.] The two-dimensionality of the human mating environment, combined with female sociality and breeding asynchrony, should facilitate female defense. Men's large size enables them to inflict damaging blows, and phylogenetic relationships also predict male contests in humans, along with some sperm competition, mate choice, and coercion. All three genera of non-human great apes show intense male contests with some female choice, and significant sperm competition and sexual coercion in *Pan* and *Pongo* (Knott, Emery Thompson, Stumpf, & McIntyre, 2009; Muller, Kahlenberg, Emery

Table 1
Variables influencing contest competition and predictions regarding humans

Variable influencing contest competition	Value of variable (prediction regarding contests)	
	Males	Females
Dimensionality of mating environment	2D (Contests)	2D (Contests)
Body size	Large (Contests)	Large (Contests)
Capability of physically constraining opposite sex	Yes (Contests)	No (No Contests)
Temporal clumping of available mates	No (Contests)	No (Contests)
Spatial clumping of mates and competitors	Multi-male/ multi-female groups (Contests reduced)	Multi-male/ multi-female groups (Contests reduced)
Body-size constraints of flight or arboreality	No (Contests)	No (Contests)
Contests in close phylogenetic relatives	Yes (Contests)	No (No contests)

Thompson, & Wrangham, 2007; Nishida & Hiraiwa-Hasegawa, 1987; Rodman & Mitani, 1987; Smuts, 1987). Only multi-male groups are predicted to reduce individual males' abilities to monopolize females, elevating the importance of other forms of sexual selection, but the influence of this variable may be mitigated in humans (see below).

Female contests are absent in humans' close phylogenetic relatives, and monopolization of mates is likely to be unfeasible in women, as well (Table 1). The multi-female structure of human groups should have hindered ancestral females from excluding their competitors from mates. Indeed, in the presence of multiple same-sex competitors, successful mate defense probably depends partly on mates' cooperation. However, evolutionary models suggest that such cooperation will tend to evolve in one sex when the other is physically dominant and thus capable of sexual coercion (Clutton-Brock & Parker, 1995). Yet, men are greater in size and physical prowess than women are, and thus, men should be prohibitively difficult to constrain in their choices. We can therefore predict that female mating competition would favor traits to attract men, rather than physically monopolize them.

Before these predictions can be evaluated, it is necessary to clarify what constitutes evidence of a trait's adaptive function in winning mates. For example, is a particular trait a weapon or an ornament, a dominance signal or a mate attraction display?

3.1. Testing evolutionary predictions

One can infer ancestral selection pressures by studying the adaptations that they produced. Natural selection is the only evolutionary process to systematically produce traits that appear engineered for specific functions (Williams, 1966). If, under scrutiny, a trait looks well-suited to a purpose that would have benefited ancestral bearers, then we can tentatively conclude that it evolved for this function. This can be demonstrated by cross-species comparison. For example, the hypothesis that horns in male beetles function in combat is supported if hornlike structures are present in species with male combat and absent in species without it. In parallel, within species, functional hypotheses are bolstered by correlations between a trait (e.g., horn size) and its proposed function (fighting efficiency). The strongest within-species evidence involves experimental manipulation that affects the trait's utility in the predicted direction. The more efficiently a trait performs its hypothesized function compared with alternative functions, the stronger support for the adaptive hypothesis.

3.2. Male contests

3.2.1. Evidence of design for male contests

All of these types of evidence support the prediction that male contests have been important in human evolution. Men are larger, stronger, faster, and more physically aggressive than women, and the degree of sexual dimorphism in these traits rivals that of species with intense male contests. The relatively modest 8% stature dimorphism in humans (Gaulin & Boster, 1985) and a difference of about 15–20% in body mass (Mayhew & Salm, 1990) might suggest that male contests are reduced compared with our closest relatives. However, human sex differences in size underestimate sex differences in the traits most relevant to contests. This is partly because women are unique among primates in having copious fat stores (Pond & Mattacks, 1987), perhaps for building the large, fatty brains of human offspring (Lassek & Gaulin, 2008), and as sexual ornamentation (see below). When fat-free mass is considered, men are 40% heavier (Lassek & Gaulin, 2009; Mayhew & Salm, 1990) and have 60% more total lean muscle mass than women. Men have 80% greater arm muscle mass and 50% more lower body muscle mass (Abe, Kearns, & Fukunaga, 2003). Lassek and Gaulin (2009) note that the sex difference in upper-body muscle mass in humans is similar to the sex difference in fat-free mass in gorillas (Zihlman & MacFarland, 2000), the most sexually dimorphic of all living primates.

These differences in muscularity translate into large differences in strength and speed. Men have about 90% greater upper-body strength, a difference of approximately three standard deviations (Abe et al., 2003; Lassek & Gaulin, 2009). The average man is stronger than 99.9% of women (Lassek & Gaulin, 2009). Men also have about 65% greater lower body strength (Lassek & Gaulin, 2009; Mayhew & Salm, 1990), over 45% higher vertical leap, and over 22% faster sprint times (Mayhew & Salm, 1990). Contrary to earlier claims, sex differences in anaerobic sprint speeds are not narrowing (Cheuvront, Carter, Deruisseau, & Moffatt, 2005; Seiler, De Koning, & Foster, 2007).

Men and boys are more physically aggressive than women and girls (Archer, 2004, 2009). Boys engage in more play-fighting, and the amount of play-fighting a boy engages

in correlates positively with peers' rankings of his dominance (Pellegrini, 1995; Pellegrini & Smith, 1998). Men report engaging in, and inclinations to engage in, nearly one standard deviation more physical aggression than women (Buss & Perry, 1992). Men perpetrate more offensive physical aggression, defined as non-defensive "attacking, hitting, and/or restraining another individual" in all societies studied (Ellis et al., 2008). The vast majority of same-sex homicides (about 95%), from every society and time period for which data are available, are committed by men (Daly & Wilson, 1988; M. Wilson & Daly, 1985). Importantly, these data do not include war killings, which occur almost entirely at the hands of men (Adams, 1983). Traumatic injuries in ancient skeletal remains indicate that interpersonal violence was especially prevalent among men throughout human history and prehistory (Walker, 2001).

Such sex differences in traumatic skeletal injuries may help explain why some aspects of men's skeletons, particularly in the face, are more robust. For example, in modern populations, the incidence of mandibular fractures is approximately five times higher in men than in women, young men are disproportionately represented, and the primary cause is typically found to be violent assault with a fist or blunt object (Adi, Ogden, & Chisholm, 1990; Haug, Prather, & Indresano, 1990; Scherer, Sullivan, Smith, Phillips, & Robson, 1989; Sojat, Meisami, Sandor, & Clokie, 2001). A similar pattern in the evolutionary past could have selected for more robust mandibles in men than in women.

Certainly, size, strength, speed, and aggression in men correlate with physical competitive ability, and manipulations that increase these variables lead to greater physical prowess. This is why many athletes abuse anabolic steroids. Relatively greater male upper-body (compared with lower-body) muscle mass and strength in particular suggest an evolutionary history of fighting (Sell et al., 2009). These traits also characterize male contests across species; males are larger, stronger and more aggressive in diverse species with male contests across the animal kingdom (Andersson, 1994). Close relatives of humans with minimal male contests, such as gibbons, lack substantial sex differences in size, strength, and aggression.

Men possess several traits that appear to function primarily in threatening rivals. For example, beards and eyebrow hair grow at puberty in males and may signal dominance through association with testosterone levels and by increasing the apparent size of the jaw and brow (Guthrie, 1970; Muscarella & Cunningham, 1996; Neave & Shields, 2008). Male faces with beards are rated as more dominant than the same faces clean-shaven (Muscarella & Cunningham, 1996; Neave & Shields, 2008). Likewise, deep, low-pitched voices increase men's apparent size (Feinberg, Jones, Little, Burt, & Perrett, 2005) and dominance (Puts, Gaulin, & Verdolini, 2006; Puts, Hodges, Cardenas, & Gaulin, 2007). Perhaps deep voices signal dominance in men partly because they correlate with high testosterone levels

(Bruckert, Lienard, Lacroix, Kreutzer, & Leboucher, 2006; Dabbs & Mallinger, 1999; Evans, Neave, Wakelin, & Hamilton, 2008). Across animals, low-pitch vocalizations generally signal dominance, and high-pitch vocalizations signal submissiveness (Morton, 1977; Morton & Page, 1992). In the laboratory, men who reported superior fighting ability tended to lower their voice pitch during mating competition, whereas those who perceived themselves to be poor fighters raised their pitch (Puts et al., 2006).

It is often claimed (e.g., Lorenz, 1966) that men lack antlers, long canines, or other weapons typical of intense contest competition. However, these traits are called "weapons" by analogy with human weapons, and for as long as there is any record, weapons have been manufactured and wielded almost entirely by men (Christensen, 2004; D'Andrade, 1974; Darwin, 1871; Gat, 2006). The first known combat weapons were also used in hunting (Christensen, 2004), which is performed nearly exclusively by men in foraging societies (Murdock, 1967). It is therefore appropriate to consider weapons a part of men's phenotype. The use of projectile weapons must have selected for targeting abilities, which show the largest known "cognitive" human sex difference, with an effect size of about 1.5 standard deviations favoring men (Hines et al., 2003; Kimura, 1999). Thus, the already large sex differences in muscle mass, strength, speed, and aggression probably underestimate the intensity of contest competition in men.

Men's anatomy and behavior seem well designed for contest competition. The alternative hypothesis that these traits evolved in the service of hunting (e.g., Lancaster & Kaplan, 2009) is unsatisfying partly because it is unparsimonious: across the animal kingdom, where one finds large, strong, aggressive males with weapons, it is almost always because males employ these traits in fights for females (Andersson, 1994). The hunting hypothesis also has difficulty explaining traits such as beards, deep voices, robust skulls, and male-male aggression that are easily explicable by male contest competition. Even targeting ability may have emerged in the context of male contests: male chimpanzees throw rocks and branches with far greater frequency than do females, and the targets are other males, not prey (Goodall, 1968; Van Lawick-Goodall, 1971). Although superior targeting ability in men was likely shaped for both male contests and efficient hunting, men also exhibit superior intercepting abilities (Watson & Kimura, 1991), which are difficult to comprehend as adaptations for hunting (Mark Flinn, personal communication). Finally, orangutans, gorillas, chimpanzees, and early hominins, such as *Australopithecus afarensis* and *A. anamenis* (Leakey, Feibel, McDougall, Ward, & Walker, 1998; Plavcan, Lockwood, Kimbel, Lague, & Harmon, 2005; Reno, Meindl, McCollum, & Lovejoy, 2003, 2005; Ward, Leakey, & Walker, 1999), all exhibit moderate to high degrees of sexual dimorphism, and intense male contests occur in all genera of extant great apes. Substantial sexual dimorphism and contests thus probably existed in the earliest hominins, yet hunting became a major

source of food only as early as perhaps 2.5 million years ago (Dominguez-Rodrigo, Pickering, Semaw, & Rogers, 2005). Greater male size and strength probably preceded hunting in our lineage, and thus could not have resulted from it.

3.2.2. Human mating systems and the role of male contests

Although it seems clear that contest competition shaped many of men's traits, it is less clear how success in male contests increased mating opportunities over human evolution. Several possibilities exist. First, coalitional aggression could have facilitated acquisition and defense of mates against other groups of males. Second, males could have used force or force threat within their groups to acquire and defend one or more long-term mates, or to obtain disproportionate short-term mating opportunities. Finally, contests could have contributed indirectly to mating success if dominant males could acquire resources, territory, or status needed to attract females. To what extent did these possibilities apply to ancestral humans?

3.2.2.1. Male coalitions and between-group competition.

The tendency of males to form alliances may have evolved in the common ancestor of humans and our closest living relatives, *Pan*, as a means of cooperative female capture and defense (Fig. 3), although coalitions may also have evolved independently in these lineages for this purpose (Geary & Flinn, 2001; Wrangham, 1999). Male coalitions are rare among primates but common in humans and *Pan*, especially common chimpanzees (*P. troglodytes*), and are strengthened by kinship (Nishida & Hiraiwa-Hasegawa, 1987). The capture of women was a primary objective of early warfare (Darwin, 1871; Hrdy, 1997; Lerner, 1986; Spencer, 1885), and among foragers, groups of men commonly raid other villages and abscond with women
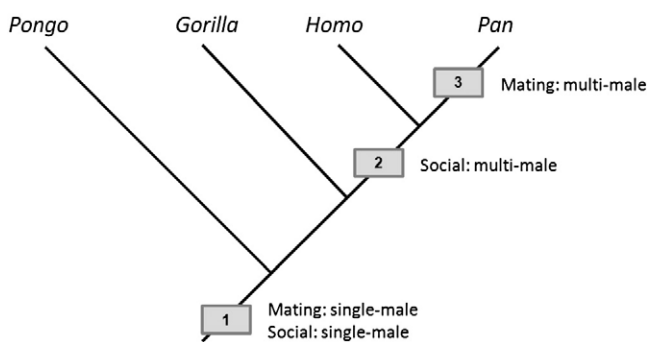

Fig. 3. From a great ape progenitor with single-male polygyny and single-male social groups (1) (Harrison & Chivers, 2007), two trajectories for African apes are depicted: a continuation of this pattern in *Gorilla*, and the evolution of multi-male groups for female defense, as in African lions, in the common ancestor of *Pan* and *Homo* (2). In *Pan*, within-group monopolization of females was difficult, and greater sperm competition thus predominated (3), resulting in lower sexual dimorphism (Jungers & Susman, 1984) but larger investments in testicular tissue (Short, 1979). In *Homo* and their immediate ancestors, individual males more effectively monopolized females, perhaps due female cooperation, between-group competition, and more intensive use of weapons.

(e.g., Chagnon, 1988). Such raids may also function in mate defense by deterring future attacks. These behaviors would tend to favor not only aggression and physical prowess, but also social intelligence for negotiating alliances (e.g., Alexander, 1989; Geary & Flinn, 2002; Mueller & Mazur, 1996; Wrangham, 1999).

3.2.2.2. Within-group competition.

Despite their relevance in *Pan* and *Homo*, alliances are open to subversion; if one member can gain a reproductive advantage, he may defect. Male chimpanzees not only cooperate to defend their community range against outside males but also fight within groups over estrous females (Nishida & Hiraiwa-Hasegawa, 1987). As noted, multi-male groups should make females more difficult to defend from other group members. The cross-cultural ubiquity of within-group aggression between men (Daly & Wilson, 1988), male violence against women over suspected infidelity (Daly & Wilson, 1988; Smuts, 1996), high levels of male sexual jealousy (Buss, Larsen, Westen, & Semelroth, 1997; Daly, Wilson, & Weghorst, 1982; Schützwohl & Koch, 2004), and evidence of moderate sperm competition (Harcourt, Purvis, & Liles, 1995; Wyckoff, Wang, & Wu, 2000) indicate that men have had to defend their mates within their groups, as well.

Yet, within multi-male groups, men form enduring mateships with one or more females and usually have near-exclusive sexual access (Daly & Wilson, 1983; Flinn, Quinlan, Ward, & Coe, 2007). Among Yanomamo hunter-gatherers, approximately 10% of offspring are sired by a man other than the mother's social partner (Chagnon, 1979). This number has been estimated to be 2% (Simmons, Firman, Rhodes, & Peters, 2004), 4% (Bellis, Hughes, Hughes, & Ashton, 2005) and 9% (Baker & Bellis, 1995) across modern societies. The cross-cultural frequency of these conditions—enduring mateships and relatively low rates of extrapair paternity—suggests that they characterized early *Homo sapiens*. Women's inconspicuous estrus also suggests a single-male mating system (Clutton-Brock & Harvey, 1976; Hrdy, 1997; Nunn, 1999) and, thus, that ancestral males could monopolize females.

Several factors may have contributed to ancestral males' ability to monopolize females. First, the importance of male alliances might have reduced within-group conflict, enabling individual males—especially those distinguished in intergroup conflict—to monopolize one or more females (Hrdy, 1997; Smuts, 1995). Among the horticultural Yanomamo of Venezuela, men who have killed enemies in intergroup conflict have more wives (Chagnon, 1988). However, male chimpanzees also form alliances but are unable to similarly monopolize females for prolonged periods.

Second, acquisition and long-term defense of females by individual males may have been promoted by enhanced cooperation from females as a result of male investment (Geary & Flinn, 2001). Serial long-term mating in particular may have been an important means by which dominant males could monopolize the reproductive careers of multiple

females while having to defend (and invest in) only one female at a time (Hill & Hurtado, 1996; Johanna, Forsberg, & Tullberg, 1995; Kaar, Jokela, Merila, Helle, & Kojola, 1998; Marlowe, 2004). However, in most societies, some men are simultaneous polygynists (Murdock, 1967), and this was probably true of all human societies until a few hundred years ago (Betzig, 1986, 1995).

Finally, ancestral males likely acquired and defended females within groups through the use of force or threat of force. This may have been facilitated by the use of lethal weapons that can be wielded at a distance. Among the Hadza hunter-gatherers of Tanzania, courtship of a female by more than one male can lead to violent, possibly fatal conflict between the males (Marlowe, 2004). Bloody and sometimes fatal club fights erupt between Yanomamo men when one suspects the other of trysting with his wife (Chagnon, 1992). In these cases, the ability to inflict serious damage to a competitor apparently functions in mate acquisition and mate retention, respectively. Certainly, the ability to inflict physical harm on competitors would have helped ancestral males win such skirmishes over mates. A reputation for—or advertisement of—fighting ability would also have enabled ancestral males to win and defend mates while avoiding many costly fights. Indeed, some male traits, such as such as deep voices and facial hair, seem more explicable as within-group dominance signals than as functioning in between-group competition.

Human males have probably not competed over short-term access to fertile females to the extent that such competition occurs in other multi-male primates, such as chimpanzees. Unlike chimpanzees, humans do not exhibit conspicuous estrus. Without a reliable indicator of female ovulatory status, males' expected reproductive return from copulations over a short duration is low (Bongaarts & Potter, 1986; Leridon, 1977). Consequently, short-term sexual access was probably seldom worth incurring the potentially large costs of physical competition. However, contest competition leading to ascension in a male dominance hierarchy would likely have ramifying reproductive benefits, including greater access to short-term mates and less retaliation after trysting with already-mated females.

3.2.2.3. Competition for mate-acquisition resources, or as sexual display. Perhaps dominant males were also more likely to be chosen by females because dominant males had access to better resources or territory, or because the victors of male contests tended to provide high quality genes. Female preferences must have affected males' ability to acquire mates and ensure their fidelity over human evolution. Thus, we now direct our attention to female choice.

3.3. Female choice

Women's preferences for men with resources and willingness to invest appear culturally ubiquitous (Buss, 1989; Cashdan, 1996; Hill & Hurtado, 1996). Men likely provide resources partly because this attracted more mates

(Buss, 1989; Hawkes, 1990, 1991) and increased mates' fidelity (Geary & Flinn, 2001), although resource provisioning can also function as parental investment (Marlowe, 2003; Trivers, 1972). However, foragers typically cannot accumulate great wealth or resources (Marlowe, 2005), and all humans were foragers prior to about 10,000 years ago. Nevertheless, women can choose mates based on less tangible benefits, such as foraging ability (Marlowe, 2004) and high status for offspring (Hill & Hurtado, 1996). Women can also obtain protection from rape and harm to offspring (Smuts, 1996). Male infanticide of unrelated offspring is prevalent among primates (Hrdy, 1979), including humans (Smuts, 1996), and is mitigated by the presence of the biological father (Daly & Wilson, 1988). Because most human reproduction occurs within long-term mateships such as marriage (Apostolou, 2007), preferences for such benefits may have evolved primarily in this context (see, e.g., Marlowe, 2004). However, women may also extract male investment from short-term mating (Buss & Schmitt, 1993; Greiling & Buss, 2000; Hawkes, 1990, 1991).

3.3.1. Good genes mate choice

A growing body of evidence suggests that women also choose mates partly on genetic quality (Roberts & Little, 2008). Because selection culls alleles associated with inferior phenotypes, the traits most relevant to fitness should lose heritability (Fisher, 1930), degrading the basis for good genes mate choice. However, mutation and fluctuating selection can maintain genetic variation. Hamilton and Zuk (1982) suggested that parasites generate important temporally varying selection on hosts. As parasites' short generation times facilitate rapid evolution, resistance to infection is an essential fitness component that might remain heritable in hosts. A preference for indicators of heritable parasite resistance could spread and be maintained in a population (Hamilton & Zuk, 1982).

Some animal research indicates that females choose mates based on parasite resistance, and this resistance is heritable (e.g., Hillgarth, 1990). An important genomic region in mediating disease resistance is the major histocompatibility complex (MHC). Greater MHC allelic diversity theoretically enables recognition of more invaders and stronger immune function. Hence, preferences for MHC-dissimilar mates are predicted. Olfactory preferences for MHC-dissimilar mates have been demonstrated in several vertebrate taxa, including fish, reptiles, birds, and rodents, and in most human studies (reviewed in Roberts & Little, 2008). Preferences for MHC dissimilarity may produce greater MHC-specific genetic dissimilarity within human couples than occurs between random pairs of individuals (Chaix, Cao, & Donnelly, 2008) and may produce attractive, healthy-looking offspring; heterozygosity at MHC loci (Lie, Rhodes, & Simmons, 2008), has been associated with facial attractiveness and healthy-looking skin (Lie et al., 2008; Roberts et al., 2005).

Women are thus expected to prefer mates with genes that confer disease resistance, and with few harmful mutations.

Two putative good-genes indicators are androgen-dependent traits and fluctuating asymmetry. Androgen-dependent, masculine traits may indicate heritable disease resistance because androgens suppress immune function (Grossman, 1985) and may be produced in proportion to inherited immunocompetence (Folstad & Karter, 1992). High androgen levels may increase competitive ability but attenuate inherited immunocompetence, so that good-genes males end up little healthier than average. Males with few harmful mutations may also be able to produce and maintain more elaborate androgen-dependent traits (Zahavi & Zahavi, 1997). Regulation of androgen levels and patterns of response to androgens may thus have evolved as a means of producing sexually selected traits in proportion to a male's ability to safely bear them (Folstad & Karter, 1992). Fluctuating asymmetry (FA) refers to asymmetry in anatomical traits that are normally bilaterally symmetric. FA may negatively indicate genetic quality because it results from developmental stresses such as mutation and parasitic infection (Moller & Pomiankowski, 1993; Parsons, 1990, 1992; van Valen, 1962) and is moderately heritable in several species (Moller & Thornhill, 1997).

As expected, women have been found to exhibit preferences for the odors (Gangestad & Thornhill, 1998; Rikowski & Grammer, 1999; Thornhill & Gangestad, 1999), faces (Gangestad, Thornhill, & Yeo, 1994; Scheib, Gangestad, & Thornhill, 1999), and voices (Hughes, Harrison, & Gallup, 2002) of men whose external features are symmetrical. Women also prefer men who are somewhat more masculine than average in height (Pawlowski & Jasienska, 2005), body build (Frederick & Haselton, 2007; Horvath, 1981), voice (Feinberg et al., 2005; Puts, 2005), and perhaps face (e.g., Johnston, Hagel, Franklin, Fink, & Grammer, 2001; but see Perrett et al., 1998). Some studies have found that men's symmetry and masculinity correlate, as might be predicted if both features index underlying genetic quality (Gangestad & Thornhill, 2003; Scheib et al., 1999).

Presumably because they are more sexually attractive to women, men of putatively high genetic quality tend to expend more effort acquiring additional mates and less effort investing in mates (Gangestad & Simpson, 2000). For example, men with high testosterone levels are more likely to have extramarital sex (Booth & Dabbs, 1993) and less likely ever to have been married (Booth & Dabbs, 1993), and unmarried men have higher testosterone levels than do married men (Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002). Similarly, symmetrical men have more extra-pair sex partners (Gangestad & Thornhill, 1997, 1999) and invest less in their current mates (Gangestad, 1993; Simpson, Gangestad, Christensen, & Leck, 1999). Consequently, masculine and symmetrical men should tend to make better sires than long-term mates.

Predictably, women's preferences for these men are greater for short-term, sexual (vs. long-term) relationships and strongest during the fertile phase of the ovulatory cycle

(reviewed in Gangestad & Thornhill, 2008). Symmetrical, physically attractive men are also more often the extra-pair sexual partners of women (Gangestad & Thornhill, 1997). Women's extra-pair, but not intra-pair, sexual interest increases near ovulation (Gangestad, Thornhill, & Garver, 2002), and this cyclic shift occurs mainly in women whose primary partners are putatively of low genetic quality (Gangestad, Thornhill, & Garver-Apgar, 2005; Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006). These findings suggest that women's sexual preferences are designed partly to recruit genetic benefits from men who may not be the women's long-term partners. Evidence of sperm competition and moderate rates of extra-pair paternity across human societies (Simmons et al., 2004) support this possibility.

3.3.2. Sexual ornaments in men?

Women's preferences raise the question of whether men's traits are better viewed as sexual ornaments or armaments. Female mate choice has been observed in virtually every primate species studied (Smuts, 1987). Paradoxically, few male primates exhibit clear sexual ornaments (Andersson, 1994). Part of the reason may be that females choosing males on genetic quality might prefer dominance and the traits associated with it, and thus male secondary sex traits adopt dual functions (Berglund, Bisazza, & Pilastro, 1996). Berglund et al. (1996) argue that secondary sexual characters usually originate through contests rather than female choice partly because signals used in contests tend to be costly to produce, are constantly tested by competitors and, thus, should provide accurate information about male quality to both competitors and potential mates.

In many species, females prefer traits that function in contests (Berglund et al., 1996; Kodrick-Brown & Brown, 1984). Low, closely-spaced vocal formant frequencies intimidate rivals among red deer stags (Reby et al., 2005) and are preferred by estrous females (Charlton, Reby, & McComb, 2007). Likewise, spur length among ring-neck pheasants is associated with both male dominance (Mateos & Carranza, 1996) and attractiveness to females (von Schantz, Wittzell, Göransson, Grahn, & Persson, 1996). Estrous females choose dominant males in a variety of nonhuman primates (Smuts, 1987); for example, dominant male orangutans are larger and possess cheek flanges, and females show greater willingness to mate with these males near ovulation (Knott et al., 2009).

These ideas help explain the origin of women's preferences for traits such as size, muscularity and deep voices that have clear utility in contests. The idea that such traits should be especially good indicators of male quality also helps explain why women tend to prefer them more for sexual relationships and during the fertile phase of the ovulatory cycle. However, even if men's traits initially arose through male combat, it is possible that female choice could have become a stronger selection pressure,

and men's traits subsequently evolved to assume a more ornamental role.

This hypothesis that men's traits evolved to be ornamental gains little support from the literature. Some male traits, such as beards, have been found to decrease attractiveness to women, yet have strong positive effects on men's appearance of dominance (Muscarella & Cunningham, 1996; Neave & Shields, 2008). In other cases, it is unclear whether women prefer more masculine males. For example, women have been found to prefer both slightly feminine-looking (Perrett et al., 1998; Rhodes, Hickford, & Jeffery, 2000) and slightly masculine-looking (DeBruine et al., 2006; Johnston et al., 2001) male faces. Despite these equivocal results, facial masculinity strongly increases the appearance of dominance, and has substantially larger effects on dominance than attractiveness when both are examined (DeBruine et al., 2006; Perrett et al., 1998). Finally, although some masculine traits, such as muscular builds (Frederick & Haselton, 2007) and deep, masculine voices (Feinberg et al., 2005; Puts, 2005, 2006) are sexually attractive, masculinity in these traits increases perceptions of dominance to a much greater degree than it increases attractiveness (Fig. 4). Even near ovulation and in the context of short-term mating (where masculine traits are maximally attractive), masculinity has been found to produce smaller positive effects on attractiveness to women than on dominance as judged by men (Puts et al., 2006) (see Fig. 4).

One might argue that there is considerable cross-cultural variation in the importance of masculine traits for attractiveness and dominance. This is certainly true, but cultural differences are unlikely to reverse the findings that masculine traits have greater positive effects on perceptions

of dominance than they do on attractiveness. For example, in societies in which nearly all adult men have beards, women may prefer facial hair on men. Yet, in such societies, facial hair will probably be even more essential to perceptions of dominance, with a lack of facial hair being perceived as childlike in men.

One might also argue that, although masculine traits appear better at increasing dominance, mating success is determined more by attractiveness. Thus, masculine traits may actually have been favored primarily through their utility as sexual ornaments. Existing evidence contradicts this possibility. For example, men's voice attractiveness predicts mating success (Hughes, Dispenza, & Gallup, 2004). Yet, when dominance and attractiveness ratings of men's voices were used simultaneously to predict mating success, dominance strongly predicted number of sex partners, whereas attractiveness did not (Puts et al., 2007).

Finally, one might argue that the masculine traits reviewed above bias a functional analysis toward the conclusion that ancestral men competed for mates mainly via contests, and that choosing a different set of traits would lead to a different conclusion. However, traits that show a high degree of sexual dimorphism, especially those that develop at sexual maturity, are the best candidates for targets of sexual selection (Andersson, 1994; Darwin, 1871). Choosing such traits in men necessitates choosing masculine traits (i.e., traits that are present to a greater degree in males), which could be ornaments or weapons. In other words, choosing masculine traits for a functional analysis amounts to choosing the best candidates for sexually selected traits without implying anything about the traits' utility in contests, mate attraction, or any other mechanism. [In long-tailed widowbirds, long tail feathers are masculine, yet male widowbirds use their long tails to attract females (Andersson, 1982).] The function of masculine traits in men was an open question, but men's traits seem better designed for contests than for attracting mates.

Are any of men's traits properly considered sexual ornaments (i.e., function primarily in mate attraction)? Men's penises are longer and thicker, both relatively and absolutely, than those of our closest relatives, chimpanzees and gorillas, and could have evolved to signal mate quality. Women report greater satisfaction with larger penises (Lever, Frederick, & Peplau, 2006), so penis size may affect a man's ability to stimulate orgasm in women (Miller, 2000). Female orgasm may boost sperm retention, facilitate sperm activation, and encourage additional copulations (reviewed in Puts & Dawood, 2006, see also Gallup et al., 2003). However, it has also been suggested that penis size may advertise vigor to other men (Diamond, 1997).

Geoffrey Miller (1998; 2000) is the leading proponent of a theory that men's brains and creativity are designed to attract females. In this view, displays of neurophysiological efficiency advertise heritable fitness. Miller's "mating-mind"
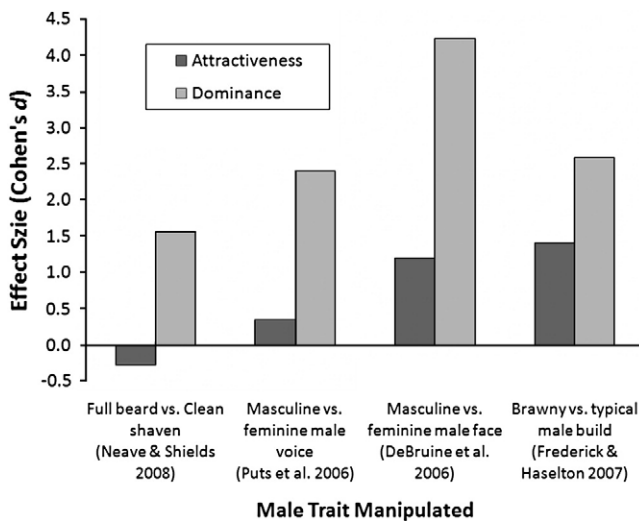

Fig. 4. Masculinity in facial hair, voice, facial structure and body build has larger positive effects on perceptions of dominance than on perceptions of attractiveness. Note: the important comparisons are the effects of masculinity on attractiveness versus dominance within each study. Between-studies comparisons are confounded by differences in the magnitude of manipulations and other methodological details.

hypothesis offers explanations for the evolution of large human brains and behaviors such as humor, music, and poetry that do not have obvious survival value. It also accords with widespread preferences for intelligent mates and the moderate heritability of intelligence, which affords the opportunity for genes associated with intelligence to be favored by mate choice.

Despite these advantages, Miller's hypothesis suffers shortcomings (Miller, 2001). Betzig (2002) notes that sexual selection tends to produce sexual dimorphism, but men's brains are only slightly larger relative to body size than women's (Ankney, 1992), and sex differences in overall intelligence, if present, are small (Irwing & Lynn, 2005). Although women may produce fewer creative displays than men do (Miller, 2000), it is unclear how ancestral women could offset the costs of producing and maintaining large brains under Miller's hypothesis.

The mating-mind hypothesis better explains men's investment in creative displays, rather than human intelligence generally (Miller, 2001). Even this narrower version encounters difficulties. Men's mental displays lack features of an ornament advertising genetic quality. As we have seen, putative good-genes indicators are preferred more in short-term, sexual mating contexts, and near ovulation (Gangestad & Thornhill, 2008). Yet, women prefer intelligence, creativity, and humor more in long-term relationships (Bressler, Martin, & Balshine, 2006; Gangestad, Garver-Apgar, Simpson, & Cousins, 2007; Kenrick, Sadalla, Groth, & Trost, 1990; Prokosch, Coss, Scheib, & Blozis, 2009). Women also do not seem to prefer intelligent men more strongly near ovulation (Gangestad et al., 2007; Prokosch et al., 2009, but see Haselton & Miller, 2006).

An intriguing possibility is that creative displays represent an alternative mating tactic to male contests. Contest competition favors not only fighting ability but also "alternative mating tactics of inferior competitors, avoiding contests with superior rivals" (Andersson, 1994, Table 1.1.1). Alternative mating tactics probably occur in most nonhuman primates, and often involve mate attraction (Smuts, 1987). For example, alpha male chimpanzees monopolize estrous females through possessive behavior, while non-alpha males form sexual consortships away from other males (Smuts, 1987). Consortships often appear to occur through mate choice, although they may sometimes result from sexual coercion (Smuts, 1987; Wrangham & Peterson, 1996). Given the importance of male investment in human reproduction (Kaplan, Hill, Lancaster, & Hurtado, 2000), creative displays may represent "super-stimuli" (Miller, 2000) designed to trigger female preferences for investing mates. Thus, while large brains cannot presently be regarded as sexual ornaments, men's creative displays may represent courtship behaviors shaped by female choice, perhaps as part of an alternative mating tactic to contest competition.

3.3.3. Does female choice drive male dominance competition?

It is possible that men engage in contest competition primarily because women prefer dominant men. Women have been shown to prefer dominant male behavior in short-term/sexual mating contexts and during the fertile phase of the menstrual cycle (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004; Snyder, Kirkpatrick, & Barrett, 2008), apparently because these preferences garnered genetic benefits ancestrally. As noted above, women also prefer the perquisites of dominance, including protection and access to resources.

However, strong sexual selection through mate choice tends to produce sexual ornaments and displays—traits favored primarily through their utility in mate attraction. Even in lekking species, where females choose dominant males, males tend to evolve sexual ornaments and displays (Andersson, 1994). But we do not see these in humans, except possibly for creative displays and large penises.

Furthermore, some evidence suggests that women had less freedom of mate choice ancestrally than they do in many modern industrial societies (Apostolou, 2007; Low, 2005; Smuts, 1995). Among foragers, reproduction occurs mainly within the context of marriage, and familial control over women's marriage decisions is prevalent (Apostolou, 2007). [Men's marriages are not as strongly influenced by family members (Apostolou, 2007).] In most societies, men may purchase women from women's families through bride-price or bride-service (Murdock, 1967), or steal women from other villages (e.g., Chagnon, 1992). Men also constrain women's choices through the threats of loss of investment and physical injury to mates and competitors. Among both traditional (Chagnon, 1992; Marlowe, 2004) and industrial societies (Daly & Wilson, 1988), men injure or kill wives whom they suspect of infidelity and injure or kill other men in competition over women. Men's greater size, strength, and physical aggressiveness contribute to an ability to sexually coerce females (Clutton-Brock & Parker, 1995). Women may have less influence over mating when they lack kin support (Smuts, 1996), and female exogamy was likely the ancestral human condition (Chapais, 2008; Fox, 1980; Wrangham, 1987). In general, men everywhere appear concerned with controlling women's reproductive capacity (e.g., Daly & Wilson, 1983; Dickemann, 1981).

This is not to say that ancestral women had little choice. In some traditional societies women choose their spouses (Marlowe, 2004), and across traditional societies women frequently influence their family's choice of a spouse, are often consulted, and occasionally elope (Apostolou, 2007). Divorce is also commonly initiated by women (Betzig, 1989). Women have affairs, although men's proprietariness over women makes this behavior risky (Kaighobadi & Shackelford, 2009; Kaighobadi, Starratt, Shackelford, & Popp, 2008; Wilson & Daly, 1993; Wilson & Daly, 1996). Given the cross-cultural frequency of these conditions (Apostolou, 2007), women probably also utilized these avenues of mate choice over human evolution (Small, 1992).

Indeed, preferences are costly and generally do not evolve without some compensatory benefit (but see, e.g., Ryan & Rand, 1995).

In a species such as *Homo sapiens*, where mate choice and contests occur simultaneously, it can be difficult to disentangle their relative contributions. Several lines of evidence reviewed above are relevant. Men's traits look designed to make men appear threatening, or enable them to inflict real harm. Men's beards and deep voices seem designed specifically to increase apparent size and dominance. Size, musculature, aggression, and the manufacture and use of weapons directly increase fighting ability. Even masculine facial structure may be designed for fighting; heavy brow ridges protect eyes from blows, and robust mandibles lessen the risk of catastrophic jaw fractures, for example. Men's traits and a human tendency toward polygyny (Murdock, 1967) indicate an evolutionary history of male monopolization of females through force. Many of men's traits are probably not generally preferred by females, and those that are appear better designed for contests than mate attraction. Various constraints on female mating, including familial control of marriage, female exogamy, male sexual coercion and mate guarding, and male exclusion of competitors by force, also challenge the notion that ancestral men competed for dominance primarily to be chosen by women. Although more work is needed before firm conclusions can be drawn, cross-species comparison, empirical evidence of design, and multiple features of human mating support the theoretical prediction that contest competition was the predominate form of sexual selection in men. The contention that "adult male hominids must have been rather peripheral characters in human evolution, except as bearers of traits sexually selected by females for their amusement value or utility" (Miller, 1998, p. 109) is almost certainly false.

3.4. Male choice

Although contest competition may have predominated in shaping men's traits, male mate choice is expected to have been more important in shaping women's. Why might women compete for mates? While men contribute far less parental care than women do across societies (Hewlett, 1992), men protect mates and offspring from predators and other men, and can provide high quality food through hunting. Men procure more food (in kcal) than women do in foraging societies, far more than they consume (Kaplan et al., 2000). In contemporary foragers, men use meat to obtain mating opportunities (Hawkes, 1991) and to invest in current mates and offspring (Kaplan et al., 2000; Marlowe, 2003), and meat probably served this dual function over human evolution. The proportion of a man's resources channeled toward parenting likely depended on his paternity confidence (Anderson, Kaplan, Lam, & Lancaster, 1999; Anderson, Kaplan, & Lancaster, 1999, 2007).

To the extent that men vary in their ability to protect and provide, women are expected to compete for these benefits (Cant, 1981; Geary & Flinn, 2001; Symons, 1979). Compared to mechanisms of sexual selection in men, the mechanism of sexual selection in women is uncontroversial. Multi-female groups and strong selection for fighting ability in men militated against female monopolization of men through force. Although ancestral females could not make themselves the only option, they could compete to be the most attractive one. Men generally value mates' physical attractiveness highly across societies (Buss, 1989), especially in mating contexts where male investment is highest (Kenrick et al., 1990). Where male investment is important, women endeavor to appear chaste and faithful, apparently to increase attractiveness as targets of investment, and their insults often derogate competitors' chastity and attractiveness (Cashdan, 1996; Fisher & Cox, 2009; Schmitt & Buss, 1996), apparently to make their rivals less attractive targets of investment (Buss & Dedden, 1990). In addition, more physically attractive women demand greater male investment and other direct and indirect benefits (Buss & Shackelford, 2008; Pawlowski & Jasienska, 2008).

Women compete to look attractive (Cashdan, 1996, 1998; Schmitt & Buss, 1996) and possess anatomical traits that appear to have been shaped by male mate choice (Barber, 1995; Thornhill & Grammer, 1999). Women's residual reproductive value peaks at sexual maturity, fecundity peaks in the mid-twenties, and both decline rapidly near menopause (Wood, 1992). It is therefore unsurprising that men prefer young women the world over (Buss, 1989). Several of women's traits increase youthful appearance, including gracile facial features, reduced body hair, and high voices —all characteristics of immature primates (Cunningham, 1986; Jones & Hill, 1993; McArthur & Berry, 1983). These traits are also preferred by men (Collins & Missing, 2003; Cunningham, 1986; Rilling, Kaufman, Smith, Patel, & Worthman, 2009). Women may have evolved to exploit a male tendency to protect and provide for infants by evolving infant-like features, but men's preferences were probably maintained because youthful traits in women reliably index reproductive value, fertility, and perhaps heritable disease resistance (Scheyd, Garver-Apgar, & Gangestad, 2008).

Women's body fat distribution also appears to be designed to attract mates (Cant, 1981; Low, Alexander, & Noonan, 1987). No other primate is sexual dimorphic in body fat distribution (Pond & Mattacks, 1987). Women deposit fat on their breasts and hips as they approach sexual maturity, which suggests that these traits are involved in mating. This possibility is reinforced by evidence that men prefer these traits (Marlowe, Apicella, & Reed, 2005; Singh, 1993, 1995; Singh & Young, 1995; Streeter & McBurney, 2003). Large body fat stores are needed for ovulation, probably to provide the necessary resources for a long pregnancy and lactation, but the placement of fat on the hips, buttocks, and breasts may advertise fecundity (Jasienska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004; Marlowe, 1998; Singh, 1993) and the

storage of essential fats for fetal and infant brain development (Lassek & Gaulin, 2008; Lassek & Gaulin, 2006). The placement of fat in these locations may also have evolved to take advantage of existing male preferences for females with more mammary glandular tissue and wider pelvises (Low, 1979; Low et al., 1987).

Whereas women's traits appear well-designed for mate attraction, they do not appear designed for contest competition. Fatty breasts and hips probably do not increase fighting ability, and feminine traits such as high-pitched voices, reduced facial hair, and gracile faces decrease the appearance of dominance and resistance to blows (see above).

4. Summary

The ancestral human mating system may have comprised groups of (often related) males cooperating in female defense. Between-group aggression, female cooperation, and the ability to inflict lethal injuries with weapons likely enabled some males to monopolize multiple females. At the same time, female defense was imperfect, promoting moderate sperm competition and female choice of both long-term mates and extra-pair sex partners. Monopolization of females was probably related to social skills and attractiveness to females, but force or threat of force seems to have been especially important. Moderate paternity confidence coupled with efficient hunting promoted male investment, which may have been elaborated as an alternative mating tactic. Females may have evolved sexual ornaments such as neotenic faces, high-pitched voices, and fatty breasts and hips to attract male investment.

5. Conclusions

Human mating is complicated. It is the stuff of operas and soap operas, full of manipulation and deception, aggression and solicitude, cooperation and selfishness. It is the culmination of multiple individual interests, sometimes overlapping, often opposing. Human mating is perhaps even more complicated than it appears in contemporary industrial societies, where men and women choose their mates largely beyond the authority of kin, women do not rely economically on men, and men are prohibited by the state from using force against mates and sexual competitors. As complicated as human mating is, it is becoming clear that contests must have been very important in determining men's reproductive success, and male mate choice must have been very important in determining women's reproductive success. We can predict this theoretically from the dimensionality of our mating environment, the structure of human groups, differential parental investment, and phylogeny. We can also see it in the traits that selection has produced.

The idea that male mate choice has been an important selection pressure on women is relatively uncontroversial,

but the importance of male contests appears to contradict a prevailing view that female mate choice has predominated in shaping men's phenotypes. It is interesting to speculate on why there has been such focus on mate choice. Perhaps it is because most research has been carried out by researchers from industrial societies, where men and women freely choose their mates. Then again, perhaps the recent focus on mate choice—and in particular female mate choice—may partly be reactionary to the scant attention females were paid in earlier sociobiological literature (see, e.g., Fedigan, 1982). Mate choice theory is also probably more alluring to researchers, posing fascinating questions about the importance of indicator models versus Fisherian runaway sexual selection, for example. The research bias toward female mate choice is not specific to human studies (Berglund et al., 1996). Researchers have also tended to interpret, incorrectly, as I have tried to make clear, the modest human sexual dimorphism in overall body mass as evidence against strong contest competition in men, ignoring large sex differences in the allocation of fat and muscle. Much, too, depends on one's choice of model organisms. It is easy to see parallels between avian mating and human social monogamy, extra-pair mating, and the like. Phylogeny and ecological selective pressures, such as the dimensionality of the mating environment, probably directed sexual selection in birds more toward mate choice than contests. Yet, phylogenetic and selective considerations predict the opposite regarding human mating competition, invalidating some inferences from avian models.

More work is needed in identifying and testing the variables affecting mechanisms of sexual selection across species. A goal of this paper is to encourage such research. The central goal, however, is to provide a framework for future research on human sexual selection. Even for those interested only in understanding mating in industrial nations, where mate choice predominates, it will help to know the contexts under which our preferences and other mating behaviors evolved. It could be harmful, for example, to underestimate the extent of male-male competition in shaping human nature; an evolutionary history of male contest competition is likely responsible—at least in part—for a host of social afflictions, including bullying, homicide, gang violence, and war. A framework for understanding human sexual selection is important because it affects how we view our anatomical and behavioral traits, and because it affects the kinds of questions that we ask about them.

Future work should investigate whether putative sexually selected traits in men and women appear better designed for contests, mate attraction, or another function by testing competing hypotheses simultaneously. Cross-cultural work, particularly in traditional societies, will be especially useful to this end. Likewise, researchers should continue to explore the determinants of mating and reproductive success across populations and assess the relative contributions of dominance and attractiveness. Further exploration of the fossil record will be essential for determining mating systems and

the extent of sexual dimorphism in our hominin ancestors. The idea that contests were the main form of sexual selection in men suggests that mate attraction through creative displays may be an alternative mating tactic, a hypothesis also inviting investigation.

Acknowledgments

References

Abe, T., Kearns, C. F., & Fukunaga, T. (2003). Sex differences in whole body skeletal muscle mass measured by magnetic resonance imaging and its distribution in young Japanese adults. *British Journal of Sports Medicine, 37*(5), 436−440.

Adams, D. B. (1983). Why there are so few women warriors. *Behavior Science Research, 18*, 196−212.

Adi, M., Ogden, G. R., & Chisholm, D. M. (1990). An analysis of mandibular fractures in Dundee, Scotland (1977 to 1985). *British Journal of Oral & Maxillofacial Surgery, 28*(3), 194−199.

Alexander, R. D. (1989). The evolution of the human psyche. In P. Mellars, & C. Stringer (Eds.), *The Human Revolution* (pp. 455−513). Princeton, NJ: Princeton University Press.

Anderson, K. G., Kaplan, H., Lam, D., & Lancaster, J. B. (1999). Paternal care by genetic fathers and stepfathers II: Reports by Xhosa high school students. *Evolution and Human Behavior, 20*(6), 433−451.

Anderson, K. G., Kaplan, H., & Lancaster, J. B. (1999). Paternal care by genetic fathers and stepfathers I: Reports from Albuquerque men. *Evolution and Human Behavior, 20*(6), 405−431.

Anderson, K. G., Kaplan, H., & Lancaster, J. B. (2007). Confidence of paternity, divorce, and investment in children by Albuquerque men. *Evolution and Human Behavior, 28*(1), 1−10.

Andersson, M. (1982). Female choice selects for extreme tail length in a widowbird. *Nature, 299*, 818−1220.

Andersson, M. (1994). *Sexual Selection.* Princeton, NJ: Princeton University Press.

Ankney, C. D. (1992). Differences in brain size. *Nature, 358*(6387), 532.

Apostolou, M. (2007). Sexual selection under parental choice: The role of parents in the evolution of human mating. *Evolution and Human Behavior, 28*(6), 403−409.

Archer, J. (2004). Sex differences in aggression in real-world settings: A meta-analytic review. *Review of General Psychology, 4*, 291−322.

Archer, J. (2009). Does sexual selection explain human sex differences in aggression? *Behavioral and Brain Sciences, 32*(3-4), 249−266.

Baker, R. R., & Bellis, M. A. (1995). *Human sperm competition: Copulation, masturbation, and infidelity.* London: Chapman and Hall.

Barber, N. (1995). The evolutionary psychology of physical attractiveness: Sexual selection and human morphology. *Ethology and Sociobiology, 16*(5), 395−424.

Bateman, A. J. (1948). Intra-sexual selection in Drosophila. *Heredity, 2*, 349−368.

Bellis, M. A., Hughes, K., Hughes, S., & Ashton, J. R. (2005). Measuring paternal discrepancy and its public health consequences. *Journal of Epidemiology and Community Health, 59*(9), 749−754.

Berglund, A., Bisazza, A., & Pilastro, A. (1996). Armaments and ornaments: An evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society, 58*, 385−399.

Betzig, L. L. (1986). *Darwinism and Differential Reproduction: A Darwinian View of History.* Hawthorne, MY: Aldine de Gruyter.

Betzig, L. L. (1989). Causes of conjugal dissolution: A cross-cultural study. *Current Anthropology, 30*(5), 654−676.

Betzig, L. L. (1995). Medieval monogamy. *Journal of Family History, 20*(2), 181−216.

Betzig, L. L. (2002). Croaks and tails or teeth and claws? Book review of Miller on mating-mind. *Psycoloquy, 13*(009), 4.

Bongaarts, J., & Potter, R. G. (1986). *Fertility, biology and behavior: An analysis of proximate determinants.* New York: Academic.

Booth, A., & Dabbs, J. M. (1993). Testosterone and men's marriages. *Social Forces, 72*, 463−477.

Boyd, I. L. (1989). Spatial and temporal distribution of Antarctic fur seals (*Arctocephalus gazella*) on the breeding grounds at Bird Island, South Georgia. *Polar Biology, 10*, 179−185.

Bressler, E. R., Martin, R. A., & Balshine, S. (2006). Production and appreciation of humor as sexually selected traits. *Evolution and Human Behavior, 27*(2), 121−130.

Brown, G. R., Laland, K. N., & Borgerhoff Mulder, M. (2009). Bateman's principles and human sex roles. *Trends in Ecology and Evolution, 24*(6), 297−304.

Bruckert, L., Lienard, J. S., Lacroix, A., Kreutzer, M., & Leboucher, G. (2006). Women use voice parameters to assess men's characteristics. *Proceedings Biological Sciences, 273*(1582), 83−89.

Buss, A. H., & Perry, M. (1992). The aggression questionnaire. *Journal of Personality and Social Psychology, 63*(3), 452−459.

Buss, D. (1996). Sexual conflict: Evolutionary insight into feminism and the "battle of the sexes". In D. Buss, & N. Malamuth (Eds.), *Sex, power and conflict: Evolutionary and feminist perspectives* (pp. 296−318). New York: Oxford University Press.

Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences, 12*, 1−49.

Buss, D. M., & Dedden, L. A. (1990). Derogation of competitors. *Journal of Social and Personal Relationships, 7*, 395−422.

Buss, D. M., & Duntley, J. D. (2006). The evolution of aggression. In M. Schaller, D. T. Kenrick, & J. A. Simpson (Eds.), *Evolution and social psychology* (pp. 263−286). New York: Psychology Press.

Buss, D. M., Larsen, R. J., Westen, D., & Semelroth, J. (1997). Sex differences in jealousy: Evolution, physiology, and psychology. *Psychological Science, 3*, 251−255.

Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review, 100*(2), 204−232.

Buss, D. M., & Shackelford, T. K. (1997). Human aggression in evolutionary psychological perspective. *Clinical Psychology Review, 17*(6), 605−619.

Buss, D. M., & Shackelford, T. K. (2008). Attractive women want it all: Good genes, investment, parenting indicators, and commitment. *Evolutionary Psychology, 6*, 134−146.

Caizergues, A., & Lambrechts, M. M. (1999). Male "macho" mammals exploiting females versus male "Don Juan" birds exploited by females: The opposite-sex exploitation (OSEX) theory. *Ecology Letters, 2*, 204−206.

Cant, J. G. H. (1981). Hypothesis for the evolution of human breasts and buttocks. *The American Naturalist, 117*, 199−204.

Cashdan, E. (1996). Women's mating strategies. *Evolutionary Anthropology, 5*, 134−143.

Cashdan, E. (1998). Are men more competitive than women? *British Journal of Social Psychology, 37*(Pt 2), 213−229.

Chagnon, N. A. (1979). Mate competition, favoring close kin, and village fissioning among the Yanomamo Indians. In N. Chagon, & W. Irons (Eds.), *Evolutionary Biology of Human Social Behavior* (pp. 86−132). North Scituate, MA: Duxbury Press.

Chagnon, N. A. (1988). Life histories, blood revenge, and warfare in a tribal population. *Science, 239*(4843), 985−992.

Chagnon, N. A. (1992). *Yanomamo.* (4th ed.) Harcourt Brace: Fort Worth.

Chaix, R., Cao, C., & Donnelly, P. (2008). Is mate choice in humans MHC-dependent? *PLoS Genetics, 4*(9), e1000184.

Chapais, B. (2008). *Primeval kinship: How pair bonding gave birth to human society.* Cambridge, MA: Harvard University Press.

Charlton, B. D., Reby, D., & McComb, K. (2007). Female red deer prefer the roars of larger males. *Biology Letters, 3*(4), 382−385.

Cheuvront, S. N., Carter, R., Deruisseau, K. C., & Moffatt, R. J. (2005). Running performance differences between men and women: an update. *Sports Medicine, 35*(12), 1017−1024.

Christensen, J. (2004). Warfare in the European Neolithic. *Acta Archaeologica, 75*, 129−156.

Christy, J. H., & Salmon, M. (1991). Comparative studies of reproductive behavior in mantis shrimps and fiddler crabs. *American Zoologist, 31*, 329−337.

Clutton-Brock, T. H., & Harvey, P. H. (1976). Evolutionary rules and primate societies. In P. P. G. Bateson, & R. A. Hinde (Eds.), *Growing points in ethology* (pp. 195−237). Cambridge: Cambridge University Press.

Clutton-Brock, T. H., & Harvey, P. H. (1984). Comparative approaches to investigating adaptation. In J. R. Krebs, & N. B. Davies (Eds.), *Behavioral ecology: An evolutionary approach* (2nd ed., pp. 7−29). Oxford: Blackwell.

Clutton-Brock, T. H., Harvey, P. H., & Rudder, B. (1977). Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature, 269*(5631), 797−800.

Clutton-Brock, T. H., & Parker, G. A. (1995). Punishment in animal societies. *Nature, 373*(6511), 209−216.

Clutton-Brock, T. H., & Vincent, A. C. J. (1991). Sexual selection and the potential reproductive rates of males and females. *Nature, 351*, 58−60.

Collins, S. A., & Missing, C. (2003). Vocal and visual attractiveness are related in women. *Animal Behaviour, 6*, 997−1004.

Connor, R. C., Richards, A. F., Smolker, R. A., & Mann, J. (1996). Patterns of female attractiveness in Indian Ocean bottlenose dolphins. *Behaviour, 133*(1-2), 37−69.

Cooper, V. J., & Hosey, C. R. (2003). Sexual dichromatism and female preference in *Eulemur fulvus* subspecies. *International Journal of Primatology, 24*(6), 1177−1188.

Crane, J. (1975). *Fiddler Crabs of the World.* Princeton, NJ: Princeton University Press.

Crockett, C. M. (1987). Howler monkeys: Diet, dimorphism, and demography: perspectives from howlers to hominids. In W. G. Kinzey (Ed.), *The evolution of human behavior: Primate models* (pp. 115−138). Albany, NY: SUNY Press.

Crook, J. H. (1972). Sexual selection, dimorphism, and social organization in the primates. In B. G. Campbell (Ed.), *Sexual selection and the descent of man 1871-1971* (pp. 231−281). Chicago: Aldine.

Cunningham, M. R. (1986). Measuring the physical in physical attractiveness: Quasi-experiments in the sociobiology of female facial beauty. *Journal of Personality and Social Psychology, 50*, 925−935.

D'Andrade, R. (1974). Sex differences and cultural institutions. In R. A. LeVine (Ed.), *Culture and Personality* (pp. 16−39). New Brunswick, NJ: Aldine Transaction.

Dabbs, J. M., & Mallinger, A. (1999). High testosterone levels predict low voice pitch among men. *Personality and Individual Differences, 27*, 801−804.

Daly, M., & Wilson, M. (1983). *Sex, evolution, and behavior.* (2nd ed.) Belmont, CA: Wadsworth.

Daly, M., & Wilson, M. (1988). *Homicide.* New York: Aldine de Gruyter.

Daly, M., Wilson, M. I., & Weghorst, S. J. (1982). Male sexual jealousy. *Ethology and Sociobiology, 3*, 11−27.

Darwin, C. (1859). *On the origin of species by means of natural selection.* London: Murray.

Darwin, C. (1871). *The descent of man, and selection in relation to sex.* London: Murray.

DeBruine, L. M., Jones, B. C., Little, A. C., Boothroyd, L. G., Perrett, D. I., Penton-Voak, I. S., et al. (2006). Correlated preferences for facial masculinity and ideal or actual partner's masculinity. *Proceedings of the Royal Society B: Biological Sciences, 273*(1592), 1355−1360.

Diamond, J. (1997). *Why is sex fun? The Evolution of human sexuality.* New York: Basic Books.

Dickemann, M. (1981). Paternal confidence and dowry competition: A biocultural analysis of purdah. In R. D. Alexander, & D. W. Tinkel (Eds.), *Natural selection and social behavior: Recent research and new theory* (pp. 417−438). New York: Chiron Press.

Dominguez-Rodrigo, M., Pickering, T. R., Semaw, S., & Rogers, M. J. (2005). Cutmarked bones from Pliocene archaeological sites at Gona, Afar, Ethiopia: Implications for the function of the world's oldest stone tools. *Journal of Human Evolution, 48*(2), 109−121.

Eberhard, W. G. (1979). The function of horns in Podischnus agenor (Dynastinae) and other beetles. In M. S. Blum, & N. A. Blum (Eds.), *Sexual selection and reproductive competition in insects* (pp. 231−258). New York: Academic Press.

Eibl-Eibesfeldt, I. (1989). *Human ethology.* New York: Aldine de Gruyter.

Ellis, L., Hershberger, S., Field, E., Wersinger, S., Pellis, S., Geary, D., et al. (2008). Sex differences: Summarizing more than a century of scientific research. New York.

Emlen, D. J. (2008). The evolution of animal weapons. *Annual Review in Ecology & Evolution System, 39*, 387−413.

Emlen, D. J., & Philips, T. K. (2006). Phylogenetic evidence for an association between tunneling behavior and the evolution of horns in dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Coleopterists Society Monographs, 5*, 47−56.

Emlen, S. T. (1976). Lek organization and mating strategies in the bullfrog. *Behavioral Ecology and Sociobiology, 1*, 283−313.

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science, 197*(4300), 215−223.

Evans, S., Neave, N., Wakelin, D., & Hamilton, C. (2008). The relationship between testosterone and vocal frequencies in human males. *Physiology and Behavior, 93*(4-5), 783−788.

Fedigan, L. M. (1982). *Primate Paradigms.* Montreal: Eden Press.

Feinberg, D. R., Jones, B. C., Little, A. C., Burt, D. M., & Perrett, D. I. (2005). Manipulations of fundamental and formant frequencies affect the attractiveness of human male voices. *Animal Behaviour, 69*, 561−568.

Fisher, M., & Cox, A. (2009). The influence of female attractiveness on competitor derogation. *Journal of Evolutionary Psychology, 7*(2), 141−155.

Fisher, R. A. (1930). *The Genetical Theory of Natural Selection.* Oxford: Clarendon Press.

Flinn, M. V., Quinlan, R. L., Ward, C. V., & Coe, M. K. (2007). Evolution of the human family: Cooperative males, long social childhoods, smart mothers, and extended kin networks. In C. Salmon, & T. Shackelford (Eds.), *Family relationships* (pp. 16−38). Oxford: Oxford University Press.

Folstad, I., & Karter, A. J. (1992). Parasites, bright males and the immunocompetence handicap. *The American Naturalist, 139*, 603−622.

Fox, R. (1980). *The Red Lamp of Incest.* New York: Dutton.

Frederick, D. A., & Haselton, M. G. (2007). Why is muscularity sexy? Tests of the fitness indicator hypothesis. *Personality and Social Psychology Bulletin, 33*(8), 1167−1183.

Fuller, R. C. (1998). Sperm competition affects male behaviour and sperm output in the rainbow darter. *Proceedings of the Royal Society B: Biological Sciences, 265*, 2365−2371.

Gallup, G. G., Burch, R. L., Zappieri, M. L., Parvez, R. A., Stockwell, M. L., & Davis, J. A. (2003). The human penis as a semen displacement device. *Evolution and Human Behavior, 24*, 277−289.

Gangestad, S. W. (1993). Sexual selection and physical attractiveness: Implications for mating dynamics. *Human Nature, 4*, 205−235.

Gangestad, S. W., Garver-Apgar, C. E., Simpson, J. A., & Cousins, A. J. (2007). Changes in women's mate preferences across the ovulatory cycle. *Journal of Personality and Social Psychology, 92*, 151−163.

Gangestad, S. W., & Simpson, J. A. (2000). On the evolutionary psychology of human mating: Trade-offs and strategic pluralism. *Behavioral and Brain Sciences, 23*, 573−587.

Gangestad, S. W., Simpson, J. A., Cousins, A. J., Garver-Apgar, C. E., & Christensen, P. N. (2004). Women's preferences for male behavioral displays change across the menstrual cycle. *Psychological Science, 15*(3), 203−207.

Gangestad, S. W., & Thornhill, R. (1997). The evolutionary psychology of extrapair sex: The role of fluctuating asymmetry. *Evolution and Human Behavior, 18*(2), 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 B: Biological Sciences, 265*(1399), 927−933.

Gangestad, S. W., & Thornhill, R. (1999). Individual differences in developmental precision and fluctuating asymmetry: A model and its implications. *Journal of Evolutionary Biology, 12*, 406−416.

Gangestad, S. W., & Thornhill, R. (2003). Facial masculinity and fluctuating asymmetry. *Evolution and Human Behavior, 24*, 231−241.

Gangestad, S. W., & Thornhill, R. (2008). Human oestrus. *Proceedings of the Royal Society B: Biological Sciences, 275*(1638), 991−1000.

Gangestad, S. W., Thornhill, R., & Garver-Apgar, C. E. (2005). Women's sexual interests across the ovulatory cycle depend on primary partner developmental instability. *Proceedings Biological Sciences, 272*(1576), 2023−2027.

Gangestad, S. W., Thornhill, R., & Garver, C. E. (2002). Changes in women's sexual interests and their partners' mate-retention tactics across the menstrual cycle: Evidence for shifting conflicts of interest. *Proceedings Biological Sciences, 269*(1494), 975−982.

Gangestad, S. W., Thornhill, R., & Yeo, R. A. (1994). Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology, 15*, 73−85.

Gat, A. (2006). *War in Human Civilization.* Oxford: Oxford University Press.

Gaulin, S., & Sailer, L. D. (1984). Sexual dimorphism in weight among the primates: The relative impact of allometry and sexual selection. *International Journal of Primatology, 5*(6), 515−535.

Gaulin, S. J. C., & Boster, J. S. (1985). Cross cultural differences in sexual dimorphism: Is there any variance to be explained. *Ethology and Sociobiology, 6*, 193−199.

Geary, D. C., & Flinn, M. V. (2001). Evolution of human parental behavior and the human family. *Parenting: Science and Practice, 1*(1), 5−61.

Geary, D. C., & Flinn, M. V. (2002). Sex differences in behavioral and hormonal response to social threat: Commentary on Taylor et al. (2000). *Psychological Review, 109*(4), 745−750.

Gladstone, W. (1987). The eggs and larvae of the sharpnose pufferfish *Canthigaster valentini* (Pisces: Tetraodontidae) are unpalatable to other reef fishes. *Copeia, 1*, 227−230.

Goodall, J. (1968). The behavior of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behavior Monographs, 1*, 165−311.

Gray, P. B., Kahlenberg, S. M., Barrett, E. S., Lipson, S. F., & Ellison, P. T. (2002). Marriage and fatherhood are associated with lower testosterone in males. *Evolution and Human Behavior, 23*(3), 193−201.

Greiling, H., & Buss, D. M. (2000). Women's sexual strategies: The hidden dimension of extra-pair mating. *Personality and Individual Differences, 28*, 929−963.

Gross, M. R., & MacMillan, A. M. (1981). Predation and the evolution of colonial nesting in bluegill sunfish (*Lepomis macrochirus*). *Behavioral Ecology and Sociobiology, 8*(3), 163−174.

Grossman, C. J. (1985). Interactions between the gonadal steroids and the immune system. *Science, 227*(4684), 257−261.

Guthrie, R. D. (1970). Evolution of human threat display organs. In T. Dobzansky, M. K. Hecht, & W. C. Steers (Eds.), *Evolutionary Biology* (pp. 257−302). New York: Appleton-Century-Crofts.

Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites? *Science, 218*(4570), 384−387.

Harcourt, A. H., Harvey, P. H., Larson, S. G., & Short, R. V. (1981). Testis weight, body weight and breeding system in primates. *Nature, 293* (5827), 55−57.

Harcourt, A. H., Purvis, A., & Liles, L. (1995). Sperm competition: Mating system, not breeding season, affects testes size of primates. *Functional Ecology, 9*, 468−476.

Harrison, M. E., & Chivers, D. J. (2007). The orang-utan mating system and the unflanged male: A product of increased food stress during the late Miocene and Pliocene? *Journal of Human Evolution, 52*(3), 275−293.

Haselton, M. G., & Gangestad, S. W. (2006). Conditional expression of women's desires and men's mate guarding across the ovulatory cycle. *Hormones and Behavior, 49*, 509−518.

Haselton, M. G., & Miller, G. F. (2006). Women's fertility across the cycle increases the short-term attractiveness of creative intelligence compared to wealth. *Human Nature, 17*(1), 50−73.

Haug, R. H., Prather, J., & Indresano, A. T. (1990). An epidemiologic survey of facial fractures and concomitant injuries. *Journal of Oral and Maxillofacial Surgery, 48*(9), 926−932.

Hawkes, K. (1990). Why do men hunt? Benefits for risky choices. In E. Cashdan (Ed.), *Risk and uncertainty in tribal and peasant economies* (pp. 146−166). Boulder, CO: Westview Press.

Hawkes, K. (1991). Showing off: Tests of an hypothesis about men's foraging goals. *Ethology and Sociobiology, 12*, 29−54.

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.

Hillgarth, N. (1990). Parasites and female choice in the ring-necked pheasant. *American Zoologist, 30*, 227−233.

Hines, M., Fane, B. A., Pasterski, V. L., Mathews, G. A., Conway, G. S., & Brook, C. (2003). Spatial abilities following prenatal androgen abnormality: Targeting and mental rotations performance in individuals with congenital adrenal hyperplasia. *Psychoneuroendocrinology, 28*(8), 1010−1026.

Horvath, T. (1981). Physical attractiveness: The influence of selected torso parameters. *Archives of Sexual Behavior, 10*(1), 21−24.

Howell, N. (1979). *Demography of the Dobe !Kung.* New York: Academic Press.

Hrdy, S. B. (1979). Infanticide among mammals: A review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology, 1*, 13−40.

Hrdy, S. B. (1997). Raising Darwin's consciousness: Female sexuality and the prehominid origins of patriarchy. *Human Nature, 8*(1), 1−49.

Hughes, S. M., Dispenza, F., & Gallup, G. G. (2004). Ratings of voice attractiveness predict sexual behavior and body configuration. *Evolution and Human Behavior, 25*, 295−304.

Hughes, S. M., Harrison, M. A., & Gallup, G. G., Jr. (2002). The sound of symmetry: Voice as a marker of developmental instability. *Evolution and Human Behavior, 23*, 173−180.

Irwing, P., & Lynn, R. (2005). Sex differences in means and variability on the progressive matrices in university students: A meta-analysis. *British Journal of Psychology, 96*(Pt 4), 505−524.

Jasienska, G., Ziomkiewicz, A., Ellison, P. T., Lipson, S. F., & Thune, I. (2004). Large breasts and narrow waists indicate high reproductive potential in women. *Proceedings of the Royal Society B: Biological Sciences, 271*(1545), 1213−1217.

Johanna, A., Forsberg, L., & Tullberg, B. S. (1995). The relationship between cumulative number of cohabiting partners and number of children for men and women in modern Sweden. *Ethology and Sociobiology, 16*, 221−232.

Johnston, V. S., Hagel, R., Franklin, M., Fink, B., & Grammer, K. (2001). Male facial attractiveness: Evidence of hormone-mediated adaptive design. *Evolution and Human Behavior, 22*, 251−267.

Jones, D., & Hill, K. (1993). Criteria of facial attractiveness in five populations. *Human Nature, 4*(3), 271−296.

Jungers, W. L., & Susman, R. L. (1984). Body size and skeletal allometry in African apes. In R. L. Susman (Ed.), *The pygmy chimpanzee: Evolutionary biology and behavior* (pp. 131−177). New York: Plenum.

Kaar, P., Jokela, J., Merila, J., Helle, T., & Kojola, I. (1998). Sexual conflict and remarriage in preindustrial human populations: Causes and fitness consequences. *Evolution and Human Behavior, 19*, 139−151.

Kaighobadi, F., & Shackelford, T. K. (2009). Suspicions of female infidelity predict men's partner-directed violence. *Behavioral and Brain Sciences, 32*(3-4), 281−282 (discussion 292-311).

Kaighobadi, F., Starratt, V. G., Shackelford, T. K., & Popp, D. (2008). Male mate retention mediates the relationship between female sexual infidelity and female-directed violence. *Personality and Individual Differences, 44*, 1422−1431.

Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology, 9*(4), 156−185.

Kenrick, D. T., Sadalla, E. K., Groth, G., & Trost, M. R. (1990). Evolution, traits, and the stages of human courtship: Qualifying the parental investment model. *Journal of Personality, 58*, 97−116.

Kimura, D. (1999). *Sex and Cognition.* Cambridge, MA: Mit Press.

Knott, C. D., Emery Thompson, M., Stumpf, R. M., & McIntyre, M. H. (2009). Female reproductive strategies in orangutans, evidence for female choice and counterstrategies to infanticide in a species with frequent sexual coercion. *Proceedings of the Royal Society B: Biological Sciences, 277*(1678), 105−113.

Kodrick-Brown, A., & Brown, J. H. (1984). The kinds of traits favored by sexual selection. *American Naturalist, 124*(3), 309−323.

Lancaster, J. B., & Kaplan, H. S. (2009). The endocrinology of the human adaptive complex. In P. T. Ellison, & P. B. Gray (Eds.), *Endocrinology of social relationships* (pp. 95−118). Cambridge, MA: Harvard.

Lassek, W. D., & Gaulin, S. (2008). Waist-hip ratio and cognitive ability: Is gluteofemoral fat a privileged store of neurodevelopmental resources? *Evolution and Human Behavior, 29*, 26−34.

Lassek, W. D., & Gaulin, S. J. (2006). Changes in body fat distribution in relation to parity in American women: A covert form of maternal depletion. *American Journal of Physical Anthropology, 131*(2), 295−302.

Lassek, W. D., & Gaulin, S. J. C. (2009). Costs and benefits of fat-free muscle mass in men: Relationship to mating success, dietary requirements, and natural immunity. *Evolution and Human Behavior, 30*, 322−328.

Le Boeuf, B. J. (1974). Male-male competition and reproductive success in elephant seals. *American Zoologist, 14*, 163−176.

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*(6680), 62−66.

Leridon, H. (1977). *Human fertility.* Chicago: University of Chicago Press.

Lerner, G. (1986). *The Creation of Patriarchy.* Oxford: Oxford University Press.

Leutenegger, W., & Cheverud, J. (1982). Correlates of sexual dimorphism in primates: Ecological and size variables. *International Journal of Primatology, 3*(4), 387−402.

Leutenegger, W., & Kelly, J. T. (1977). Relationship of sexual dimorphism in canine size and body size to social, behavioral, and ecological correlates in anthropoid primates. *Primates, 18*(1), 117−136.

Lever, J., Frederick, D. A., & Peplau, L. A. (2006). Does size matter? Men's and women's views on penis size across the lifespan. *Psychology of Men and Masculinity, 7*, 129−143.

Lie, H. C., Rhodes, G., & Simmons, L. W. (2008). Genetic diversity revealed in human faces. *Evolution, 62*(10), 2473−2486.

Lindenfors, P., Froberg, L., & Nunn, C. L. (2004). Females drive primate social evolution. *Proceedings of the Royal Society B: Biological Sciences, 271*(Suppl 3), S101−S103.

Lindenfors, P., Tullberg, B. S., & Biuw, M. (2002). Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. *Behavioral Ecology and Sociobiology, 52*, 188−193.

Lorenz, K. (1966). *On aggression.* New York: Harcourt Brace Jovanovich.

Low, B. S. (1979). Sexual selection and human ornamentation. In N. A. Chagnon, & W. Irons (Eds.), *Evolutionary biology and human social behavior: An anthropological perspective* (pp. 462−487). North Scituate, MA: Duxbury.

Low, B. S. (2005). Women's lives there, here, then, now: A review of women's ecological and demographic constraints cross-culturally. *Evolution and Human Behavior, 26*(1), 64−87.

Low, B. S., Alexander, R. D., & Noonan, K. M. (1987). Human hips, breasts and buttocks: Is fat deceptive? *Ethology and Sociobiology, 8*(4), 249−257.

Marlowe, F. W. (1998). The nubility hypothesis: The human breast as an honest signal of residual reproductive value. *Human Nature, 9*(3), 263−271.

Marlowe, F. W. (2003). A critical period for provisioning by Hadza men Implications for pair bonding. *Evolution and Human Behavior, 24*, 217−229.

Marlowe, F. W. (2004). Mate preferences among Hadza hunter-gatherers. *Human Nature, 15*, 365−376.

Marlowe, F. W. (2005). Hunter-gatherers and human evolution. *Evolutionary Anthropology, 14*, 54−67.

Marlowe, F. W., Apicella, C. L., & Reed, D. (2005). Men's preferences for women's profile waist-to-hip ratio in two societies. *Evolution and Human Behavior, 26*, 458−468.

Mateos, C., & Carranza, J. (1996). On the intersexual selection for spurs in the ring-necked pheasant. *Behavioral Ecology, 7*(3), 362−369.

Mayhew, J. L., & Salm, P. C. (1990). Gender differences in anaerobic power tests. *European Journal of Applied Physiology and Occupational Physiology, 60*(2), 133−138.

McArthur, L. Z., & Berry, D. S. (1983). Impressions of baby-faced adults. *Social Cognition, 2*, 315−342.

Miller, G. F. (1998). How mate choice shaped human nature: A review of sexual selection and human evolution. In C. B. Crawford, & D. Krebs (Eds.), *Handbook of evolutionary psychology: Ideas, issues, and applications* (pp. 87−130). Mahwah, NJ: Lawrence Erlbaum Associates.

Miller, G. F. (2000). *The mating mind: How sexual choice shaped the evolution of human nature.* New York: Doubleday.

Miller, G. F. (2001). Mating-mind. *Psycoloquy, 12*(008), 1.

Moller, A. P., & Pomiankowski, A. (1993). Fluctuating assymmetry and sexual selection. *Genetica, 98*, 267−279.

Moller, A. P., & Thornhill, R. (1997). A meta-analysis of the heritability of developmental stability. *Journal of Evolutionary Biology, 10*, 1−16.

Morton, E. S. (1977). One the occurrence and significance of motivation—structural rules in some bird and mammal species. *The American Naturalist, 111*, 855−869.

Morton, E. S., & Page, J. (1992). *Animal talk: Science and the voices of nature.* New York: Random House.

Mueller, U., & Mazur, A. (1996). Facial dominance of West Point cadets as a predictor of later rank. *Social Forces, 74*(3), 823−850.

Muller, M. N., Kahlenberg, S. M., Emery Thompson, M., & Wrangham, R. W. (2007). Male coercion and the costs of promiscuous mating for female chimpanzees. *Proceedings of the Royal Society B: Biological Sciences, 274*(1612), 1009−1014.

Murdock, G. P. (1967). *Ethnographic Atlas.* Pittsburgh: University of Pittsburgh Press.

Muscarella, F., & Cunningham, M. R. (1996). The evolutionary significance and social perception of male pattern baldness and facial hair. *Ethology and Sociobiology, 17*, 99−117.

Neave, N., & Shields, K. (2008). The effects of facial hair manipulation on female perceptions of attractiveness, masculinity, and dominance in male faces. *Personality and Individual Differences, 45*, 373−377.

Nishida, T., & Hiraiwa-Hasegawa, M. (1987). Chimpanzee and bonobos: Cooperative relationships among males. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate Societies* (pp. 165−177). Chicago: University of Chicago Press.

Noble, G. K. (1938). Sexual selection among the fishes. *Biological Reviews, 13*, 133−158.

Nunn, C. L. (1999). The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. *Animal Behaviour, 58*(2), 229−246.

Parsons, P. A. (1990). Fluctuating asymmetry: An epigenetic measure of stress. *Biological Reviews of the Cambridge Philosophical Society, 65*(2), 131−145.

Parsons, P. A. (1992). Fluctuating asymmetry: A biological monitor of environmental and genomic stress. *Heredity, 68*(Pt 4), 361−364.

Pawlowski, B., & Jasienska, G. (2005). Women's preferences for sexual dimorphism in height depend on menstrual cycle phase and expected duration of relationship. *Biological Psychology, 70*(1), 38−43.

Pawlowski, B., & Jasienska, G. (2008). Women's body morphology and preferences for sexual partners' characteristics. *Evolution and Human Behavior, 29*(1), 19−25.

Payne, R. B. (1984). Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. *Ornithological Monographs, 33*, 1−53.

Pellegrini, A. D. (1995). A longitudinal study of boys' rough-and-tumble play and dominance during early adolescence. *Journal of Applied Developmental Psychology, 16*, 77−93.

Pellegrini, A. D., & Smith, P. K. (1998). Physical activity play: The nature and function of a neglected aspect of playing. *Child Development, 69*(3), 577−598.

Perrett, D. I., Lee, K. J., Penton-Voak, I., Rowland, D., Yoshikawa, S., Burt, D. M., et al. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature, 394*(6696), 884−887.

Pillsworth, E. G., & Haselton, M. G. (2006). Male sexual attractiveness predicts differential ovulatory shifts in female extra-pair attraction and male mate retention. *Evolution and Human Behavior, 27*, 247−258.

Plavcan, J. M., Lockwood, C. A., Kimbel, W. H., Lague, M. R., & Harmon, E. H. (2005). Sexual dimorphism in Australopithecus afarensis revisited: How strong is the case for a human-like pattern of dimorphism? *Journal of Human Evolution, 48*(3), 313−320.

Plavcan, J. M., & van Schaik, C. P. (1997). Intrasexual competition and body weight dimorphism in anthropoid primates. *American Journal of Physical Anthropology, 103*(1), 37−68.

Pond, C. M., & Mattacks, C. A. (1987). The anatomy of adipose tissue in captive macaca monkeys and its implications for human biology. *Folia Primatologica, 48*, 164−185.

Prokosch, M. D., Coss, R. G., Scheib, J. E., & Blozis, S. A. (2009). Intelligence and mate choice: Intelligent men are always appealing. *Evolution and Human Behavior, 30*(1), 11−20.

Puts, D. A. (2005). Mating context and menstrual phase affect women's preferences for male voice pitch. *Evolution and Human Behavior, 26*, 388−397.

Puts, D. A. (2006). Cyclic variation in women's preferences for masculine traits: Potential hormonal causes. *Human Nature, 17*(1), 114−127.

Puts, D. A., & Dawood, K. (2006). The evolution of female orgasm: Adaptation or byproduct? *Twin Research and Human Genetics, 9*(3), 467−472.

Puts, D. A., Gaulin, S. J. C., & Verdolini, K. (2006). Dominance and the evolution of sexual dimorphism in human voice pitch. *Evolution and Human Behavior, 27*, 283−296.

Puts, D. A., Hodges, C., Cardenas, R. A., & Gaulin, S. J. C. (2007). Men's voices as dominance signals: Vocal fundamental and formant frequencies influence dominance attributions among men. *Evolution and Human Behavior, 28*, 340−344.

Quinn, T. P., Adkison, M. D., & Ward, M. B. (1996). Behavioral tactics of male sockeye salmon (*Oncorhynchus nerka*) under varying operational sex ratios. *Ethology, 102*, 304−322.

Quinn, T. P., Hendry, A. P., & Buck, G. P. (2001). Balancing natural and sexual selection in sockeye salmon: Interactions between body size, reproductive opportunity and vulnerability to predation by bears. *Evolutionary Ecology Research, 3*, 917−937.

Reby, D., McComb, K., Cargnelutti, B., Darwin, C., Fitch, W. T., & Clutton-Brock, T. (2005). Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proceedings of the Royal Society B: Biological Sciences, 272*(1566), 941−947.

Reno, P. L., Meindl, R. S., McCollum, M. A., & Lovejoy, C. O. (2003). Sexual dimorphism in Australopithecus afarensis was similar to that of modern humans. *Proceedings of the National Academy of Sciences of the United States of America, 100*(16), 9404−9409.

Reno, P. L., Meindl, R. S., McCollum, M. A., & Lovejoy, C. O. (2005). The case is unchanged and remains robust: Australopithecus afarensis exhibits only moderate skeletal dimorphism. A reply to Plavcan et al. (2005). *Journal of Human Evolution, 49*(2), 279−288.

Rhodes, G., Hickford, C., & Jeffery, L. (2000). Sex-typicality and attractiveness: Are supermale and superfemale faces super-attractive? *British Journal of Psychology, 91*(Pt 1), 125−140.

Rikowski, A., & Grammer, K. (1999). Human body odour, symmetry and attractiveness. *Proceedings Biological Sciences, 266*(1422), 869−874.

Rilling, J., Kaufman, T., Smith, E., Patel, R., & Worthman, C. (2009). Abdominal depth and waist circumference as influential determinants of human female attractiveness. *Evolution and Human Behavior, 30*(1), 21−31.

Roberts, S. C., & Little, A. C. (2008). Good genes, complementary genes and human mate preferences. *Genetica, 134*(1), 31−43.

Roberts, S. C., Little, A. C., Gosling, L. M., Jones, B. C., Perrett, D. I., Carter, V., et al. (2005). MHC-assortative facial preferences in humans. *Biology Letters, 1*(4), 400−403.

Robertson, D. R., & Hoffman, S. G. (1977). The roles of female mate choice and predation in the mating systems of some tropical labriod fishes. *Zeitschrift für Tierphysiologie, 45*, 298−320.

Rodman, P. S., & Mitani, J. C. (1987). Orangutans: Sexual dimorphism in a solitary species. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate Societies* (pp. 146−154). Chicago: University of Chicago Press.

Ryan, M. J., & Rand, A. S. (1995). Female responses to ancestral advertisement calls in tungara frogs. *Science, 269*(5222), 390−392.

Savalli, U. M. (2001). Sexual selection. In C. W. Fox, D. A. Roff, & D. J. Fairbairn (Eds.), *Evolutionary ecology: Concepts and case studies* (pp. 207−221). Oxford: Oxford University Press.

Scheib, J. E., Gangestad, S. W., & Thornhill, R. (1999). Facial attractiveness, symmetry and cues of good genes. *Proceedings of the Royal Society B: Biological Sciences, 266*(1431), 1913−1917.

Scherer, M., Sullivan, W. G., Smith, D. J., Jr., Phillips, L. G., & Robson, M. C. (1989). An analysis of 1,423 facial fractures in 788 patients at an urban trauma center. *Journal of Trauma, 29*(3), 388−390.

Scheyd, G. J., Garver-Apgar, C. E., & Gangestad, S. W. (2008). Physical attractiveness: Signals of phenotypic quality and beyond. In C. B. Crawford, & D. Krebs (Eds.), *Foundations of Evolutionary Psychology* (2nd ed., pp. 239−260). Hillsdale, NJ: Erlbaum.

Schmitt, D. P., & Buss, D. M. (1996). Strategic self-promotion and competitor derogation: Sex and context effects on the perceived effectiveness of mate attraction tactics. *Journal of Personality and Social Psychology, 70*(6), 1185−1204.

Schützwohl, A., & Koch, S. (2004). Sex differences in jealousy: The recall of cues to sexual and emotional infidelity in personally more and less threatening context conditions. *Evolution and Human Behavior, 25*(4), 249−257.

Schwagmeyer, P. L., & Woontner, S. J. (1986). Scramble competition polygyny in thirteen-lined ground squirrels: The relative contributions of overt conflict and competitive mate searching. *Behavior Ecology and Sociobiology, 19*, 359−364.

Seiler, S., De Koning, J. J., & Foster, C. (2007). The fall and rise of the gender difference in elite anaerobic performance 1952-2006. *Medicine and Science in Sports and Exercise, 39*(3), 534−540.

Sell, A., Cosmides, L., Tooby, J., Sznycer, D., von Rueden, C., & Gurven, M. (2009). Human adaptations for the visual assessment of strength and fighting ability from the body and face. *Proceedings of the Royal Society B: Biological Sciences, 276*(1656), 575−584.

Short, R. V. (1979). Sexual selection and its components parts, somatic and genital selection, as illustrated by man and the great apes. *Advances in the Study of Behavior, 9*, 131−158.

Simmons, L. W., Firman, R. C., Rhodes, G., & Peters, M. (2004). Human sperm competition: Testis size, sperm production and rates of extrapair copulations. *Animal Behaviour, 68*, 297−302.

Simpson, J. A., Gangestad, S. W., Christensen, P. N., & Leck, K. (1999). Fluctuating asymmetry, sociosexuality, and intrasexual competitive tactics. *Journal of Personality and Social Psychology, 76*(1), 159−172.

Singh, D. (1993). Body shape and women's attractiveness: The critical role of waist-to-hip ratio. *Human Nature, 4*(3), 297−321.

Singh, D. (1995). Female health, attractiveness and desirability for relationships: Role of breast asymmetry and waist-to-hip ratio. *Ethology and Sociobiology, 16*, 465−481.

Singh, D., & Young, R. K. (1995). Body weight, waist-to-hip ratio, beast and hips: Role in judgements of female attractiveness and desirability for relationships. *Ethology and Sociobiology, 16*, 483−507.

Small, M. F. (1992). The evolution of female sexuality and mate selection in humans. *Human Nature, 3*(2), 133−156.

Smuts, 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: University of Chicago Press.

Smuts, B. (1995). The evolutionary origins of patriarchy. *Human Nature, 6* (1), 1−32.

Smuts, B. (1996). Male aggression against women: An evolutionary perspective. In D. M. Buss, & N. M. Malamuth (Eds.), *Sex, power, conflict. evolutionary and feminist perspectives* (pp. 231−268). New York: Oxford University Press.

Snedden, W. A. (1990). Determinants of male mating success in the temperate crayfish *Orconectes rusticus*: Chela size and sperm competition. *Behaviour, 15*(1-2), 100−113.

Sneddon, L. U., Huntingford, F. A., & Taylor, A. C. (1997). Weapon size versus body size as a predictor of winning in fights between shore crabs, *Carcinus maenas* (L.). *Behavioral Ecology and Sociobiology, 41*(4), 237−242.

Snyder, J. K., Kirkpatrick, L. A., & Barrett, H. C. (2008). The dominance dilemma: Do women really prefer dominant mates? *Personal Relationships, 15*, 425−444.

Sojat, A. J., Meisami, T., Sandor, G. K. B., & Clokie, C. M. L. (2001). The epidemiology of mandibular fractures treated at the Toronto General Hospital: A review of 246 cases. *Journal of the Canadian Dental Association, 67*(11), 640−644.

Spencer, H. (1885). *The Principles of Sociology.* New York: Appelton.

Streeter, S. A., & McBurney, D. H. (2003). Waist–hip ratio and attractiveness: New evidence and a critique of "a critical test". *Evolution and Human Behavior, 24*, 88−98.

Symons, D. (1979). *The Evolution of Human Sexuality.* New York: Oxford University Press.

Thornhill, R., & Gangestad, S. W. (1999). The scent of symmetry: A human sex pheromone that signals fitness? *Evolution and Human Behavior, 20*, 175−201.

Thornhill, R., & Grammer, K. (1999). The body and face of woman: One ornament that signals quality? *Evolution and Human Behavior, 20*, 105−120.

Tobalske, B. W., & Dial, K. P. (2000). Effects of body size on take-off flight performance in the Phasianidae (Aves). *Journal of Experimental Biology, 203*(Pt 21), 3319−3332.

Trivers, R. R. (1972). Parental investment and sexual selection. In B. Cambell (Ed.), *Sexual selection and the descent of man, 1871-1971* (pp. 136−179). London: Heinemann.

Turner, G. F. (1993). Teleost mating behaviour. In T. J. Pitcher (Ed.), *Behaviour of Teleost Fishes* (2nd ed., pp. 307−332). London: Chapman and Hall.

Van Lawick-Goodall, J. (1971). Tool using in primates and other vertebrates. In D. S. Lehrman, R. A. Hinde, & E. Shaw (Eds.), *Advances in the study of behavior, 3.* (pp. 195−250). New York: Academic Press.

van Valen, L. (1962). A study of fluctuating asymmetry. *Evolution, 16*, 125−142.

von Schantz, T., Wittzell, H., Göransson, G., Grahn, M., & Persson, K. (1996). MHC genotype and male ornamentation: Genetic evidence for the Hamilton-Zuk model. *Proceedings Biological Sciences, 263*, 265−271.

Walker, P. L. (2001). A bioarcheological perspective on the history of violence. *Annual Review of Anthropology, 30*, 573−596.

Ward, C., Leakey, M., & Walker, A. (1999). The new hominid species Australopithecus anamensis. *Evolutionary Anthropology, 7*, 197−205.

Watson, N. V., & Kimura, D. (1991). Nontrivial sex differences in throwing and intercepting: Relation to psychometrically-defined spatial functions. *Personality and Individual Differences, 12*, 375−385.

Watson, P. J. (1990). Female-enhance male competition determines the first mate and principle sire in the spider *Linyphia litigiosa*. *Behavioral Ecology and Sociobiology, 26*, 77−90.

Williams, G. C. (1966). *Adaptation and natural selection.* Princeton, NJ: Princeton University Press.

Wilson, M., & Daly, M. (1985). Competitiveness, risk taking, and violence: The young male syndrome. *Ethology and Sociobiology, 6*, 59−73.

Wilson, M., & Daly, M. (1993). An evolutionary psychological perspective on male sexual proprietariness and violence against wives. *Violence and Victims, 8*(3), 271−294.

Wilson, M. I., & Daly, M. (1996). Male sexual proprietariness and violence against wives. *Current Directions in Psychological Science, 5*(1), 2−7.

Wood, J. W. (1992). *Dynamics of human reproduction: Biology, biometry, demography.* Aldine de Gruyter: Hawthorne, NY.

Wrangham, R. W. (1987). The significance of African apes for reconstructing human social evolution. In W. G. Kinzey (Ed.), *The evolution of human behavior: Primate models* (pp. 51−71). Albany, NY: SUNY Press.

Wrangham, R. W. (1999). Evolution of coalitionary killing. *American Journal of Physical Anthropology* (Suppl 29), 1−30.

Wrangham, R. W., & Peterson, D. (1996). *Demonic Males.* Boston: Mariner Press.

Wyckoff, G. J., Wang, W., & Wu, C. I. (2000). Rapid evolution of male reproductive genes in the descent of man. *Nature, 403*(6767), 304−309.

Zahavi, A., & Zahavi, A. (1997). *The Handicap Principle.* New York: Oxford University Press.

Zeh, D. W. (1987). Life history consequences of sexual dimorphism in a chernetid pseudoscorpion. *Ecology, 68*, 1495−1501.

Zihlman, A. L., & MacFarland, R. K. (2000). Body mass in lowland gorillas: A quantitative analysis. *American Journal of Physical Anthropology, 113*, 61−78.