A Review of Sexual Selection and Human Evolution: How Mate Choice shaped Human Nature

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1 Introduction

The application of sexual selection theory to human behavior has been the greatest success story in evolutionary psychology, and one of the most fruitful and fascinating developments in the human sciences over the last two decades. Ironically, this development would have seemed absurd only twenty years ago. At that time, many biologists considered sexual selection through mate choice to be Darwin's least successful idea: if not outright wrong, it was at most a minor, uninteresting, even pathological evolutionary process. At that time, any `Darwinization' of the human sciences would have had to rely on natural selection theory, which bears much less directly on human social, sexual, and cultural behavior.

Instead, something remarkable happened: sexual selection theory was revived over the last two decades through the combined efforts of researchers in theoretical population genetics, experimental behavioral biology, primatology, evolutionary anthropology, and evolutionary psychology. Today, although natural selection theory serves as the conceptual and rhetorical foundation for evolutionary psychology (see Tooby & Cosmides, 1990, 1992), sexual selection theory seems to guide more actual day-to-day research (see Buss, 1994; Ridley, 1993; Wright, 1994).

This chapter reviews the current state of sexual selection theory, and outlines some applications to understanding human behavior. Sexual selection theory has been revived so recently that, while extraordinary opportunities exist for further research, many old misconceptions persist. These include the mistaken ideas that sexual selection:(1) always produces sex differences,(2) does not operate in monogamous species,(3) is weaker than natural selection, and(4) had nothing to do with the evolution of human intelligence, language, or creativity. One goal of this chapter will be to dispel some of these myths, and to bring evolutionary psychology up to date with respect to the biological literature on sexual selection. Sections 2 through 4 review the history and basic theory of sexual selection. Sections 5 and 6 contextualized human mate choice by covering sexual selection in primates and hominids. Sections 7 through 9 survey some possible roles of mate choice in shaping the human body, the human mind, and human culture. Finally, section 10 concludes with some academic and existential implications of applying sexual selection theory to understand human nature. -

2 History of sexual selection theory

Darwin (1859, 1871) realized that his theory of natural selection through differential survival could not explain extravagant male traits such as the peacock's tail, because such traits actually decrease survival ability. Rather, he reasoned that in a sexually-reproducing species, any heritable traits that help in competing for sexual mates will tend to spread through the species, even if they compromise survival somewhat. This process of *sexual selection* may favor, for example, better sensory and motor abilities for finding mates, gifts and ornaments to attract them, weapons and bluffs for repelling same-sex competitors, endurance for lasting through the breeding season, and genitals and gametes that maximize fertilization rates. Within the sexual selection process, Darwin distinguished between male competition for female mates (which typically gives rise to weapons), and female choice of male mates (which typically gives rise to gifts and ornaments). But he recognized that female choice and male competition are often two sides of the same coin, because mate choice by one sex usually implies competition by the other sex, either through direct 'interference competition' (e.g. physical fights over the opposite sex) or through indirect 'exploitation competition' (e.g. scrambles to find and seduce the opposite sex before someone else does). Darwin had no real explanation of why males usually compete harder for mates than females do — why males court, and females choose —though he offered a staggering amount of evidence that this pattern holds from insects through humans (Darwin, 1871).

Sexual selection was a radical idea for several reasons. First, it was a truly novel concept. Whereas the theory of natural selection had been anticipated by many 18th and 19th century thinkers such as Jean-Baptiste de Lamarck, Etienne Geoffroy Saint-Hilaire, Frederic Cuvier, Thomas Malthus, and Robert Chambers (see Richards, 1987), and was co-discovered by Alfred Russell Wallace (1870, 1889), the notion that mate choice could shape organic form was without scientific precedent. Second, sexual selection embodied Darwin's conviction that evolution was a matter of differential reproduction rather than differential survival. Animals expend their very lives in the pursuit of mates, against all the expectations of natural theology. Finally, Darwin recognized that the agents of sexual selection are literally the brains and bodies of sexual rivals and potential mates, rather than the insensate features of a physical habitat or a biological econiche. Psychology haunts biology with the spectre of half-sentient mate choice shaping the otherwise blind course of evolution (see Miller, 1994; Miller & Todd, 1995). For Darwin, the choice of mates by female animals was no different in kind from artificial selection by human breeders:

> "All animals present individual differences, and as man can modify his domesticated birds by selecting the individuals which appear to him the most beautiful, so the habitual or even occasional preference by the female of the more attractive males would almost certainly lead to their modification; and such modification might in the course of time be augmented to almost any extent, compatible with the existence of the species." (Darwin, 1871, p. 750-751).

Because female animals exercised most mate choice, and sexual selection through mate choice came very close to creative, conscious artificial selection by humans, Darwin's ideas put females in a very powerful evolutionary role —a role that made most (male) Victorian biologists deeply uncomfortable. Thus, male competition was widely accepted by Darwin's peers as an important, necessary, and general evolutionary process, but the possibility of female choice driving evolution was almost universally mocked and dismissed (Cronin, 1991).

For example, even Alfred Russell Wallace, the co-discoverer of natural selection (Wallace, 1870), was deeply skeptical about sexual selection through female choice. He doubted that the perceptual systems of female animals could shape male courtship ornaments, and viewed such ornaments as arising from a simple male "surplus of strength, vitality, and growth-power which is able to expend itself in this way without injury" (Wallace, 1889, p. 293). Wallace's skepticism is strange because his insightful analyses of camouflage, mimicry, and warning coloration all presupposed a form of 'perceptual selection' by female (and male) predators hunting prey (see Wallace, 1870, 1889). If female predators could shape the evolution of bright warning colors in their prey, why couldn't they shape the evolution of bright courtship colors in their males? Even now, we hear echoes of Wallace's fallacious surplus-of-energy argument in most psychological and anthropological theories about the 'self-expressive' functions of human art, music, language, and culture. After Darwin (1871), sexual selection received such a frosty reception from Wallace and others that it was virtually forgotten (Mayr, 1972; Cronin, 1991). The Modern Synthesis of Mendelian genetics and Darwinism in the 1930s viewed male competition as a sub-class of natural selection, while continuing to reject female choice. Sexual ornaments were assumed to intimidate other males, or were 'species recognition markers' to help animals avoid cross-species mating (e.g. Huxley, 1938; Cott, 1940). Sexual selection remained hidden in biology's blind spot for many decades. The reasons are clear in retrospect. Sexual selection is hard to analyze mathematically. Behaviorist psychology ignored evolution, denied instincts, and disregarded the ecological validity of psychology experiments, so was not prone to doing realistic experiments on mate choice. A fallacious form of group-selectionism viewed costly courtship ornaments as 'bad for the species' and therefore implausible. Freud's vain attempt to leapfrog past Darwin without really understanding sexual selection (see Sulloway, 1979) led to psychoanalysis supplanting evolutionary biology as the early 20th century's leading account of human sexuality. Not least, persistent sexism in biology denied the power of female choice until the 1970s (see Miller, 1993). However, during sexual selection's long exile from biology, it was sometimes adopted by early evolutionary psychologists such as Edward Westermark (1894) and Havelock Ellis (1905, 1934), who used it to explain many aspects of the human body and mind.

R. A. Fisher (1915, 1930) was one of the few biologists to take-sexual selection seriously. He viewed mate preferences as legitimate biological traits subject to heritable variation, and this insight led him to postulate a process he called *runaway sexual selection*.. In runaway, an evolutionary positive-feedback loop gets established between female preferences for certain male traits, and the male traits themselves. Given a nudge in the right direction (e.g. an initial bias in female preferences), Fisher's model could account for the wildly exaggerated male traits seen in many species, such as the peacock's plumage (details follow in section 3.3). But Fisher did not explain the evolutionary origins of female preferences themselves, nor did he develop formal genetic models of runaway sexual selection. Huxley's (1938) hostile, deeply confused critique of Fisher's theory and of sexual selection in general consigned the field to continued neglect until the 1970s.

Sexual selection's revival has been swift, dramatic, and unique: Darwin's idea is, to my knowledge, the only major scientific theory ever to have been accepted after a century of condemnation. A centenary volume on sexual selection (B. Campbell, 1972) drew some attention to Darwin's neglected ideas. Trivers (1972) finally explained why males court and females choose, when he pointed out that the higher levels of necessary 'parental investment' by females of most species make females a limiting resource over which males must compete: sex differences in parental investment drive sex differences in the intensity of sexual selection. Zahavi (1975) set off intense debate with his ‘handicap principle’, suggesting that the extravagance and costliness of many sexual ornaments function to guarantee their reliability as displays of genetic quality (e.g. only healthy peacocks can afford to grow such huge, handicapping tails.) The debate over sociobiology (Wilson, 1975) attracted interest in the evolution of social and sexual behavior. The new population genetics models of O'Donald (1980), Lande (1981), and Kirkpatrick (1982) showed the mathematical feasibility of Fisher’s runaway sexual selection process. New behavioral experiments on animals showed that females of many species do exhibit strong preferences for certain male traits (e.g. Andersson, 1982; Catchpole, 1980; Moller, 1988; Ryan, 1985). Important edited volumes appeared on sexual selection theory (Bateson, 1983; Bradbury & Andersson, 1987), and on sexual selection in insects (Blum & Blum, 1979) and humans (Betzig, Borgerhoff Mulder, & Turke, 1987). Eberhard (1985) argued that the only feasible explanation for the wildly complex and diverse male genitalia of many species is female choice for certain kinds of genital stimulation. Finally, primatologists began to appreciate the role of sexual selection in primate social systems (e.g. De Waal, 1982; Dunbar, 1988; Smuts, 1985; Byrne & Whiten, 1988), and Symons (1979) applied sexual selection theory to humans more thoroughly than ever before. Once biologists started taking the possibility of female choice seriously, evidence for its existence and significance came quickly and ubiquitously (see Andersson, 1994; Cronin, 1991).

Currently, sexual selection is one of the fastest-growing and most exciting areas of evolutionary biology and animal behavior. Recent biological work permeates the journals *American Naturalist, Animal Behavior, Behavioral Ecology and Sociobiology, Evolution, Heredity, Journal of Theoretical Biology, Nature,* and *Science.* Research on sexual selection in humans appears most often in the journals *Behavioral and Brain Sciences, Ethology and Sociobiology, Human Nature,* and *Psychological Review.* The best recent theoretical and empirical review of sexual selection is Andersson (1994); the best historical review is Cronin (1991). Darwin’s (1871) foundational work *The Descent of Man, and Selection in Relation to Sex* still rewards careful and repeated reading. Accessible introductions to sexual selection in humans include Batten (1992), Buss (1994), H. Fisher (1992), Daly and Wilson (1988), Ridley (1993), and Wright (1994).

It is important to understand the peculiar history of sexual selection theory because virtually all of 20th century psychology, anthropology, paleontology, primatology, and cognitive science, as well as the social sciences and humanities, developed without recognizing that sexual selection could have played any important role in the evolution of the human body, the human mind, human behavior, or human culture. Since biologists have embraced sexual selection, we must face the possibility that most current theories of human behavior and culture are inadequate, because they may have vastly under-estimated the role of sexual competition, courtship, and mate choice in human affairs.

3 Mate choice criteria and sexual selection mechanisms

The simplest way to review the current state of sexual selection theory is to explore the different kinds of criteria that animals can use to choose mates. This is because we can often view sexual competition within each sex as an outcome of mate choice by the other sex — if “choice” is understood broadly to include processes both conscious and unconscious, and both psychological and physiological. Recently, there have been two major schools of thought about mate choice criteria. Champions of Zahavi's (1975) handicap principle have emphasized selection for *genetic indicators* — also called “good genes”, “good sense”, or "healthy-offspring" selection. Champions of R. A. Fisher's (1930) runaway process have emphasized selection for *aesthetic displays* — also called "good taste" or "sexy son" selection. In evolutionary biology, these different mate choice criteria are often considered competing models of how sexual selection works, but there is now sufficient evidence for each (see Andersson, 1994) that they can be considered well-established, often complementary selective forces. Of course, mate choice can favor many other important qualities, including parental ability and resources (see Clutton-Brock, 1991; Hoelzer, 1989; Price, Schluter, & Heckman, 1993), fertility (e.g. sperm quality in males or fecundity in females — see Baker& Bellis, 1995; Singh, 1993), optimal genetic distance (to avoid inbreeding with close relatives or outbreeding with the wrong species — see N. Thornhill, 1991, 1993), and similarity in appearance, behavior, and personality (see Buss, 1985; Rushton, 1989; Thiessen & Gregg 1980). But before discussing these various classes of mate choice mechanisms, we must understand their origins.

3.1 The origins of mate preferences

Mate choice is the behavioral outcome of mate preferences. These preferences are usually "mental adaptations" implemented as complex neural circuits, and constructed through the interaction of many genes and environmental conditions, which bias mating in favor of individuals with certain perceivable traits. In most species, such systems may function without conscious awareness, deliberation, or complex aesthetic feelings; but we might expect mate choice to be among the *least unconscious* of an animal's decisions, because it requires the integration of such diverse information, and has such important fitness consequences. Mate choice operates by rejecting some potential mates and accepting or soliciting to others. In almost all species, females can effectively resist copulation attempts by unwanted males, and in many species, females actively solicit copulations from desired males. Likewise, males actively pursue desired females, and ignore solicitation attempts by unwanted females. Although sexual harassment of females is common in nature, 'successful' rape seems fairly rare, being reported in only a small collection of species such as ducks, squid, dolphins, orangutans, and humans (Brownmiller, 1975; Rodman & Mitani, 1987; R. Thornhill &N. Thornhill, 1992). Generally, mutual choice and mutual cooperation are necessary for breeding.

Why do these mechanisms for mate choice evolve? Being choosy requires time, energy, and intelligence, and these costs of mate choice can impair survival and can decrease the likelihood of sexual selection operating at all (Pomiankowski, 1987; Reynolds& Gross, 1990). The basic rationale is that random mating is stupid mating. It pays to be choosy because in a sexually reproducing species, the genetic quality of your mate will determine half the genetic quality of your offspring. Ugly, unhealthy mates yield ugly, unhealthy offspring. By forming a joint genetic venture with an attractive, high-quality mate, one's genes are much more likely to be passed on. Even modern women who deny the "role of genes in human behavior" tend to choose their sperm donors quite carefully (see Scheib, 1994). Mate choice is simply the best eugenics and genetic screening that female animals are capable of carrying out under field conditions, with no equipment but their senses and their brains.

Mate choice mechanisms can evolve through direct selection for mate-choice efficiency (i.e. better preferences lead to more or better offspring), and through three other less predictable, less adaptive processes: (1) mutation, (2) genetic drift, and(3) genetic linkage with another trait that is undergoing genetic drift, natural selection, or sexual selection. These last three processes will typically produce harmful changes in mate choice mechanisms, so will usually be selected out. But some changes will persist, through chance, utility, or Fisher's runaway effect. The unpredictability of these three processes is important in explaining the diversity of sexually-selected ornaments across similar, closely-related species (Eberhard, 1985; Miller & Todd, 1995).

The following sections review some of the major kinds of mate choice and sexual selection. But in addition to the mate choice criteria discussed below, most animals also have mechanisms to ensure that they mate with partners of the appropriate species, sex, age, and genetic distance, at an appropriate place and time (see Bateson, 1983; Andersson, 1994).

3.2 **Selection for indicators**

Probably the most fundamental form of sexual selection is mate choice for various "indicators" of viability (likelihood of survival) and fertility (likelihood of reproduction). These can take many forms. Almost any perceivable bodily or behavioral trait can function as an indicator — revealing age, health, nutritional status, size, strength, aggressive dominance, social status, disease resistance, or overall vigor. Such indicators may reveal both heritable genetic traits that would be passed on to offspring (selection for 'good genes'), and chances that the mate will survive to give provisioning, protection, and support to offspring (selection for 'good parents').

No one is surprised when animals avoid mating with the dead, the injured, or the sick. All such mating decisions must rely on observable cues of viability. The idea of indicators is that the cues used in such assessments will tend to be exaggerated over eons of mate choice. Weak, ambiguous, unreliable, incidental cues of being non-dead and non-sick will become strong, clear, reliable, specially-adapted indicators of being vigorous and healthy. For example, dead peacocks have rather drab tails. And peacocks with inferior tails get eaten more often by predators (Petrie, 1992). So tail quality probably reflects some underlying physiological quality that correlates with predator-escape ability, and that could be inherited by offspring. This gives an incentive for peahens to choose males for tale quality, and for peacocks to display large, healthy tails as vigorously as possible (Petrie, Halliday, & Sanders, 1991). Other classic examples of indicators include color and condition of bird plumage in other species (Hamilton & Zuk, 1982; Moller, 1988), loudness and complexity of bird song (Catchpole, 1980, 1987), antler size and symmetry (e.g. Goss, 1983), and raw body size (Ryan, 985). But almost any body part or behavior that is expensive to produce and that varies in magnitude can serve as an indicator.

The importance of indicators in sexual selection has been emphasized by R. A. Fisher (1915), Williams (1966), and Zahavi (1975). Indicators, like animal signals in general, are subject to the *handicap principle* the game-theoretic constraint that they must be costly in order to be reliable because if not, they can be faked too easily (Zahavi, 1975, 1991). Indicators evolve most easily when they are 'condition-dependent', such that healthier animals grow bigger or better indicators(e. g. larger, more colorful tails) or 'revealing', such that healthier animals take better care or make better use of the indicators they have (e.g. the tails are better-groomed and better-displayed).

Despite initial skepticism about the handicap principle, computer simulations and mathematical models have helped to convince most biologists that condition-dependent and revealing indicators are common outcomes of sexual selection. For example, simulations by Andersson (1986) showed that condition-dependent indicators could evolve even in perfectly monogamous species, given viability differences of only a few percent. An important mathematical analysis by Iwasa, Pomiankowski, and Nee (1991) confirms that indicators can evolve under sexual selection even if mate preferences are costly, as long as mutations are usually harmful. Other, more recent models suggest that 'good parenting' indicators can evolve to display even non-heritable resources such as good territories (Grafen, 1990; Heywood, 1989; Hoelzer, 1989; Price et al., 1993). Thus, not all indicators are necessarily advertising genetic quality; they could simply be advertising resources and health relevant to raising offspring. Indicators often evolve better when runaway sexual selection is also operating on the relevant traits and preferences (Andersson, 1986; Heywood, 1989; Pomiankowski, 1988; Tomlinson, 1988). However, indicators alone, even without the runaway process, can suffice for the evolution of extravagant male ornaments and extreme female preferences (Grafen, 1990). See Andersson (1994, chapter 3) for a comprehensive review of indicator models and data.

The idea of genetic indicators has been criticized because of the `lek paradox' (e.g. Williams, 1975; Maynard Smith, 1976; Kirkpatrick, 1987; Pomiankowski, 1987, 1995; Reynolds& Gross, 1990). *Leks* are aggregations of animals such as sage grouse, where females pick their mates very carefully from among dozens of males displaying in large groups, and females receive nothing but sperm from the males they choose. The most attractive male sage grouse may achieve over 30 matings in a single morning, while average males usually win none (Boyce, 1990). Under such intense selection for attractive traits, we might expect the preferred traits to go to fixation (100% frequency) in the gene pool very quickly (R. A. Fisher, 1930). Once fixated, there would be no further incentive for females to be choosy, because all of the males should have the same genes and hence be equally attractive. Indicators would become irrelevant once the population became genetically homogeneous, without any heritable variation in fitness or attractiveness.

However, three processes can maintain heritable fitness variation: temporal variation in selection, spatial variation in selection, and mutation pressure (see Andersson, 1994). Temporally varying selection can result from co-evolution between ecological competitors, between predators and prey, or, perhaps most importantly, between hosts and parasites(Hamilton & Zuk, 1982; Hamilton, Axelrod, & Tanese, 1990; Low, 1990). Spatially varying selection in different geographic areas, combined with migration, can maintain heritable variation in a population. Mutation pressure can also maintain heritable fitness variation because most mutations are harmful, and give rise to an excess of low-fitness individuals (Lande, 1981; Charlesworth, 1987; Kondrashov, 1988; Rice, 1988). Indeed, genetic models show that indicators evolve more easily under biased mutation (Iwasa et al., 1991). Some recent studies even suggest that sexually-selected traits have much *higher* heritabilities and genetic variances than naturally-selected traits, despite strong directional selection (Moller & Pomiankowski, 1993; Pomiankowski, 1995; Wilcockson, Crean, & Day, 1995). The importance of heritable fitness variation is also confirmed by experiments in which females that are allowed to choose their mates have offspring with higher phenotypic (and, by inference, genetic) quality than females not allowed to choose(e.g. Partridge, 1980; Reynolds & Gross, 1992). Through female choice, males have been forced to evolve clear windows onto the quality of their genes, so that females can weed out the bad ones. In this sense, females shape males to function as a kind of genetic sieve for the species (Atmar, 1991; Michod & Levin, 1988): out with the bad genes, in with the good.

3.3 **Selection for aesthetic displays**

Some traits have been shaped as aesthetic displays, sometimes in addition to functioning as indicators. Aesthetic displays play upon the perceptual biases of receivers to attract attention, provoke excitement, and increase willingness to mate. That is, seducers manipulate perceptions. The perceptual biases open to manipulation can arise in two, often complementary, ways: (1) they may already exist as 'latent preferences' — side-effects of previous evolutionary processes, reflecting basic psychophysical effects, general principles of perception, or perceptual adaptations to particular environments — and (2) they may co-evolve with the courtship traits they prefer, through Fisher's runaway process.

Several species have been shown to have 'latent preferences' for particular ornaments, even though the ornaments have not yet evolved in the species. Burley (1988) showed that female zebra finches prefer males whose legs have been experimentally decorated with red or black plastic bands, but males with blue and green bands were rejected. Basolo (1990) showed that female platyfish prefer males with colorful plastic 'swords' glued on the ends of their tails, suggesting that this preference also pre-dated the evolution of such ornaments in their close relatives the swordtails. Ryan (1985, 1990) found that females frogs of some species prefer the courtship calls (deep "chuck" sounds) of male frogs if they are played back at artificially lowered frequencies, as if produced by extra-large frogs. Ridley (1981) suggested that tails with multiple eye-spots, such as those of the peacock and the Argus pheasant, play upon a widespread responsiveness to eye-like stimuli in animal perception.

In response to such findings, several theorists have emphasized the role of perceptual biases in sexual selection, using terms such as 'sensory drive' (Endler, 1992, 1993), 'sensory trap' (West-Eberhard, 1984), 'sensory exploitation'(Eberhard, 1985; Ryan, 1990; Ryan & Keddy-Hector, 1992), 'signal selection' (Zahavi, 1991), and 'the influence of receiver psychology on the evolution of animal signals' (Guilford & M. S. Dawkins, 1991; see also Enquist & Arak, 1993). As any perceptual psychologist might predict, animals typically prefer displays that are louder, larger, more colorful, more frequent, more varied, and more novel than average (Ryan & Keddy-Hector, 1990; Miller, 1993). But such perceptual biases may also vary substantially across species, in accord with ecological specializations of the perceptual systems. For example, birds that eat blue berries may evolve blue-sensitive eyes, which would tend to favor blue ornaments; whereas birds that eat red berries may evolve red-sensitive eyes that favor red ornaments. These perceptual specializations may help explain the rapid divergence of sexually-selected traits across closely-related species (Endler, 1992, 1993). The effectiveness of aesthetic displays in courtship supports the R. Dawkins and Krebs (1978) theory that animal signals often evolve to manipulate receivers in the signaller's interest, not to communicate truthful information (as indicators do) for the benefit of both.

But latent preferences are not necessary, according to R. A. Fisher's (1930) runaway theory. Even chance fluctuations in mate preferences, combined with a strange kind of evolutionary positive-feedback loop, could produce quite extreme mate preferences and quite exaggerated courtship traits (see Miller & Todd, 1993; Todd & Miller, 1993). Suppose that mate preferences vary somewhat randomly within a bird population, so that in one particular generation, some females happen to prefer long tails on males, while others don't care. Suppose male tail length also varies randomly. Could the preference (for long tails) and the trait (of having a long tail) evolve together in a positive-feedback loop? This possibility was first considered and dismissed by T. H. Morgan (1903) to ridicule Darwin's sexual selection theory:

> "Shall we assume that . . . those females whose taste has soared a little higher than that of the average (a variation of this sort having appeared) select males to correspond, and thus the two continue heaping up the ornaments on one side and the appreciation of the ornaments on the other side? No doubt an interesting fiction could be built up along these lines, but would anyone believe it, and if he did, could he prove it?"

R. A. Fisher (1930) believed it, but couldn't prove it:

> "The two characteristics affected by such a process, namely plumage development in the male and sexual preference in the female, must thus advance together, and so long as the process is unchecked by severe counterselection, will advance with ever-increasing speed. "

Recent population genetics models (e.g. Lande, 1981; Kirkpatrick, 1982; Pomiankowski, Iwasa, & Nee, 1991) have finally proved it:

> "Females that prefer to mate with long-tailed males will mate with such males more often than females that prefer short-tailed males. Following mating and genetic recombination, the genes for long-tail preference and the genes for the long tail itself will become correlated: an individual carrying a gene for long tails will tend to carry a gene for the corresponding preference. "(Kirkpatrick, 1987, pp. 74-75).

The argument looks a bit circular, but then all positive-feedback processes look a bit circular. The only thing keeping runaway going is the 'momentum' conferred by genetic linkage and the risk to individuals of failing to display exaggerated traits or choosy preferences given that momentum. The peacock's tail grows longer and longer because of a despotic treadmill of fashion: "Each peahen is on a treadmill and dare not jump off lest she condemn her sons to celibacy" (Ridley, 1993, p. 135). The treadmill doesn't go on forever though: eventually, runaway would be counter-acted by the survival costs of elaborate ornaments (R. A. Fisher, 1930). At evolutionary equilibrium, the survival costs of an ornament should balance the reproductive advantages (Kirkpatrick, 1982).

Runaway can happen in any sensory modality. Animals' eyes respond to color and form on tails and faces; ears respond to loud complex songs by birds and whales; noses respond to intense pheromones such as musk deer scent; skin responds to grooming, foreplay, and genital stimulation. Electric fish may even respond to galvanic courtship (Kramer, 1990). But there is much more to animal cognition than low-level sensation, so courtship behaviors may have evolved to play on higher-level mental processes of categorization, symbolism, memory, expectation, communication, and curiosity (Miller, 1993).

Runaway is a fairly robust and pervasive force that emerges even in genetic models of indicators (Pomiankowski et al., 1991; Kirkpatrick, 1992), but it also a highly stochastic process, quite sensitive to initial conditions and therefore capable of explaining the capricious divergence of sexual ornamentation observed across species (Eberhard, 1985; Miller & Todd, 1993, 1995). The three basic assumptions of Fisher's model have been moderately well-supported by recent empirical work (see Andersson, 1994): (1) individuals with large sexual ornaments have higher mating success but lower survival than those with smaller ornaments (all else being equal), (2) the relevant traits and preferences show heritable genetic variation, and (3) there is genetic linkage between the relevant traits and preferences (e.g. Bakker, 1993; Houde & Endler, 1990). The runaway process is also supported by findings that some animals copy each others' mate choices, as if following an arbitrary fashion rather than a reliable indicator (Balmford, 1991; Dugatkin, 1992; Pruett-Jones, 1992).

3.4 **Selection for sperm competition**

Sexual selection does not stop when copulation begins. Indeed, gonads and genitals are the clearest expressions of sexual selection, because they are most directly responsible for fertilization, and they typically serve no survival functions. The traditional view that 'primary sexual characters' such as penises are "necessary for breeding and hence are favored by natural selection" (Andersson, 1994, p. 14) is misleading. If sexual competition and mate choice can affect genitals, then genitals can be shaped by sexual selection.

In many species, females mate with more than one male, so *sperm competition* becomes important: males evolve larger testicles, larger ejaculates, faster-swimming sperm, various devices to remove previous competitors' sperm from the female reproductive tract, and various plugs to keep future competitors' sperm excluded entirely (Smith, 1984; G. Parker, 1984). The results can be dramatic: the male North Atlantic right whale reputedly has 2000-pound testicles to pump out gallons of semen and billions of sperm per ejaculate.

In primates, testicle size increases with intensity of sperm competition across species (Harcourt & Harvey, 1984); female chimpanzees are highly promiscuous, so male chimpanzees have evolved large 4-ounce testicles. Male humans have medium-sized testicles by primate standards, and produce a respectable 400 million sperm per ejaculate, suggesting that ancestral females had multiple lovers within a month fairly often (Baker & Bellis, 1995).

Female choice does always not stop when copulation starts, either. Eberhard (1985) has argued that male genitals often function as 'internal courtship devices' to stimulate females into accepting sperm from the copulating male. The length, variety, and vigor of human copulation suggests that this type of internal courtship has been highly elaborated in our species. Human female orgasm may function partially to suck sperm into the uterus, thereby promoting fertilization by sexually exciting males (Baker& Bellis, 1995).

3.5 **Selection for provisioning, territories, and protection**

Females can gain nongenetic benefits from mate choice by favoring males that offer material gifts (Searcy, 1982). The main examples of such provisioning come from male insects giving nuptial gifts such as spermatophores or caught prey(see R. Thornhill & Alcock, 1983), male birds provisioning offspring and building nests in socially monogamous bird species (see Clutton-Brock, 1991), and sex-for-meat exchanges (e.g. prostitution and marriage) in humans(H. Fisher, 1982, 1992). Male provisioning is useful to females because it eases the nutritional and energetic burden of producing eggs, gestating young, and feeding them. But male provisioning of females during courtship is not common across species, and male provisioning of offspring after birth is quite rare except in monogamous birds (Clutton-Brock, 1991). Often, male provisioning may represent mating effort more than paternal effort, if females prefer males that have provisioned previous offspring (Seyfarth, 1978; Smuts, 1985). Biologists may often mistake the grudgingly generous step-father for the committed dad.

Selection for direct provisioning must not be confused with the more common pattern of selection for good territories that happen to be defended by particular males. Socioecologists have long recognized that female animals tend to distribute themselves around their habitat to exploit the available food resources and protect themselves against the local predators, and the males distribute themselves to exploit the available females as reproductive resources (Davies, 1991; Dunbar, 1988). In such cases, males often fight to exclude competitors from prime territories, and females prefer to mate with males that hold prime territories. Such systems are called ‘resource defense polygyny', because males that are successful at excluding other males from areas desired by females will reap a disproportionately high number of offspring with multiple females. Male territoriality can be viewed in two ways: as female choice in favor of sexy, healthy, high-status, land-holding aristocrats, or as female acquiescence to a Machiavellian protection racket, where violent, harassing males extort sex for access to food, and then leave females with all the burdens of parenting.

Males can sometimes serve as convenient if unreliable protectors from predators or from other males. Thus, mate choice in favor of protectors is especially favored in species where females and/or infants are subject to strong predation risk or strong risk of infanticide by rival males (see Hausfater & Hrdy, 1984). Again, the protection racket metaphor may be apt: males extort sex in exchange for a commitment not to kill a female’s offspring, and a willingness to keep other males from killing them. Moreover, much of what appears to be ‘protection’ behavior by males may function as mate-guarding to minimize sexual competition from rival males, and may not reflect female choice. Biologists have recently begun taking a darker view of male provisioning, territoriality, and protection behavior — a view surprisingly concordant with recent feminist analyses of human patriarchy, prostitution, marriage, sexual exploitation, and the economic oppression of women (see Brownmiller, 1975; Buss & Malamuth, in press; Haraway, 1989; Lancaster, 1991; Smuts, 1991).

3.6 **Summary of sexual selection modes**

The scope of sexual selection through mate choice is rather broad: it can operate in almost any animal species capable of making discriminations among potential mates and in responding more positively towards some than towards others. Mechanisms that cause selective mating can arise from several sources, both as adaptations in their own right and as side-effects of other adaptations (e. g. as sensory biases). Once in place, these mechanisms can influence the evolution of sexual ornamentation and courtship behaviors. If the selected trait correlates with general viability as a conditional or revealing handicap, and if genetic variance in viability is maintained somehow, e.g. by biased mutation or convolution, then Zahavi's handicap principle will work to elaborate both trait and preference (Iwasa et al., 1991). Even if the selected trait is purely ornamental and does not correlate with general viability, as long as genetic variance in the trait is maintained, then Fisher’s runaway process can elaborate both trait and preference (Pomiankowski et al., 1991). Often, Zahavi's and Fisher’s processes will be mutually reinforcing, such that a trait is elaborated both as a viability indicator that increases offspring survival rates and as an aesthetic ornament that increases offspring attractiveness. For example, “a peacock’s tail is, simultaneously, a testament to naturally selected female preferences for eye-like objects, a runaway product of despotic fashion among peahens, and a handicap that reveals its possessor’s condition. ” (Ridley, 1993, pp. 161-162). These processes can operate even in the face of substantial natural selection to evolve costly male traits and costly female preferences. Sexual selection will work in pseudo-monogamous and polygynous species through differential mating success, and will work in truly monogamous species if animals mate assortatively with respect to viability-indicators, or if animals that mate earlier have more offspring (Darwin, 1871; Kirkpatrick, Price, & Arnold, 1990).

4 Sex **differences and sexual selection**

Sexual selection through mate choice would be expected to operate in any sexually-reproducing lineage, regardless of whether there were distinct sexes such as males and females. If hermaphrodites exercise mate choice, they can evolve sexual ornaments. Thus, sexual selection does not necessarily require or produce sex differences.

However, in almost all sexually-reproducing lineages on earth, distinct sexes have evolved, consisting of 'males' that produce small gametes called sperm and 'females' that produce large gametes called eggs. Bateman (1948) and Trivers (1972) pointed out that since females invest more matter and energy into producing each egg than males invest in producing each sperm, eggs form more of a limiting resource for males than sperm do for females. Thus, males should compete more intensively to fertilize eggs than females do to acquire sperm, while females should be choosier than males. Males compete for quantity of females, and females compete for quality of males. In short, males court, and females choose (see Daly& Wilson, 1983; Reynolds & Harvey, 1994; Trivers, 1985).

In female mammals the costs of internal fertilization, gestation, and long-term lactation are especially high, leading to even more striking differences between male competitiveness and female choosiness. For example, the minimum parental investment by female humans under ancestral conditions would have been a harrowing 9-month pregnancy followed by at least three years of breast-feeding and baby-carrying (Shostak, 1981); whereas the minimum paternal investment would have been a few moments of copulation and a teaspoonful of semen (Symons, 1979). The result is an enormous difference in maximum lifetime reproductive success. King Moulay Ismail the Bloodthirsty, a medieval despot of Morocco, sired over 800 children by the women in his harem, and the first emperor of China, around 3000 years ago, was reputed to have sired even more through his much larger harem (Betzig, 1986). By contrast, the world record for a woman is 69 children, many of which were triplets (Daly & Wilson, 1983). Even under relatively egalitarian tribal conditions, some men can father several dozen children by several different women, whereas no woman bears more than 10 or so children (Chagnon, 1983).

Thus, a man's reproductive success generally increases with his number of sexual partners (in the absence of contraception), whereas a woman reaches her reproductive limit rather quickly as her number of sexual partners increases. This is because males can opt out of parental investment in a way that women cannot — nature can't enforce child support laws any better than modern governments, Of course, women under ancestral conditions probably used abortion and infanticide to avoid maternal investment during difficult times (see Hausfater & Hrdy, 1984), but they could not induce another woman to bear a child for them. Maternal investment was obligatory in hominids; paternal investment was not.

There are usually trade-offs between courtship effort and parental effort. Males usually invest more in the former, and females more in the latter. In females, the marginal costs of sexually-selected traits will be higher (because the demands of maternal investment push females closer to their physiological limits), and their benefits will be lower (because males are less choosy), so females often invest less time and energy in growing and displaying such traits than males do. The result is *sexual dimorphism:* a sex difference in the expression of the courtship or reproductive trait. The most ancient and reproductively central sexual dimorphism are usually qualitative: males have testicles, whereas females have ova. More recently evolved courtship traits usually retain only quantitative dimorphism: many male birds have longer, brighter feathers than females, but females often retain some discreet ornamentation. Female mammals have breasts, but males retain nipples. All the qualitative sexual dimorphism started out as quantitative ones.

Sexual dimorphism is a common but not necessary outcome of sexual selection. Two major factors limit sexual dimorphism: the mutuality of mate choice, and 'genetic linkage' between the sexes. The effects of mutual choice are easy to understand: if both males and females are somewhat choosy and somewhat competitive, as in many monogamous species, then sexual selection will apply to males and females roughly equally, and sexually selected ornaments and indicators will evolve to similar magnitudes in each. Whenever males must invest time, effort, and energy in courtship, they have incentives to be at least slightly choosy about which females they choose to court — but male choice has been studied only rarely, and may have often been overlooked. For example, Trail (1990) observed that in about a quarter of lek-breeding birds (which provide the best opportunities for female choice), ornaments are equally elaborate in males and females, suggesting that male choice was operating as well. Also, whenever high-quality males are in short supply, females have an incentive to compete with each other to attract and retain such males. Competition to retain the paternal investment and protection of male partners will also lead to substantial variance in the number of offspring raised to maturity by females; measuring variance in number of offspring born would completely miss a major stage of female reproductive competition, which occurs after birth (Dunbar, 1988; Miller, 1993). Males also vary less in their lifetime reproductive success than in their day-by-day success, because male success follows a typical life-history trajectory (adolescent frustration, young adult violence, older adult coalition-building, and gradual senescence). Therefore, short-term measures will over-estimate variance in male reproductive success and under-estimate female variance (Dunbar, 1988). Thus, sexual selection often applies to both sexes, and can drive the evolution of indicators and aesthetic displays in both sexes.

Especially under monogamy, mutual mate choice can yield strong sexual selection without much sexual dimorphism. Sexual selection can work in monogamous species if the sex ratio is skewed, if extra-pair copulations undermine the putative monogamy, or, most importantly, if mates differ in genetic quality (Darwin, 1871; R. A. Fisher, 1930). For example, if animals mate assortatively with respect to quality (e.g. the healthy marry each other, leaving the unhealthy no option but to marry other unhealthier), then indicators of genetic quality can still evolve under sexual selection (see Darwin, 1871). Thus, traits that improve the ability to compete for mates will be favored even under strict monogamy (Jones & Hunter, 1993; Kirkpatrick et al., 1990). Moreover, female competition over mates will be stronger under monogamy, so females may evolve ornaments as extravagant as those of males. Mate choice must also be somewhat mutual in species that use interactive courtship displays (which ethologists used to call 'pair-bonding rituals'), such as coordinated dances, song duets, mutual sexual foreplay, and conversations (Miller, 1993). Only-the pure Fisherian runaway process is undermined by monogamy, because it depends on some individuals obtaining a disproportionate number of mates.

Genetic linkage between the sexes also constrains the evolution of sexual dimorphism. Because males and females within a species grow from very similar genes and developmental mechanisms, most traits are homologous (developmentally and anatomically similar) across sexes, and the male trait cannot initially evolve separately from the female trait. This constraint holds for any traits that still have quantitative rather than qualitative sexual dimorphism. Sons will tend to inherit their mothers' mate preferences, and daughters will tend to inherit their fathers' sexually-selected traits. Darwin (1 871) called this the "Law of Equal Inheritance": all else being equal, even if only one sex is exercising selective mate choice, both the selected traits and the selective preferences will tend to be expressed in both sexes. For example, if female choice favored large penises over many generations in some species, the clitoris (female homolog of the penis) would tend to enlarge along with the penis, assuming no other selection operated on the clitoris.

Lande (1980, 1987) showed that this sort of genetic linkage between the sexes makes the evolution of sexual dimorphism a very slow process. Typically, sexual dimorphism evolves a few orders of magnitude slower than sexually-selected traits themselves do. For example, Rogers and Mukherjee (1992) applied Lande's model to data on the cross-sex heritability of human height and other body dimensions, and found that if female choice alone were favoring tall males, and males were not selecting females for height, sexual dimorphism in height would evolve around 65 times slower than height itself. That is, female height would increase over 98°/0 as fast as male height increases, purely as a correlated response to selection on males. This argument also applies to sexually-selected behavioral and mental traits: any female choice for some courtship capacity in the male would be expected to produce a correlated response in the female. In an extraordinary passage, Darwin revealed his belief in the importance of mate choice in human mental evolution, and in the importance of genetic linkage between the sexes:

> “It is fortunate that the law of equal transmission of characters to both sexes prevails with mammals; otherwise it is probable that man would have become as superior in mental endowment to woman, as the peacock is in ornamental plumage to the peahen.” (Darwin, 1871)

Now that we have reviewed sexual selection theory, we can explore how that theory applies to primates, hominids, and modern humans.

5 **Sexual selection in primates**

To a first approximation, ecological circumstances determine mating patterns in primates. Generally, the distribution of food determines the distribution of females, and the distribution of females determines the distribution of males. When females must forage on their own, males disperse to pair with the lone females, giving rise to monogamy; this pattern is fairly rare in primates, being restricted to gibbons, some lemurs, and some African and South American monkeys. When females can afford to forage in small groups to protect each other against female competitors, predators (Dunbar, 1988) and infanticide by strange males (Hrdy, 1979), a single male can exclude other males from each female group, giving rise to the common ‘harem system’ of unimale polygyny, as in hamadryas -baboons, colobus monkeys, some langurs, and gorillas. Unimale polygyny usually imposes strong sexual selection for aggressiveness, including male size, strength, and weaponry (e.g. large canine teeth), resulting in high degrees of sexual dimorphism in body size and behavior. When females can forage in larger groups (of more than 10 or so) males must usually form coalitions to exclude other males from the female group, resulting in a complex system of multimale polygyny, as in some baboons, macaques, ring-tailed lemurs, howler monkeys, and chimpanzees. In multimale polygyny, males compete at several levels: female promiscuity leads to sperm competition; female preferences for dominant males lead to status competition, individual aggressiveness, and coalition-formation; and female preferences for nice males lead males to groom females, protect their offspring, and guard them from other males (see De Waal, 1989). Hominids and humans probably evolved in fairly large groups under multimale polygyny, so we will focus here on sexual selection in large-group primates.

Male primates fight more often and more intensely when estrus females are in their group. These fights usually result in a linear dominance hierarchy among the males, with high-ranking males usually obtaining more matings because they can chase lower-ranking males away from estrus females(Silk, 1987). However, lower-ranking males can use a number of *alternative mating strategies,* because females often prefer novel males, long-term friends, and ex-dominant older males, to the currently dominant male (Smuts, 1985, 1987). Sometimes, these alternative strategies are as successful as achieving high dominance rank, though they may often be making the best of a bad situation. Males can also form coalitions to take over groups, repel outside males, achieve higher dominance rank within groups, and acquire estrus females (Smuts, 1987). Male primates often use different strategies at different ages, as their physical and social powers wax and wane (Dunbar, 1988).

Given multi-male, multi-female primate groups, how does mate choice work? Female primates can exercise choice by joining groups that contain favored males, initiating sex with them during estrus, supporting them during conflicts, and developing long-term social relationships with them. Females can reject disfavored males by refusing to cooperate during copulation attempts, driving males away from the group, or leaving the group. But female mate choice criteria remain obscure for most primate species. In contrast to modern humans, female primates rarely favor males that can provide resources or paternal care of offspring. The sporadic male care that is observed, such as watching, carrying, and protecting infants, may represent mating effort rather than paternal investment (Seyfarth, 1978; Smuts, 1985), because it is often performed by a male unlikely to be the father of the infant, who is interesting in mating with the infant's mother. Rather, the only consistent female preferences observed have been for (1) high-ranking males capable of protecting females and offspring from other males, (2) specific males with whom a special short-term consortship or long-term friendship has been formed through mutual grooming and affiliation, and male food-giving and infant protection, and(3) new males from outside the group, to avoid inbreeding and protect against the infanticide they might commit if they knew that none of the local offspring were theirs. Clearly, these criteria conflict somewhat: high-ranking males have insufficient time to maintain special friendships with all local females; and new males by definition cannot yet be long-term friends, nor can they attain high-rank immediately. In addition, females may choose to mate promiscuously, to maximize sperm competition and to confuse paternity, thereby inducing several males to protect the offspring, and to guard against infanticide (Hrdy, 1979; Small, 1993). Despite Darwin's (1871) discussion of sexual selection for the various beards, tufts, and colorful hair styles that adorn male primates, female choice for aesthetic displays and indicators has rarely been investigated in primates, perhaps because the relevant sexual selection theory has been developed only recently. However, female primates often exhibit preferences that cannot be accounted for on the basis-of male rank, age, novelty, grooming effort, or protection effort. Sometimes, primates just seem to like each other based on appearance, behavior, and personality.

Although primates follow the general animal pattern of male sexual competition and female choosiness, female competition and male mate choice is also important (Smuts, 1987). In monogamous callitrichids such as marmosets and tamarins, female compete to form pairs with quality males and drive off competing females. In unimale polygynous systems, the dominant male's sperm becomes a limiting resource, and high-ranking females prevent low-ranking females from mating through aggression and harassment (Small, 1988). In multimale groups, females compete to form consortships and friendships with favored males. Such patterns of female competition suggest some degree of male mate choice. When the costs of sexual competition and courtship are high, as they are for most primates, males have incentives to be choosy about how they allocate their competitive effort, courtship effort, and sperm among the available females. Males compete much more intensely for females that show signs of fertility such as sexual maturity, estrus behavior, absence of lactation, and presence of offspring (Smuts, 1987). Male primates almost always avoid adolescent, low-ranking, nulliparous (no-offspring) females and prefer older, high-ranking, multiparous (several offspring) females who have already demonstrated their fertility, viability, social savvy, and mothering skills. Marriage (i.e. legally-imposed life-long monogamy) has overturned this male mate choice pattern in modern human societies by pushing males to compete for unmarried, nulliparous young women of unproven fertility and uncertain status — a recent pattern that Symons (1979), Buss (1989, 1994), and others have projected into the ancestral past. Like females, male primates also show strong individual preferences for particular mates with whom they have developed special relationships (Smuts, 1985). The myth that romantic love is a recent invention of Western patriarchy denies not only the warm sexual relationships of humans in other cultures and historical epochs, but also those of other primate species.

In summary, sexual selection in multi-male, multi-female primate groups is intense because the social context of mating is so complex and dynamic. Both sexes compete, both sexes are choosy, both sexes have dominance relations, and both sexes form alliances. Sexual relationships develop over weeks and years rather than minutes. Under these relentlessly social conditions, reproductive success came to depend on mental capacities for "chimpanzee politics" (De Waal, 1982, 1989), "Machiavellian intelligence" (Byrne & Whiten, 1988), "special friendships" (Smuts, 1985), and creative courtship (Miller, 1993) rather than simple physical ornaments and short-term courtship behaviors as in most other animals.

6 Sexual selection in hominids

It is hard to reconstruct sexual selection patterns in extinct animals because mate preferences and courtship behaviors don't fossilize. However, it seems reasonable to suppose that the primate tradition of intense sexual selection within highly social groups persisted in our hominid ancestors, with ever-larger group sizes, and ever-more-complex relationships and sexual strategies. We are the products of this primate heritage refracted through a unique hominid sequence of habitats and econiches (Foley, 1987), combined with the unpredictable effects of runaway social competition for Machiavellian intelligence (Byrne & Whiten, 1988; Dunbar, 1992), and runaway sexual selection for various courtship behaviors (Miller, 1993).

Fossils and genetic markers suggest that hominids diverged from other anthropoid apes around 6 million years ago (mya), leading to increasing bipedalism, group size, and omnivory in the sequence *Australopithecus ramidus*, *A. afarensis*, and *A. africanus*. By two mya, hominids had divided into two main branches (see Foley, 1987): *Paranthropus* (also known as *Australopithecus*), including *P. robustus* and *P. boisei*, and *Homo*, including successively *Homo habilis* (2.0- 1.8 mya), *Homo erectus* (1.8-0.5 mya), and *Homo heidelbergensis* (400,000-120,000 years ago). This latter type split into two species (see Stringer & Gamble, 1993): the Neanderthals (*Homo neanderthalensis*, 200,000-40,000 years ago), and modern *Homo sapiens* (120,000 years ago to the present). Because the Pleistocene period covers the era from two mya until recently, and *Homo sapiens* probably evolved and migrated out of Africa quite recently (see Gamble, 1993), hominids and humans are largely a product of Pleistocene Africa.

Mating among our ancestors probably occurred in the context of small, mobile hunter-gatherer tribes. As with most primates, social life was probably centered on matrilines (female kin groups and their offspring), with the males largely fending for themselves, hovering around the periphery, and trying to insinuate themselves into the powerful female bands (see Dunbar, 1988). Under these conditions, the central mating problem for males was inseminating mature, attractive, viable, fertile females (Buss & Schmidt, 1993). The central mating problem for females was obtaining good sperm and good genes from high-quality males, and perhaps some provisioning and protection from a few males whose presence was not more trouble than it was worth. Equally unlikely are the tough-minded view of the Pleistocene as a brutal, male-dominated era of continuous warfare, frequent rape, and anarchy (e.g. Ardrey, 1976), and the tender-minded picture of life-long pair-bonded monogamy and heavy male investment (Lovejoy, 1981). Male scientists have been reluctant to recognize that, for the most part, 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.

Hominids probably did not live in discrete tribes with mutually-exclusive and stable memberships, well-defined territories, or coherent group movements. Social organization was more complex and multi-layered, as it is in other primates (Dunbar, 1988). Thus, mates may have been chosen not from within the small bands that characterize day-to-day foraging, but from the much larger congregations that occurred at special times(e.g. food-rich seasons, or “harvest carnivals”) and places (e.g. water sources, or “beaches”). Social and sexual relations were probably at least as fluid, complex, and ad hoc as they are today, with plenty of polygamy, serial monogamy and infidelity(see H. Fisher, 1992; Ford & Beach, 1951; Lockard & Adams, 1991; Shostak, 1981). Without marriage, mortgages, or money, why stick with just one lover during a lifetime? Given this social complexity and fluidity, each sex probably evolved a multitude of flexible strategies for pursuing their mating goals (Buss & Schmidt, 1993; Simpson& Gangestad, 1992). An individual’s current strategy might depend on their personal attributes(e.g. age, health, attractiveness, parenting skill, social skills, and seduction skills), the state of their kin network and social network(e.g. number of dependable child-care helpers), and various ecological conditions(e.g. reliability and patchiness of resources, foraging costs and dangers) and demographic conditions (e.g. operational sex ratio).

Primates and especially hominids are extremely ‘K-selected’ taxa: we have much slower development, larger bodies, fewer offspring, higher survival rates, and longer lifespans than more ‘r-selected’ taxa such as insects, fish, or rodents (Harvey, Martin, & Clutton-Brock, 1986). The more K-selected the species, the more important sexual selection usually becomes compared to natural selection (Miller& Todd, 1995). We might expect that as hominids evolved to be more and more K-selected, the relative importance of sexual selection increased. K-selection usually *reduces* the relative energetic demands of reproduction on the female and almost eliminates the need for male help, because slow gestation spreads maternal investment over a longer period, and small litters of large, well-developed offspring are easier to care for. However, human brains grow so large that infants must be born relatively immature to fit through the female pelvic canal: “human gestation is really 21 months long, with 9 months in the uterus followed by 12 months in the mother’s care” (Martin, 1992, p. 87). The helplessness and expense of human infants increases both the nongenetic and genetic benefits from mating: choosing males for their provisioning and protection ability eases the energetic burden of motherhood, but choosing males for their indicators of genetic quality and their aesthetic displays reduces the risk of producing sickly, unattractive offspring that may never reproduce. Thus, whereas infant dependency favors male provisioners, infant expense favors males with good genes and good displays. Foley (1992) provides life-history and nutritional evidence that the latter was more important: human infants do not grow using more energy per month than other ape infants, as paternal provisioning would have made possible — they simply grow for a longer time. Such data undermine the common assumption that male hunting was somehow important in feeding infants and mothers, and in supporting the energetic costs of encephalization (cf. Buss, 1992, 1994; Lovejoy, 1981; Knight, Power, & Watts, 1995).

Many people assume that the opportunities for mate choice would have been severely limited under ancestral conditions, due to the supposed prevalence of arranged marriages, the exchange of women as chattel between families and tribes, the influence of cultural rules concerning incest, outbreeding, marriage, monogamy, and adultery, and the generally low status of women under patriarchy. But there is good archaeological and ethnographic evidence that many of these factors arose within the last 10, 000 years, where they arose at all (see H. Fisher, 1992). The economic and geographic demands of agriculture distorted human mate choice patterns, because agriculture requires long-term investment in preparing and maintaining a plot of land, and thereby reduces the physical and social mobility that underlay the free choice of sexual mates in hunter-gatherer tribes. Modern mating behavior may not accurately reflect ancestral patterns of sexual selection. But we will turn next to modern human morphology — which, being less influenced by culture, is more reliable evidence of ancestral mate choice patterns.

7 Sexual selection and human morphology

Humans show sexual dimorphism in several traits. Compared to females, males on average have more height and mass, more upper-body strength, higher metabolic rates, more facial and bodily hair, deeper voices, larger brains, and riskier life histories, with higher juvenile mortality, later sexual maturity, and earlier death (Ankney, 1992; Daly & Wilson, 1983, 1988; Ghesquiere, Martin, & Newcombe, 1985; Rushton, 1995; Short& Balaban, 1994). Our moderate size dimorphism is consistent with our species having evolved under a moderately polygynous mating system, with more intense sexual competition between males than between females (Fleagle, Kay, & Simons, 1980; Martin, Winner, & Dettling, 1994). But human bodies reveal much more than just the degree of ancestral polygyny; they indicate a wide array of mate choice criteria used by our male and female ancestors.

Compared to other anthropoid apes, humans have less hair on our bodies, more on our heads, whiter eyes, longer noses, larger ear lobes, more everted lips, smaller and safer teeth, more expressive faces, more dextrous hands, and better-developed pheromone systems (Margulis & Sagan, 1991; Miller, 1993; Morris, 1985; Napier, 1993; Stoddart, 1990). Also, male humans have rather long, thick, and flexible penises compared to other primates, larger beards, and sometimes baldness later in life; female humans have greatly enlarged breasts and buttocks, a greater orgasmic capacity, and continual ‘sexual receptivity’ throughout the monthly cycle. Many of these traits show hallmarks of having evolved under the capricious power of sexual selection: they are uniquely elaborated in our species, show considerable sexual dimorphism, are grown only after puberty (sexual maturity), become engorged and displayed during sexual arousal, are manifestly valued as sexual signals, and are selectively elaborated through ornament and make-up (Miller, 1993; Morris, 1985). Such traits probably evolved both as indicators (of fertility, viability, age, health, and lack of infestation by pathogens and parasites) and as aesthetic displays (that play upon pre-existing or co-evolved perceptual biases). Sexual selection research has focused particularly on the human face, the breasts and buttocks, the penis, and the clitoris. These will be examined in turn.

The human face is a major target of selective mate choice during all stages of courtship, from flirtation through face-to-face copulation. Research on human facial aesthetics has boomed in the last few years (Alley& Cunningham, 1991; Brown& Perrett, 1993; Langlois & Roggman, 1990; Perrett, May, & Yoshikawa, 1994), revealing that average faces are attractive, but that females with more `neotenous' (child-like) faces, including large eyes, small noses, and full lips, are still more attractive, as are males will testosterone-enlarged features such as high cheekbones, strong jaws, strong chins, and large noses (R. Thornhill &

Gangestad, 1993). Bilateral symmetry is another important determinant of facial beauty, because symmetry correlates with "developmental competence"- resistance to disease, injury, and harmful mutations that cause "fluctuating asymmetry" during development (Moller & Pomiankowski, 1993; R. Thornhill & Gangestad, 1993). Also, as Darwin (1872) emphasized, human facial musculature is uniquely well-developed for displaying a variety of expressions, many of which are used in courtship.

Darwin (1871) assumed that genitals evolve purely through natural selection for fertilization ability, but Eberhard (1985, 1991) has demonstrated a substantial role for female choice in the evolution of male genitalia. The human penis is a prime example: men have the longest, thickest, and most flexible penises of any living primate. Gorillas, orangutans, and chimpanzees have very thin `filiform' penises less than three inches long when fully erect, and made rigid by muscular control combined with a *baculum* (penis bone). By contrast, human penises average over 5 inches long and one and a quarter inches in diameter, and use an unusual system of vasocongestion (blood inflation) to achieve erection(Sheets-Johnstone, 1990; Short, 1980). The size and flexibility of the human penis is more likely the result of female choice than sperm competition because sperm competition generally favors large testicles, as in the small-penised chimpanzee (Baker& Bellis, 1995; Harcourt & Harvey, 1984; G. Parker, 1984; Smith, 1984).

The female clitoris is anatomically homologous to the male penis, and although its structure probably did not evolve directly under male mate choice, clitoral orgasm has two important roles in sexual selection. First, as a female mate choice mechanism, clitoral orgasm favors males capable of providing high levels of sexual stimulation. Over the short term, orgasm promotes vaginal and uterine contractions that suck sperm into the uterus and minimize post-coital`flowback' therefrom (Baker & Bellis, 1995). Over the long term, pleasurable orgasms promote future copulations with the favored male through reinforcement learning and emotional attachment. Some male scientists (e.g. Gould, 1987; Symons,1979)have questioned whether human female orgasm is an adaptation at all, because it can be hard to achieve. But is makes sense for a 'choosy clitoris' to produce orgasm only given substantial foreplay and emotional warmth, because this would reinforce only sex with males who have the willingness and skill to provide the right kinds of sexual stimulation. Thus, the sexual dimorphism between penis and clitoris could be viewed as a direct physical manifestation of the two components of Fisher's runaway process: a highly elaborated male trait (the penis) designed to stimulate, and-a highly discerning female preference (the clitoral orgasm) designed to respond selectively to skillful stimulation. The second role for orgasms is to advertise happiness to lovers. Given the fact that orgasms come hard, only when sex is long, varied, and exciting rather than brief, mechanical, and perfunctory, orgasms can serve as fairly reliable indicators of female sexual satisfaction, commitment, and fidelity. Thus, some aspects of female orgasm may have evolved through male mate choice to promote male certainty of paternity (and hence male protection and investment). If so, we can understand why females advertise their orgasms through clear tactile, visual, and auditory signals such as strong vaginal contractions and hip movements, the sexual blush over face and chest, and passionate vocalizations (see Morris, 1985).

Female human breasts and buttocks have undergone sexual elaboration through mate choice by males. These organs store substantial amounts of fat, so could function as indicators of female nutritional status and hence fertility (Low, Alexander, & Noonan, 1987; Szalay & Costello, 1992). Singh (1993) showed that males prefer women who display a low waist-to-hip ratio (WHR), ideally about 0.70, concordant with enlarged buttocks indicating sufficient fat reserves, and a narrow waist indicating non-pregnancy. Permanent enlargement of breasts and buttocks is also fairly effective at concealing ovulation (Margulis & Sagan, 1991;

Szalay & Costello, 1992). Females who do not reveal their menstrual or lactational cycles may benefit from male uncertainty by being able to solicit male attention and investment even when they are not really fertile: "From hairy, flat-chested ape to modern buxom woman … males were kept guessing about when females were ovulating" (Margulis & Sagan, 1991, p. 96). More generally, the loss of a specific estrus period, combined with 'concealed ovulation' and 'continuous sexual receptivity', may have allowed females to attract more continuous attention (e.g. protection, provisioning, social support) from males even when they were not ovulating (Alexander & Noonan, 1979; H. Fisher, 1982; Hrdy, 1981, 1988; Hrdy & Whitten, 1987; Tanner, 1981).

Sexually-selected morphological features are important to the study of evolution and human behavior for three main reasons. First, there is no sharp division between body and brain: apparently simple bodily adaptations also have physiological, neurological, and psychological features. The richly-innervated penis, clitoris, nipple, and mouth are as much psychological organs as physical objects. Second, the mate choice mechanisms that assess bodily features are easy to study experimentally and may lead to insights about mate choice with respect to more complex mental and behavioral traits. Finally, body features reveal patterns of ancestral mate choice relevant to understanding human mental evolution. Mate choice by males has shaped female breasts, buttocks, and orgasms; mate choice by females has shaped male body size, beards, and penises. Mutual mate choice has probably influenced human hair, skin, eyes, lips, ears, face shape, hands, and pheromones. If our male and female ancestors were both selecting for bodily traits, it seems likely that they were also both selecting for mental and behavioral traits. By overcoming the Cartesian split between body and mind, we can better appreciate the role of mate choice in shaping both.

8 Sexual selection and human mental evolution

> "Most evolutionary anthropologists now believe that big brains contributed to reproductive success either by enabling men to outwit and outscheme other men (and women to outwit and outscheme other women), or because big brains were originally used to court and seduce members of the other sex. "(Ridley, 1993, p. 20).

Could sexual selection have shaped not only the human body, but the human mind? Darwin (1871) clearly thought so, but most 20th century theorists have viewed natural selection as the exclusive director of human mental evolution. Even those who granted a role to sexual selection focused more on male sexual competition than on mate choice. Chance (1962) suggested that sexual selection would have favored young males that show intelligence and caution in challenging dominant males, and in forming coalitions to take territories and intimidate females. Fox (1972) argued along similar lines that sexual selection would have favored male hunting prowess, leadership, and tool making. Alexander (1971) viewed organized warfare for possession of females and mating-relevant resources as a major force in human evolution. Caspari (1972) considered oratory as an arena of male competition and suggested a role for sexual selection in the evolution of language. In a fairly sketchy but provocative paper, S. Parker (1987) proposed that sexual selection could help account for the evolution of bipedalism, canine reduction, tool-making, fire-using, shelter-construction, and language. This emphasis on male competition made sense when Darwin's theory of female choice was still considered unfounded. But given the resurgence of interest in mate choice in other species, perhaps the role of mate choice in human mental evolution deserves another look.

But why bother with sexual selection? What's wrong with the traditional story that natural s-election just generally favored intelligence, learning, tool-making, and culture? The problem is that the evolution of big brains is so rare, so recent, so capricious, and seemingly so unrelated to the demands of habitat or econiche (Miller, 1993). Brain size in our lineage has tripled over the last two million years, reflecting the evolution of unprecedented mental and behavioral capacities. Over three million years ago, our ancestors were already successful, social, fairly bipedal, tool-making hunter-gatherers on the African savanna — and they had brains only slightly larger than the chimpanzees. Then, two million years ago, for no apparent reason, brain size started growing exponentially in our lineage but not in other closely-related hominid species who shared the same habitat, such as *Paranthropus boisei* and *robustus.* Encephalization then stopped about 100, 000 years ago, again for no apparent reason, long before the Neolithic revolution in technology and art 40, 000 years ago. Extreme encephalization also happened in some species of cetaceans (dolphins and whales) and proboscis (elephants) living in quite different environments, but has not occurred in other primates living in quite similar environments (e.g. baboons, chimpanzees, *Paranthropus* hominids).

The speed, uniqueness, and capriciousness of this encephalization process has prompted many theorists to accept that human mental evolution must have been driven by some sort of positive-feedback process that is sensitive to initial conditions. There have been two traditional contenders. In the runaway social competition model (Byrne& Whiten, 1988; Humphrey, 1976; Whiten, 1991; also see Miller, in press), hominids got smarter to predict and manipulate each others' behavior, leading to a social-intelligence arms race between mind-reading and deception. In the runaway gene-culture co-evolution model, hominids got smarter to learn and use material culture (e.g. tools and survival techniques), which was itself evolving (Durham, 1991; Lumsden & Wilson, 1982; Wills, 1993). Yet these theories overlook the clearest and best-established case of positive-feedback evolution in nature: runaway sexual selection. The runaway process is a good fit to the human evolution data because it begins and ends unpredictably, without much relation to the external environment, but it is extremely powerful and directional once underway (Miller, 1993; Miller& Todd, 1993).

As we saw in section 6, hominid social life probably allowed considerable scope for mate choice by both males and females. Our ancestors lived in hunter-gatherer tribes that probably had rather fluid, complex, and polygynous mating patterns, rather different from the modern ideals of lifelong monogamy and nuclear family. The mate choice patterns permitted by tribal life could have favored several classes of courtship behaviors that function as indicators: 'viability-indicators' that demonstrate physical health, energy, and freedom from disease, deformity, or deleterious mutation, 'age-indicators' that reveal age, reproductive status, and survival prospects, 'social-success-indicators' that reveal social skills for dominance, competition, aggression, deception, peace-making, communication, and unpredictability, and 'cognition-indicators' that reveal mental capacities for perception, attention, memory, planning, and creativity. In addition, perceptual biases in mate choice would have favored 'aesthetic displays' of complex, interesting, innovative behaviors that are less closely correlated with fitness in other domains. Together, these forms of mate choice could have set up runaway sexual selection for more complex and creative 'behavioral courtship displays' such as stories, myths, jokes, rituals, dance, music, art, and sexual foreplay.

If the brain evolved through runaway sexual selection, what were the relevant traits and preferences? Two uniquely elaborated aspects of the human brain are its creativity (Boden, 1991, 1994; D. Campbell, 1960; Freyd, 1994) and its neophilia, or love of novelty

(Zuckerman, 1984). Perhaps creativity itself became a trait subject to sexual selection by neophilia as a mate preference. More technically, mental capacities for generating ‘protean’ (adaptively unpredictable) courtship displays may have been subject to `neophilic' mate preferences in both sexes (on proteanism see Driver& Humphries, 1988).

Neophilia influences mate choice in many species. Darwin (1871) observed that “mere novelty, or slight changes for the sake of change, have sometimes acted on female birds as a charm, like changes of fashion with us.” Males of many species are more sexually excited by novel females (Dewsbury, 1981). Females of several bird species prefer males who display larger song repertoires with greater diversity and novelty (Catchpole, 1980, 1987; Podos, Peters, Rudnicky, Marler, & Nowicki 1992). Such neophilic mate choice may account for the creativity of male blackbirds, nightingales, sedge warblers, mockingbirds, parrots, and mynahs. Small (1993) emphasized neophilia in primate mate choice: “The only consistent interest seen among the general primate population is an interest in novelty and variety. ” Neophilia (termed ‘openness’) is one of the ‘Big Five’ personality traits in humans (see Buss, 1991), and shows moderate heritability (Plomin & Rende, 1991; Zuckerman, 1984). Of course, in modern society, human neophilia is the foundation of the art, music, television, film, publishing, drug, travel, pornography, fashion, and research industries, which account for a substantial proportion of the global economy. Before such entertainment industries amused us, we had to amuse each other on the African savanna — and our neophilia may have demanded ever-more creative displays from our mates. This hypothesis can explain the mysterious ‘cultural’ capacities that are universally and uniquely developed in humans, such as language, music, dance, art, humor, intellectual creativity, and innovative sexual play. These are all highly valued during mate choice and highly useful during courtship. Such displays all use a uniquely human trick: the creative recombination of learned semantic elements(e.g. words, notes, movements, visual symbols) to produce novel arrangements with new emergent meanings (e.g. stories, melodies, dances, paintings). This trick allows human courtship displays not just to tickle another’s senses, but to create new ideas and emotions right inside their minds, where they will most influence mate choice.

The gradual evolution of language was especially important, because it allowed hominids to display complex ideas and images to one another using an increasingly complex, structured, open-ended, combinatorial system (Pinker, 1994). Language gave potential mates a unique window into each other’s minds, so allowed much more direct sexual selection on the mind itself. Also, language permits gossip, which can transform mate choice from an individual decision to a social decision that integrates information from family and friends. With language and gossip, courtship displays need not be observed directly; they need only be witnessed by someone who can talk later to potential mates. The feedback loop between sexual selection, language complexity, and mental complexity was probably the mainspring of human mental evolution.

The lack of sexual dimorphism in human mental capacities is not a fatal problem for this sexual selection theory. We would expect men and women to have similar minds given the genetic linkage between the sexes, the mutuality of mate choice, the interactiveness of courtship behaviors(e.g. conversation, dance, and musical dueting), and the overlap between perceptual capacities for judging complex behaviors (e.g. understanding language) and motor capacities for generating complex behaviors (e.g. speaking language). The general notion of mental evolution through mate choice has been presently more fully elsewhere (Miller, 1993, 1994, 1995, in press; Miller& Pratto, 1992; Miller& Todd, 1993, 1995; Todd& Miller, 1993).

A methodological problem arises: how could one demonstrate that a mental adaptation really evolved through mate choice? As section 5 showed, sexually-selected human bodily traits can be identified by being uniquely elaborated in our species, growing only after puberty, becoming engorged and displayed during sexual arousal, being selectively elaborated through ornament and make-up, being manifestly valued as sexual signals, and showing sexual dimorphism. Similar criteria for special design features can also be applied to mental and behavioral traits. If a behavior is uniquely human, is selectively displayed by adult humans during courtship and sexual competition, is displayed in different forms and frequencies by males and females, and is clearly valued as a sexual display, then it is worth investigating as a sexually-selected adaptation. By these adaptationist criteria, many aspects of human cognition and culture would thus fall under the rubric of courtship behavior: language, art, music, humor, acting, mimicry, metaphor, sports, games, ritual, myth, ideology, religion, politics, and science. More generally, sexually-selected adaptations are expected to show complex organization specially attuned to reliably, efficiently, and flexibly perform certain functions in sexual competition and/or courtship (on adaptations, see Williams, 1966; Tooby & Cosmides, 1990). Such adaptations can also be identified through the comparative method (Harvey & Pagel, 1991) by examining the distribution of traits across related species with known phylogenies, to discern when and where evolutionary innovations occurred. New methods in cognitive neuroscience (see Gazzaniga, 1995) should also allow localization of the mental adaptations underlying these courtship capacities, and comparison to homologous structures in other primates.

One might also check whether such adaptations are currently under sexual selection, by seeing whether (1) the trait shows heritable variation (e.g. a moderate coefficient of additive genetic variation — see Moller & Pomiankowski, 1993), and whether (2) individuals exhibiting one form of the trait have greater mating success (e.g. number of copulations, partners, or offspring) than individuals exhibiting other forms. One might also show that individuals can (consciously or unconsciously) discriminate among variants of the trait, and do exhibit a preference for one variant. To further establish that a trait functions as an indicator, one must show that variants of the trait correlate with some indicated quality such as age, health, fertility, or social status. To establish that a trait is evolving at least partially under the runaway process, one must show genetic linkage between the trait and the corresponding preference. However, all such questions of utility in current societies are a bit tangential to the question of adaptive function under ancestral conditions.

9 **Sexual selection and human culture**

Theories of human mental evolution are theories of human nature, and theories of human nature are the foundation of psychology, the social sciences, and the humanities (Tooby & Cosmides, 1992). So, if sexual selection played a major but little-appreciated role in shaping human evolution, and if sexually-selected traits are the most central, distinctive, and long-overlooked components of the human mind, then the standard model of human nature used in the social sciences and humanities probably focuses too heavily on the economics of survival and not enough on the mental, material, and cultural demands of courtship. Sexual competition probably underlies many political, economic, sociological, anthropological, criminological, cultural, ideological, religious, moral, and artistic phenomena (e.g. see Barkow, 1989; Betzig, 1986, 1992; Daly& Wilson, 1988; L. Ellis, 1993; Frank, 1985; Ridley, 1993; Wright, 1994), but it has been almost entirely overlooked as an explanatory principle. Instead, 'culture' has become the dominant explanation for all human social and communicative behavior, despite its vagueness as a scientific concept (see Cosmides & Tooby, 1994; Sperber, 1994; Tooby & Cosmides, 1992). Rather than viewing culture as the reason for individual human behavior, we might view culture as an emergent phenomenon arising from sexual competition among vast numbers of individuals pursuing different mating strategies in different display arenas.

For example, only sexual selection theory can provide a coherent, non-circular account of 'cultural dimorphism': why have males always dominated political, economic, and cultural life in every known society? Most feminist theories of 'patriarchy' simply beg the question by viewing male power as a self-sustaining tradition, without offering any plausible explanation of its origins. Traditional religious, reactionary, and sexist ideologies also beg the question, by invoking unexplained 'natural' or divinely ordained sex differences. But if most 'economic behavior' is mating effort by males to acquire material resources for attracting and provisioning females, and if most 'cultural behavior' is male mating effort to broadcast courtship displays to multiple female recipients, then cultural dimorphism is easily explained by sexual selection.

The age and sex demographics of cultural production are almost the same as the demographics of homicide (Miller, 1995; see Daly & Wilson, 1988) :males produce about an order of magnitude more art, music, literature, and violent death than women, and they produce it mostly in young adulthood. This suggests that, like violent sexual competition, the production of art, music, and literature functions primarily as a courtship display. For males, the mating benefits of public cultural displays are large because every additional short-term mating achieved through impressing some receptive female represents a substantial increase in expected fitness. Because male reproductive success can be virtually unlimited, the amount of energy and time that talented men are motivated to invest in cultural displays should be virtually unlimited. For example, although the gifted guitarist Jimi Hendrix died at age 27 from a drug overdose, he had affairs with hundreds of groupies, and fathered children in the U. S., Germany, Britain, and Sweden. Composer J. S. Bach fathered 8 children by his first wife and 11 by his second. The sexual conquests of Picasso, Chaplin, and Balzac are legendary. As every teenager knows and most psychologists forget, cultural displays by males increase their sexual success.

But for females, the genetic benefits of public cultural displays are smaller, because their maximum reproductive success is constrained directly by their maternal investment ability (i.e. the time required for pregnancy and lactation), not by the number of short-term matings they can achieve. Rather than broad-casting her courtship displays to all males indiscriminately and risking sexual harassment from undesirables, it may be more effective for a woman to narrow-cast her courtship displays to a few select males who are capable of giving her the long-term care, attention, and resources she wants. This could be called the 'Scheherezade strategy', after the woman who retained a sultan's intellectual attention, sexual commitment, and paternal investment by inventing fantastic stories throughout a thousand and one nights. Thus, cultural dimorphism is much more likely to reflect a difference in motivation and sexual strategy than a difference in basic mental capacity.

10 Conclusion

In sexually-reproducing 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. However, sexual selection has long been overlooked in the human sciences, partially because evolutionary biologists themselves were skeptical about Darwin's most innovative theory until quite recently, and partially because various ideological biases kept sex marginalized as a topic too messy, too mystical, too embarrassing, and too arousing for scientific analysis. We have to face the possibility that if human evolution was a film, it would be X-rated.

This chapter has reviewed the history of sexual selection theory, the diversity of mate choice criteria (selection for indicators, aesthetic displays, sperm competition, provisioning, territories, and protection), the logic and limits of sex differences, the patterns of sexual selection in primates and hominids, and the parts of the human body, the human mind, and human culture that have probably evolved through sexual selection. But this is all only the tip of the sexberg: a snap-shot of the sometimes eager, sometimes resistant human sciences trying to absorb an unexpectedly large and potent body of biological theory and evidence. The rapture will be mutual though, because a new appreciation of sexual selection allows the tightest possible fit between (1) well-established biological theory and data, (2) universal and important aspects of human nature and human psychology, and(3) universal and important aspects of human culture and social life. This integration, though necessary for future progress, will be difficult for the social sciences and the humanities because it undermines and replaces some of their cherished models of human nature(e.g. Freud, Marx, social-constructivism), and because it demands research concerning the adaptive functions rather than just the proximate mechanisms of human social, sexual, and cultural behavior. But if we recognize the role of sexual selection in the evolution of human intelligence, creativity, and culture, perhaps some of the old dichotomies — passion/reason, mind/body, nature/culture, sex/science — can finally be reconciled.

Future histories of science will probably look back at our era as a critical point during which human self-understanding was challenged and re-cast more deeply than ever before. While the conceptual novelties of Copernicus, Adam Smith, Marx, Einstein, and Freud have lost their revolutionary edge, the Darwinian revolution continues to dig deeper and more sharply into the human soul (see Dennett, 1995; Ridley, 1993; Wright, 1994). Just when we thought we were comfortable with the idea of blind natural selection shaping human nature, the eerie, half-sentient process of sexual selection came back from the dead, more powerful and ubiquitous than ever. A full recognition of the role of mate choice and sexual competition in human affairs and human evolution may shake not only our psychology, but our psyches. It remains to be seen whether we have the intellectual creativity, the sexual self-confidence, and the existential courage to pursue these inquiries to their completion.

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