# Kindness, fidelity, and other sexually-selected virtues

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Abstract

Moral evolution theories have emphasized kinship, reciprocity, group selection, and equilibrium selection. Yet moral virtues are also sexually attractive, and Darwin argued that sexual attractiveness may suffice to explain many aspects of human morality. This paper updates his argument by integrating recent research on mate choice, person perception, individual differences, costly signaling, and virtue ethics. Many human virtues evolved in both sexes through mutual mate choice, to advertise both good genetic quality and good parenting abilities. Such virtues may include kindness, fidelity, magnaminity, and heroism, plus quasi-moral traits such as intelligence, conscientiousness, agreeableness, mental health, religiosity, and social status. This theory leads to 20 testable predictions about the phenotypic features, genetic bases, and social-cognitive responses to human moral virtues.

“Human good turns out to be the activity of the soul exhibiting excellence."

-- Aristotle (*Nichomachean Ethics*, 350 B.C.)

We feel lust for other people’s bodies, but we fall in love with their mental and moral traits. Many sexually attractive facial and bodily traits evolved to reveal phenotypic condition and genetic quality, including health, fertility, and longevity (Fink & Penton-Voak, 2002; Henderson & Anglin, 2003; Langlois et al., 2000). This paper explores that possibility that our distinctively human moral traits evolved through sexual selection to serve an analogous display function. The most romantically attractive mental traits – intelligence, wisdom, kindness, bravery, honesty, integrity, and fidelity – often have a moral or quasi-moral status.

Recent empirical research suggests that many of these moral traits are sexually attractive, and can serve as mental fitness indicators: they reliably reveal good mental health, good brain efficiency, good genetic quality, and good capacity for sustaining cooperative sexual relationships and investing in children (e.g. Alvard & Gillespie, 2004; Hawkes & Bliege Bird, 2002). Thus, the moral virtues that we consider sexually attractive are not culturally or evolutionarily arbitrary. Rather, they evolved to advertise one’s individual fitness in hard-to-fake ways that can be understood through a combination of sexual selection theory (Andersson, 1994) and costly signaling theory (Zahavi & Zahavi, 1997).

This paper develops a theory that sexual selection shaped many of our distinctively human moral virtues as reliable fitness indicators. It updates and builds upon chapter 7 (“Virtues of good breeding”) in my book *The Mating Mind* (Miller, 2000a), and emphasizes relevant empirical and theoretical work since 2000. It tries to integrate person perception research with person-level approaches to moral philosophy, especially virtue ethics (Flanagan, 1991; Hursthouse, 1999; Pence, 1984; Stohr & Wellman, 2002) and naturalistic approaches to understanding moral intuitions (e.g. Nesse, 2001; Ridley, 1996).

The paper has twelve sections. First, it introduces the idea of sexual selection for moral virtues by considering the role of morality and romantic virtues in human courtship. Second, it emphasizes that this sexual selection model does not imply that morality is illusory, superficial, or covertly sexual. Third, it considers moral judgments of whole persons rather than isolated behavioral acts, in the general context of person perception, social attribution, and mate choice; this usefully blurs the distinction between ‘moral’ virtues and other sexually attractive virtues such as intelligence, creativity, humor, charisma, bravery, mental health, physical health, strength, fertility, and beauty. Fourth, it reviews new ‘costly signaling’ and ‘fitness indicator’ models of sexual selection for ‘good genes’ and ‘good parents’ in relation to human altruism. Fifth, it explains how sexual selection in a socially monogamous species such as ours, with mutual mate choice, can result in minimal sex differences in the moral virtues. Sixth, it examines which specific moral virtues seem best explained by sexual selection. Seventh, it reviews evidence that the moral virtues really are sexually attractive to both sexes, across many cultures. Eighth, it reviews behavior genetics evidence that the moral virtues and vices remain genetically heritable in our species, providing a continuing incentive for mate choice. Ninth, it examines moral and quasi-moral traits from the perspective of psychological research on individual differences in intelligence, personality, and psychopathology. Tenth, it considers how sexual selection may have interacted with other selection pressures (kinship, reciprocity, group selection, and equilibrium selection) to shape moral virtues. Eleventh, it identifies 20 testable empirical ways to assess whether particular moral virtues evolved through sexual selection, and illustrates how to apply these assessments in the case of one specific virtue, sexual fidelity. Finally, this paper considers this theory’s sobering implications for the practice of normative ethics by philosophers (i.e. sexually mature human males and females whose moral intuitions have been shaped by millennia of sexual selection).

## Romantic Virtues and Moral Virtues

This sexual selection theory of moral virtues may appear bizarre at first to moral philosophers and moral psychologists. From Saint Augustine through Sigmund Freud, sexuality has been viewed as morality’s nemesis. It was hard to imagine that virtues might arise through mate choice when Western thought was gripped by the traditional dichotomies of body vs. spirit, lust vs. virtue, and sinners vs. saints. Also, most philosophers after Aristotle have focused on evaluating the morality of isolated acts rather than the moral virtues of whole people. This made it hard to view ethics as a branch of person-perception or individual-differences psychology. Even within evolutionary theories of morality, moral capacities have traditionally been seen as pragmatic tools to increase individual or group survival prospects, rather than as costly, conspicuous signals to increase individual reproductive prospects.

To overcome these intellectual biases, it may help to take a step back and think about moral virtues in the context of real human mate choice. Apart from physical appearance and social status, which traits most excite our romantic impulses? People often fall in love based on (unconscious) assessments of each other’s generosity, kindness, honesty, courage, social sensitivity, political idealism, intellectual integrity, empathy to children, respectfulness to parents, or loyalty to friends. The most romantic personal traits are often those that have been considered praise-worthy moral virtues by the world’s most influential philosophical and religious traditions from ancient Greece, Israel, Arabia, India, China, and Japan. These loveable virtues overlap almost entirely with a combination of Nietzsche’s (1887, 1888) ‘pagan virtues’ (e.g. leadership, bravery, strength, skill, health, fertility, beauty, tolerance, joy, humor, and grace) and the traditional ‘Christian virtues’ (e.g. faith, hope, charity, love, kindness, fairness, equality, humility, and conscience).

Moral virtues are, among other things, personal traits that we are proud to display during courtship. Indeed, courtship in most cultures can be viewed as a ritualized test of diverse moral virtues, such as kindness in gift-giving and food-sharing, conscientiousness in keeping dates and promises, empathy in talking and listening, and sexual self-control. Courtship is a moral obstacle course that we set up for each other, in which we test each others’ generosity, sympathy, patience, fidelity, honesty, and etiquette. For courtship to be reliable, valid, and discriminating as a moral test, it must lead to a perceivable range of moral failures (e.g. broken promises, revealed prejudices, irritabilities, infidelities, impatient sexual pressures) that reflect an underlying distribution of stable moral character-traits.

In prototypical romance stories across cultures, both characters fall in love, enjoy bliss, get lazy, make some moral errors, have a moral crisis, recognize their moral failures, resolve to improve their moral character, magnanimously forgive each other, and live happily ever after. It is not romantic for characters to make and forgive purely perceptual failures (e.g. failures of depth perception or color constancy) or purely cognitive failures (e.g. base rate neglect or hindsight bias). If neither individual in a sexual relationship cares about projecting moral virtues (as in relations between prostitutes and clients, masters and slaves, or presidents and interns), then the relationship is considered superficial and unloving.

Our romantic emotions seem to amplify the subjectively perceived variance in moral character across potential lovers. When we fall in love, new lovers seemed morally exemplary; when they make moral errors, they seem morally treacherous; when they make amends, they seem morally redeemed; when they divorce us, they seem morally repulsive. Borderline personality disorder (the tendency to view intimate partners in unstable, dichotomized ways, as extremely good or extremely evil – see Koenigsberg et al., 2002) is just an exaggerated form of the normal human tendency to alternately over-value and under-value our lovers’ virtues.

Conversely, moral vices are character flaws that we would be embarrassed to reveal to potential mates. These sexually embarrassing vices include not just obviously anti-social behaviors (killing, raping, lying, cheating), but also victimless addictions (sloth, gluttony, greed, envy, pride, drinking, smoking, drug-taking, gambling, masturbating), failures of pro-social magnaminity (under-tipping waiters, ignoring starving children, fleeing combat), and acts of symbolic meanness (kicking dogs, burning flags, cursing the gods). The common denominator in these moral vices is that they lead potential mates to hold our moral character in lower esteem, so they are less likely to breed with us. Across cultures, the leadings causes of divorce (infidelity, abuse, addiction, unemployment – see Betzig, 1989) are almost all seen as serious moral failures. To many moral psychologists and philosophers, the sexual costs of moral vice may seem tangential to an evolutionary account of human morality. Yet to evolutionary biologists, a direct connection between moral vice and impaired reproductive success should be highly suggestive.

## Sexually Selected Functions versus Sexual Motivations

To suggest that human moral virtues evolved through mate choice is not to suggest that morality is ‘really all about getting laid’ at the level of individual motivation. Evolutionary functions must not be confused with proximate motivations (Radcliffe Richards, 2000). Just as sexual selection can produce genuinely beautiful peacock tails and genuinely creative nightingale songs, it can produce genuine psychological altruism, not just fake generosity as a seduction tactic (Miller, 2000a). Most sexually-selected adaptations do not include a little copy of their adaptive function inside themselves as a secret libidinous motive. Male beards and female breasts have no doubt been shaped by mate choice (Barber, 1995), but neither beards nor breasts need to contain any subconscious sex drive to remind them that they are supposed to be attractive.

Why does this distinction between adaptive functions and subjective motives seem so clear when we think about beards and buttocks, but so fuzzy when we think about moral behavior? Perhaps one reason is that we have evolved a high degree of wariness about being sexually exploited. Some people are sexually predatory, and consciously produce behaviors that they know will be sexually attractive just to seduce us (Mealey, 1995; Wilson et al., 1996). If such a person admits that their apparently moral behavior was just aimed at fornication, we rightly get upset and worry that they are a Machiavellian psychopath. Some over-generalize this response to stigmatize any evolutionary psychologists who try to identify any reproductive benefits for any form of altruism.

Evaluating Moral Persons versus Moral Acts

This paper considers moral judgments and moral virtues at a level of description that is still fairly unusual in moral philosophy – the level of whole persons, not isolated behavioral acts. It argues that much of human morality emerged through the co-evolution of our moral virtues as personality-type dispositions, and our social-cognitive adaptations for judging those moral virtues in others. This moral-person level of description is the domain of mate choice in evolutionary psychology, person perception in social psychology, virtue ethics in moral philosophy, parole decisions in criminal justice, and voter choice of political leaders in democratic elections. By contrast, the moral-act level of description is the domain of adaptive decision-making in evolutionary psychology, social attribution in social psychology, act ethics in moral psychology, and guilt-or-innocence decisions in criminal law.

On this account, we rarely made moral judgments about isolated behavioral acts in prehistory. Rather, we made a hierarchy of inferences – about moral personality traits (virtues or vices) from behavioral acts, and inferences about the ethical merit of whole persons from estimates of their moral personality traits. This is because we had to choose whether, when, and how to interact with a particular person as a whole package of morally valenced personality traits. They could be favorite offspring or black sheep, friend or enemy, lover or ex-lover. We could not pick and choose our social interactions trait-by-trait.

Also, an individual’s actions were probably assessed against the background of their age, sex, health, fitness, personality, intelligence, and other individual-differences dimensions, which jointly determine our expectations about their likely moral capacities. For example, we tolerate theft by toddlers more than theft by adults. We forgive unkind words spoken during high fevers by the sick. We do not expect a keenly empathic Theory of Mind in the severely brain-damaged or autistic.

Further, an individual’s actions were probably assessed in the context of their actual social, sexual, tribal, and/or genetic relationships to us. Different social-interaction domains called for different moral-judgment criteria, focused on different virtues. In mate choice, we may give great weight to the virtues of intelligence, kindness, fidelity, and honesty, plus a few romantic virtues such as beauty, youth, and humor. By contrast, in kin altruism, we may give higher weight to the kinship-specific virtues of genetic similarity and expected future reproductive success, while caring little about kindness, gentleness, or honesty. This is why mothers can love psychopathic sons, and why fathers can love the selfish, screaming semi-clones called babies. It is mainly in the domain of social reciprocity with unrelated acquaintances that we see the sort of Tit-for-Tat moral accounting that corresponds to the traditional moral philosopher’s emphasis on the moral evaluation of isolated behavioral acts.

The moral-person level of description is different in some key respects from the moral-act level of description. First, we generally accept as a conversational implicature that ‘ought implies can’ when we judge moral acts (Sinnott-Armstrong, 1984), but we do not necessarily follow this implicature in judging the morality of whole persons. That is, we typically do not expect someone to follow a normative moral principle (an ‘ought’) in a particular behavioral instance if they can not, due to some overwhelming external or internal constraint. We don’t expect quadriplegics to jump in front of trolleys to save children, or crack addicts to vote conscientiously. However, when judging the morality of whole persons in real socio-sexual relationships, we are rarely so forgiving. If a potential mate has Tourette’s syndrome and can’t refrain from screaming ‘Crack-head slut!’ repeatedly in public during a first date, there is unlikely to be a second date, no matter how much we understand about verbal disinhibition in neurological disorders. If a potential hunting partner had a severe head injury that renders him too clumsy to hunt effectively, we may pity him, but will still exclude him from the hunt. When the fitness stakes are high, as in real socio-sexual relationships, we hold people morally accountable even for faults that are not their own. If we did not, then we would be logically incapable of shunning even serial-rapist psychopaths, who, after all, must be a joint product of their genes, environment, and random developmental events (Dennett, 2003; Pinker, 2002).

Second, ‘morality’ means something different at the person-level compared to the act-level. A moral act may be one that obeys some rationally defensible, universalizable, deontic or consequentialist principle. However, a moral person, from the point of view of a standard prehistoric hunter-gatherer, is someone who embodies pro-social virtues that make them a good mate, friend, relative, or trading partner. In economic terms, a moral person is one whose individual behavior brings ‘positive externalities’ to their social relationships. In game-theory terms, a moral person is simply one who attaches positive utility to the welfare of others, such that they tend to play Pareto-dominant equilibria in mixed-motive games. In evolutionary terms, a moral person is one who pursues their ultimate genetic self-interest through psychological adaptations that embody a genuine, proximate concern for others (de Waal, 1997; Nesse, 2001). All three of these working definitions are descriptive rather than normative. They are each open to quantitative, empirical verification by measuring the net positive externalities, Pareto-dominance, or proximate empathy levels manifest by individuals in real social interactions.

## Costly Signaling Theory, Fitness Indicators, and Moral Virtues

Since about 1990, new theories concerning ‘costly signalling’ have revolutionized the study of both sexual selection and human altruism (Gintis et al., 2001; McAndrew, 2002). Most animal communication is relentlessly narcissistic, advertising the signaler’s own individual species, sex, age, health, fertility, social status, phenotypic condition, and/or genetic quality (Bradbury & Vehrencamp, 1988). Only rarely do animals communicate any referential information about the external world. The trouble with self-referential signals is that often, animals have incentives to lie about themselves, in order to attract more mates, solicit more parental investment, or deter predators and rivals. Why should animals ever believe any self-referential signals produced by other animals?

Costly signalling theory offers a solution: if a signal is so costly that only high-health, high-status, high-condition animals can afford to produce it, the signal can remain evolutionarily reliable (Zahavi & Zahavi,1997). Almost any sort of fitness-related cost will work: matter, energy, time, or risk. For example, a peacock’s tail is burdensome in all four senses: its growth and maintenance requires several hundred grams of mass, many calories, much time to grow, and much risk (it is harder to escape from peacock-eating tigers). Very often, the most complex, elaborate, and puzzling signals observed in nature are the result of sexual selection through mate choice (Darwin, 1871). These sexual ornaments almost always impose high costs on the bearer, guaranteeing their reliability as indicators of condition and fitness.

This paper argues that many human virtues evolved through sexual selection as costly signals, as fitness indicators. This hypothesis has been advanced by a few previous researchers (e.g. Hawkes, 1991; Tessman, 1995), and its empirical testing has been one of the most active areas of evolutionary psychology and evolutionary anthropology in the last few years. Indeed, many pro-social behaviors that were assumed to arise through kinship or reciprocity are now thought to have emerged as costly signals of individual fitness, favored by social and sexual selection.

For example, it was often assumed that risky big-game hunting evolved because the best hunters could better feed their own offspring (Lee & DeVore, 1968). However, most hunted meat from big game is distributed too widely in hunter-gatherer clans for this paternal provisioning theory to work. Rather, recent research suggests that the most successful hunters are willing to provide the pro-social ‘public good’ of hunted meat because they attract more high-quality female mates (Alvard & Gillespie, 2004; Hawkes & Bliege Bird, 2002; Smith & Bliege Bird, 2000).

Costly signaling theory has intellectual roots in many traditions and academic fields, some of which explicitly applied it to explain human morality. In the Hasidei Ashkenaz movement of 13th century German Judaism, more difficult moral acts (e.g. charity when one is poor, forgiveness when one is righteously angry) were considered more praiseworthy. In Friedrich Nietzsche’s (1887) *Genealogy of Morals*, pagan virtues were considered attractive signals of health and power. In Thorstein Veblen’s *Theory of the Leisure Class* (1899), conspicuous consumption and conspicuous charity were seen as hard-to-fake signals of wealth and social status. In mid-20th century economics, corporate advertising was interpreted as a costly, conspicuous signal of market power to competitors and of corporate profitability to investors, rather than just a way to entice consumer purchases (Dorfman & Steiner, 1954). In 1970s biology, Amotz Zahavi (1975) viewed many animal traits and signals as hard-to-fake indicators of animal fitness.

Our mate preferences for moral virtues may be explained by costly signalling theory. If a young woman places a single’s ad stating “SHF, 26, seeks kind, generous, romantic, honest man”, we can translate this in evolutionary terms as “single Hispanic female, 26, seeks a healthy male of breeding age with a minimal number of personality disorders that would impair efficient coordination and parenting in a sustained sexual relationship, and a minimal number of deleterious mutations on the thousands of genes that influence the development of brain systems for costly, conspicuous, altruistic displays of moral virtue.” Of course, the single’s ad itself is not the costly signal – it is cheap and easy to fake. Rather, the ad identifies some desired moral virtues that would be hard to fake consistently during a lengthy courtship.

Sexually-selected costly signals typically advertise two classes of traits: good genes or good parenting abilities (Iwasa & Pomiankowski, 1999; Kokko et al., 2002). Different moral virtues might advertise one or the other, or both. Good genes indicators advertise general ‘genetic quality’, which probably reflects having a low ‘mutation load’ (Eyre-Walker & Keightley, 1999; Ridley, 2001). By favoring mates with a lower-than-average number of harmful mutations, sexually reproducing organisms can increase the expected survival and reproductive prospects of their offspring – even if their mate contributes nothing as a parent after fertilization (Houle & Kondrashov, 2002). Moral virtues may function as good genes indicators by being difficult to display impressively if one has a high mutation load that impairs the precision of body and brain development. For example, displaying a sophisticated, empathetic social intelligence requires the development of a complex Theory of Mind, which might be easily disrupted by a variety of mutations associated with autism, schizophrenia, mental retardation, social anxiety, and language impairments (Baron-Cohen, 2000). Thus, a conspicuously expert level of empathy may function as a sort of neurogenetic warranty.

By contrast, good parent indicators advertise phenotypic traits that help care for offspring, such as feeding them, grooming them to remove parasites, protecting them from predators, resolving sibling rivalries, and teaching life-skills through play and practice (Hoelzer, 1989; Iwasa & Pomiankowski, 1999). So, a conspicuously empathic personality may also function as a good-parent warranty, guaranteeing the likely patience, kindness, protectiveness, playfulness, and conscientiousness that helps children thrive.

## Sexual Selection without Large Sex Differences

In most of the other 4,600+ mammalian species, sexual selection acts much more strongly on males than on females, since females do almost all of the parental care, so have incentives to be much choosier about their mates than males are (Andersson, 1994). Humans are unusual in having evolved a mating/parenting system of intensive offspring care by both mothers and fathers (Geary, 2000; Kaplan et al., 2000), which favors social monogamy (at least medium-term pair-bonded relationships with expectations of sexual fidelity). This in turn can favor mutual mate choice by both males and females (Kokko & Johnstone, 2002; Miller, 2000a). Of course, males are not very choosy about short-term sexual partners, but become as choosy as females about committing to long-term serious relationships likely to produce children (Kenrick et al., 1991). Thus, human mate choice is mutual, with both males and females choosing carefully when forming the long-term partnerships most likely to result in reproduction.

Sexual selection is not restricted to explaining sex differences; it can also explain sexual similarities in extravagant traits when mutual mate choice is at work (Miller, 2000a). These mutually-selected traits usually show at least some of the following criteria: (1) large differences even between closely-related species (e.g. humans vs. other great apes), (2) full maturation only after puberty, (3) sexual attractiveness to both sexes, during at least some phases of mate choice, (4) cultural embellishment through body ornamentation (for physical traits) or skill-learning (for mental traits). The human morphological traits that evolved through mutual mate choice probably include long head hair, relatively hairless bodies, everted lips, and visible white scleras around the iris of the eye (Barber, 1995). The mutually-selected human mental traits that show very low average sex differences include general intelligence, cognitive abilities for language, art, music, humor, and ideology, and many moral virtues (Miller, 2000a).

Thus, a sexual selection account of moral virtues absolutely does not imply that males evolve all the conspicuous virtues and females play the passive role of virtue-assessment (cf. Darwin, 1871). Rather, it implies that both sexes evolved the complementary adaptations for morality: moral virtues that tend to be displayed selectively in high-payoff social and sexual contexts, and person-perception mechanisms for judging the moral virtues of others.

Although this sexual selection model does not predict uniformly large sex differences across all moral virtues, it does predict some specific sex differences that cannot be explained by other models. Human males face higher variance and skew in reproductive success, so are predicted to allocate more energy, time, and risk to mating effort, including costly, dangerous, public displays of moral virtue. For example, this model naturally explains why males are over-represented among pro-social heroes who risk their lives to save unrelated strangers (Farthing, 2005; Johnson, 1996), and why males remain over-represented in high-risk, under-paid, altruistic professions such as the police, fire, rescue, paramedic, and other emergency services.

Which Moral Virtues can be Explained by Sexual Selection?

The moral virtues most readily explained by sexual selection are those most clearly manifest in sexual courtship, in long-term sexual relationships, and in child-rearing. Courtship generosity is the most obvious class of sexually-selected moral behaviors. It has obvious parallels to ‘courtship feeding’ by animals, in which ‘nuptial gifts’ are given by males to females as good-genes indicators and good-parent investments (Vahed, 1998). Human courtship generosity would include altruism, kindness, and sympathy to the sexual partner, to his or her children from previous relationships (one’s step-children), and to his or her family members (one’s in-laws). Since this sort of courtship generosity is directed at non-relatives and is not expected to be reciprocated, it is hard to explain through kin selection or reciprocal altruism, and it qualifies as evolutionary altruism by traditional definitions.

Courtship generosity may even include much of the paternal effort that is usually assumed to arise through kin selection (where ‘kin’ include ‘offspring’), since most divorced fathers cut off their paternal investment as soon as they are cut off from sexual access to mothers (Anderson, 2000; Anderson et al., 1999; Hofferth & Anderson, 2003). Thus, what looks like unproblematic paternal investment by males for the sake of perpetuating one’s genes in one’s children may turn out to be better described as ongoing courtship generosity by males in order to maintain sexual access to the mothers of those children.

Other sexually-selected moral virtues may include sexual patience, sexual fidelity, and sexual generosity. Sexual patience is the opposite of sexual harassment, sexual stalking, and sexual coercion (rape). If a potential male mate shows a virtuous degree of sexual self-restraint throughout a long courtship period, this is valuable for several reasons. It does not compromise a woman’s power of mate choice, which is the foundation of sexual selection. It reliably signals that the mate is not just looking for an opportunistic short-term affair, but would value a longer-term committed relationship. It also signals that the mate is not a sexually predatory psychopath, and reveals efficient frontal-lobe control over limbic impulses.

Similarly, sexual fidelity is valuable for both practical and signaling reasons. Practically, fidelity minimizes the spread of sexually-transmissible pathogens, the risk of cuckoldry (a male investing in offspring that were sired by another male), and the costs of polygyny (a female losing investment in her own children if a male sires children by another female). Sexual fidelity also carries much the same signaling power as sexual patience: attractive partners who remain faithful despite credible opportunities for extra-pair copulation are revealing that they expect the long-term relationship with you to yield higher net fitness benefits than a series of short-term flings with others. That is, they treasure, value, and love you above all others, and have the self-control to remember that even in the face of temptation. Along these lines, although males are attracted to promiscuous females as potential short-term mates (Oliver & Sedikides, 1992; Schmitt et al., 2001), neither sex respects high levels of promiscuity in potential long-term mates (Marks & Fraley, 2005; Milhausen & Herold, 1999; O’Sullivan, 1995).

Sexual generosity during foreplay and copulation certainly brings proximate benefits in terms of sexual pleasure, but that begs the ultimate, evolutionary question: why does successful mutual orgasm in humans require such a high degree of attentiveness, sympathy, communication, mind-reading, and previous experience with a particular partner? Other great apes, such as chimpanzees and bonobos, of both sexes, appear to reach orgasm without such an investment of time, energy, touch, and mindfulness (Anestis, 2004; Hohmann & Fruth, 2000). Only humans seem to have transformed copulation itself into a moral test of each partner’s Theory of Mind (and Theory of Body). If orgasms came easily and often to us, they would be useless for discriminating altruistic partners from selfish partners, or good-genes partners from bad-genes partners (Miller, 2000a; Thornhill et al., 1995). Just as human females are choosier early in courtship (in deciding whether to have sex) and human males become choosier later in courtship (in deciding whether to stick around after a bit of sex), female sexual excitement is hard to achieve early in courtship, and male sexual excitement is hard to achieve after the first few years of marriage (Clement, 2002). In each case, humans have apparently evolved an orgasm-resistant brain precisely to test the partner’s degree of sexual altruism – i.e. their ongoing level of commitment, patience, sympathy, and creativity.

A third class of sexually-selected moral virtues may include ideological extremism among young adults, who are near the peak of mating effort. Adolescents and young adults often adopt social, political, and religious views that are more extreme than any they held before puberty, and that become much less extreme in mid-life after they settle down into stable monogamy and child-rearing (Miller, 1996; Tilley, 2002; Visser & Krosnick, 1998). As young adults age, extreme and idiosyncratic attitudes tend to soften, increasing participation in mainstream elections, organized religions, and nonprofit charities. Conspicuous displays of ideological fervor (e.g. organizing political protests, leading revolutions) may function as reliable personality-indicators. Under some oppressive regimes, they may also function as very high-risk heroic altruism indicators, especially among young males at the peak of mating effort. This may explain the moral fervor of the young Akhenaten, Buddha, St. Paul, Muhammed, Martin Luther, Thomas Jefferson, Karl Marx, Vladimir Lenin, Mao Tse-tung, Malcolm X, and Nelson Mandela -- who all launched major ideological movements around age 30.

Precursors of many human moral virtues, such as empathy, fairness, and peace-making, have been found in other great apes (de Waal, 1997, 2000; Preston & de Waal, 2002). My claim is not that sexual selection created our moral virtues from scratch in our species alone, without any primate foundation. Rather, my claim is that sexual selection amplified our standard social primate virtues into uniquely elaborated human forms.

Are the Moral Virtues Really Sexually Attractive?

The two largest cross-cultural studies of mate preferences have been coordinated by David Buss (1989) and David Schmitt (2004). Buss and his collaborators (1989) asked 10,047 people from 37 cultures to rate and rank-order the desirability of several traits in a sexual partner. Among the top ten traits most desired by both men and women across almost all cultures were: kindness, intelligence, exciting personality, adaptability, creativity, chastity, and beauty. Each of these has at least quasi-moral status in many cultures. Schmitt and collaborators (2004a,b) gathered data on 17,804 people from 62 cultures, and found that sexual promiscuity, infidelity, and ‘mate poaching’ were predicted by low agreeableness, low conscientiousness, and high extraversion (Schmitt, 2004a, b). Thus, three of the ‘Big Five’ personality traits (Goldberg, 1990) carry a sexual-morality valence that would be important in mate choice. Also, 49 out of 62 cultures (79%) endorsed a normative ideal of ‘secure’ romantic attachment, as opposed to dismissing, preoccupied, or fearful attachment (Schmitt et al., 2004). That is, most people in 79% of sampled cultures supported a moral ideal that couples should strive for a stable, low-conflict, high-mutual-valuation relationship. Also, many studies show that single’s ads across cultures often advertise and seek moral traits -- especially kindness, generosity, honesty, fidelity, and capacity for commitment (e.g. Koziel & Pawlowski, 2003; Oda, 2001). Thus, morality and mate choice are tightly interwoven across human cultures.

In addition to these large-scale cross-cultural studies, research has confirmed that many particular moral virtues are sexually attractive and relationship-stabilizing; these include:

* Kindness: emotional responsiveness to the needs of others (e.g. Jensen-Campbell et al., 1995; Karney & Bradbury, 1995; Li et al., 2002);
* Empathy: lovingness, affection, fondness, commitment, forgivingness, trust, and perspective-taking (e.g. Miller & Rempel, 2004; Wieselquist, et al., 1999);
* Niceness: emotional stability, conscientiousness, agreeableness, non-irritability, and non-violence (Bouchard et al.,1999; Gottman et al., 1998; Herold & Milhausen, 1999; Shackelford & Buss, 2000; Urbaniak & Kilman, 2003);
* Honesty (e.g. DePaulo & Kashy, 1998; Haselton et al., 2005; Shackelford & Buss, 1996; Williams, 2001);
* Generosity to partner, children, and strangers (e.g. Buss & Schmitt, 1993; Goldberg, 1995);
* Capacity for self-control, self-respect, and self-disclosure (e.g. Byers & Demmons, 1999; Finkel & Campbell, 2001); and
* Heroism (e.g. Farthing, 2005; Johnson, 1996; Kelly & Dunbar, 2001).

Of course, these moral-virtue preferences are typically stronger when seeking a serious long-term partner than a short-term lover (Herold & Milhausen, 1999; Scheib, 2001; Urbaniak & Kilman, 2003).

Apart from the sexual attractiveness of moral virtues, sexual competition seems to explain the evolution of many specific moral vices and anti-social behaviors. For example, most male violence, homicide, and warfare seems to reflect direct sexual competition for mates, for mating-relevant resources, and for mate-attracting social status (Daly & Wilson, 1988; Ellis, 2001; Summers, 2005). This probably explains the dramatic sex differences in aggressive risk-taking across many domains (Byrnes et al., 1999), and the high rates of violence perpetrated by young males at peak mating effort across cultures (Daly & Wilson, 2001; Wrangham & Peterson, 1996). In males, testosterone seems important in organizing and activating these intra-sexual competition adaptations, including aggressiveness, sensation-seeking, risk-seeking, and sexual motivation (Aluja & Garcia, 2005; Harris et al., 1996). Thus, testosterone could be construed as an ‘anti-virtue hormone’ in some sense. Over the longer term, many forms of intimate cruelty, such as derogating, abusing, and beating sexual partners, can be seen as ‘mate retention tactics’ (Buss & Shackelford, 1997). Thus, sexual selection seems to explain not only the attractive, pro-social virtues (mostly through inter-sexual mate choice), but also the anti-social vices (mostly through intra-sexual competition).

An apparent inconsistency arises: does human female choice really favor niceness or dominance, lovers or fighters, dads or cads? It seems to depend on the relationship context, the male’s sexual strategy, and the male’s other traits. Males who are low on ‘sociosexuality’ (interest in multiple short-term matings) tend to project a ‘nice guy’ image that is attractive for committed long-term relationships (Simpson et al., 1999). Male dominance is especially attractive when combined with a pro-social demeanor (Jensen-Campbell et al., 1995). Women seeking a long-term mate were more attracted to niceness, whereas women seeking a short-term mate are more attracted to physical appearance (Urbaniak & Kilman, 2003). By contrast, women at peak fertility, mid-cycle, when they would gain the greatest benefits from short-term good-genes mate choice, tend to prefer dominance to niceness (Gangestad et al., 2004). As in other species, adaptive female choice requires an extraordinary sensitivity to the costs vs. benefits of male dominance and aggressiveness – which can increase male intra-sexual competitive ability and short-term sexiness, but which also predict a male’s likelihood of using sexual coercion (Cristopher et al., 1993).

## Are the Moral Virtues Really Heritable?

If the moral virtues are favored as good genes indicators, and if they are heritable, then sexual selection should favor them and increase their frequency in the population. Yet, if the virtues are driven to fixation (100% genetic prevalence) in the population, then there would no longer be any heritable variation in virtues, so the incentives for good genes mate choice would evaporate. Thus, we might expect good genes mate choice to cannibalize the heritability of the traits that it favors. Is this a big problem for my model?

Actually, this is a special case of what biologists call the ‘lek paradox’: the puzzling fact that sexual ornaments remain conspicuously variable and heritable even when females choose males in large courtship-display congregations called ‘leks’, in which good genes sexual selection is very strong. Biologists used to worry a lot more about the lek paradox, but they think there are some pretty good solutions now. For example, sexual ornaments may remain heritable because they are enormously complex and depend on many, many genes; sexual selection is constantly removing harmful mutations that have arisen in some of these genes, but new mutations are constantly arising in other genes (Rowe & Houle, 1996; Tomkins et al., 2004). This mutation-selection balance maintains a large number of harmful mutations at equilibrium, on average. Yet it also tends to maintain a large variance in mutation load across individuals, and this is what keeps sexual ornaments heritable – why not all peacocks have equally spectacular tails, and why not all humans are equally virtuous.

This mutation-selection resolution of the lek paradox may sound fine in theory, but is there any evidence that the moral virtues are heritable in our species? There is much more behavior genetics work on the vices than on the virtues. Over 50 studies report substantial heritability for various forms of anti-social behavior and its personality correlates, such as psychopathy, sensation-seeking, and disagreeableness (e.g. Agrawal et al., 2004; Eley et al., 2003; Jang et al., 1998; Krueger et al., 2001; Rhee & Waldman, 2002; Taylor et al., 2003) .

The heritability of pro-social virtues has been less well-studied. Moderate heritability for altruism, empathy, nurturance, and/or responsibility has been found in a few twin studies (e.g. Beatty et al., 2002; Davis et al., 1994; Zahnwaxler et al., 1992). For example, Rushton (2004) recently found moderate heritability for altruism, empathy, nurturance, and responsibility in 322 twin pairs. Several other morally relevant traits are known to be heritable, including social attitudes (e.g. conservatism, authoritarianism) and religiosity (e.g. D’Onofrio et al., 1999; Koenig et al., 2005; McCourt et al., 1999; Olson et al., 2001).

The general message from behavior genetics is that virtually every reliably measurable human behavioral trait shows a heritability of about .50, plus or minus .20 (Bouchard & McGue, 2003; Plomin et al., 2001). We should not be surprised that the moral virtues fit this pattern, so there are continuing evolutionary incentives for good genes mate choice based on moral virtues displayed in courtship.

## Moral and Quasi-Moral Traits in Individual Differences Psychology

The best-studied individual differences dimensions in psychology – intelligence, personality traits, and psychopathologies – all have moral or quasi-moral status when they are assessed in social and sexual interaction. That is, the most important individual differences dimensions are morally valenced, and their morally praise-worthy extremes increase sexual attractiveness.

### Cognitive Traits

Intelligence (in the sense of general cognitive ability, the *g* factor, or IQ) is a morally valenced concept, which is why it has been so controversial throughout a century of psychometrics. In every domain of life, smart is good, and stupid is bad. This is not just because intelligence predicts objective performance and learning ability across all important life-domains that show reliable individual differences (Jensen, 1998; Deary, 2000). It is also because having higher intelligence predicts many behaviors that we consider morally virtuous, such as being emotionally sensitive to the needs of others (Schulte et al., 2004), being an effective group leader (Judge et al., 2004), working conscientiously (Gottfredson, 1997; Kuncel et al., 2004; Lynn & Vanhanen, 2001), staying healthy through exercize and diet (Gottfredson, 2004; Gottfredson & Deary, 2004), and staying happily married (Gottfredson, 1997; Jensen, 1998). Conversely, having lower intelligence predicts many behaviors that most people consider morally objectionable, such as murder, rape, assault, alcoholism, drug addiction, absenteeism, child abuse and neglect, passing along sexually-transmissible infections, and causing fatal traffic accidents (Gordon, 1997; Gottfredson, 1997; Lubinski & Humphreys, 1997). This may be one reason why intelligence is so attractive when both men and women consider potential long-term partners (Kenrick et al., 1990; Li et al., 2002; Miller, 2000c).

One might object that intelligence is not really a ‘moral virtue’; it just happens to predict a wide range of specific moral behaviors. Yet, what is a ‘moral virtue’, if not an individual-differences dimension, a psychological construct, an attributed trait, that predicts a wide range of specific moral behaviors? Moral virtues are socially attributed traits that carry predictive information about morally relevant behaviors. If kindness is a moral virtue because it predicts specific pro-social behaviors, and is valued as such, then intelligence must also be a moral virtue – besides being an academic, economic, and epistemological virtue.

### Personality Traits

Each of the ‘Big Five’ personality dimensions (Goldberg, 1990) seems to have a moral valence that is positively correlated with its sexual attractiveness. These traits can be remembered with the acronym ‘OCEAN’: openness to experience, conscientiousness, extraversion, agreeableness, and neuroticism.

Openness to experience implies intelligence, curiosity, tolerance, and broad-mindedness. It predicts emotional sensitivity (Schutte et al., 1998), social tolerance (Dollinger, Leong, & Ulicni, 1996), political liberalism (McCrae, 1996), and support for universalist values – the sort that would be supported by Kant’s categorical imperative (Roccas et al., 2002). People low in openness to experience tend show unvirtuous traits such as being more prejudiced, racist, sexist, and anthropocentric, and higher on ‘right-wing authoritarianism’ and ‘social dominance orientation’ (Ekehammar et al., 2004; Heaven & Bucci, 2001; Van Hiel et al., 2004).

Conscientiousness implies fulfilling promises, respecting commitments, and resisting bad habits. It subsumes individual differences in industriousness, self-control, responsibility, and several other virtues (Roberts et al., 2005). It predicts emotional maturity (McCrae et al., 1999), romantic loveability in relationships (Engel et al., 2002), team cooperation ability (Barrick et al., 1998), and not killing people by driving safely (Arthur & Graziano, 1996). It also predicts pro-social civic and organizational engagement (Organ & Ryan, 1995; Penner et al., 2005), and honesty, integrity, dependability, trustworthiness, and reliability at work (Sackett & Wanek, 1996). Further, conscientiousness positively predicts virtually every health-related behavior that increases longevity, including eating a healthy diet, exercizing, and avoiding tobacco, excessive alcohol, addictive drugs, risky sexual behavior, risky driving, and suicide (Bogg & Roberts, 2004). Conscientiousness is also closely related to the capacity for self-control, which is a key virtue. Prefrontal brain damage, as in the famous case of Phineas Gage, tends to reduce conscientiousness and disinhibits impulsive anti-social behavior, so it reduces both moral virtue and long-term sexual attractiveness.

Extraversion implies gregariousness, social intelligence, self-esteem, and leadership – some Nietzschean pagan virtues. It predicts pro-social volunteerism (Carlo et al., 2005), and happiness and optimism (Furnham & Cheng, 1999; Lucas et al., 2000). However, extraversion is closely related to social attention-seeking (Ashton et al., 2002), so depending on whether virtue or vice attract more attention, extraversion may be associated with pro-social or anti-social behavior.

Agreeableness implies kindness, sympathy, and non-aggressiveness; it predicts benevolence and respect for moral traditions (Roccas et al., 2002), the quality and peacefulness of social relationships (Asendorpf & Wilpers, 1998), and success in jobs requiring teamwork and social interaction (Mount et al., 1998). It is probably the most morally valenced of all the Big Five traits, with conscientiousness a close second.

Emotional stability (the opposite of neuroticism and anxiety) implies dependability, maturity, confidence, self-control, and equanimity. Its strongly predicts happiness (DeNeve & Cooper, 1998), which is sexually attractive. It also predicts marital satisfaction in many studies (e.g. Caughlin et al., 2000). Emotional stability is also related to the ‘secure attachment’ style that predicts stability, intimacy, and fidelity in sexual relationships (Allen & Baucom, 2004; Bogaert & Sadava, 2002), and that is valued across cultures (Schmitt et al., 2004).

All of the morally positive, socially desirable ends of the ‘Big Five’ dimensions tend to be valued in mate choice and marital satisfaction (Berry & Miller, 2001; Botwin et al., 1997; Bouchard et al., 1999; Donnellan et al., 2004). Mate choice for the Big Five traits may reflect both good genes and good parent effects. All of the Big Five are moderately heritable (Plomin et al., 2001). Yet good parenting ability is also positively predicted by openness, conscientiousness, extraversion, agreeableness, and emotional stability (Kochanska et al., 2004; Metsapelto & Pulkkinen, 2003; Spinath & O’Connor, 2003).

Psychologists typically avoid morally evaluative labels for personality traits, to avoid mixing descriptive science with normative ethics. However, one can remain perfectly descriptive by stepping back and considering person perception as a morally evaluative function of social cognition: our social-attribution systems tend to attribute moral valences to most personality traits when we observe them in other people. Indeed, this is one reason for the runaway success of the Implicit Association Test in recent social cognition research: it reveals the deeply evaluative nature of implicit person perception (Greenwald et al., 2002).

Moral philosophers have lately rediscovered the old social psychology critiques of personality psychology, as in the ‘person vs. situation’ debate (Mischel, 1968), and work on the ‘fundamental attribution error’ (Ross, 1977). Social psychology’s concern was that apparently stable personality traits may not really exist, but may be projections of a biased social-attribution system. Citing this literature, Gilbert Harman (1999, 2000) argued that virtue ethics cannot succeed because social psychology shows there are no stable personality traits that could correspond to virtues. Unfortunately, virtue ethicists have usually responded to Harman’s critique with rather weak theoretical arguments (e.g. Merritt, 2000; C. Miller, 2003), rather than by citing the now well-established reliability, validity, stability, and heritability of personality traits (Funder, 2004; Matthews et al., 2003), across cultures and even across species (Gosling, 2001; King et al., 2005). Also, there have been some incisive critiques of situationist research in social psychology (e.g. Andrews, 2001; Sabini et al., 2001) that may undermine some of Harman’s grounds for concern.

### Psychopathology Traits

All major psychopathologies tends to increase perceived selfishness, and to decrease perceived moral virtue, sexual attractiveness, and social status (McGuire et al., 1994; Wakefield, 1999). This seems especially true for the most common and severe psychopathologies, such as psychopathy, major depression, and schizophrenia (Nesse, 2000; Shaner et al., 2004; Wilson et al., 1996). Many personality disorders, such as paranoid, narcissistic, and borderline disorders, also predict anti-social behavior (Coid, 2003). Signs of mental illness typically lead to social and sexual rejection by others – i.e., to stigmatization through negative social attributions (Corrigan, 2000; Crisp et al., 2000). Serious mental illness almost always reduces reproductive success by reducing sexual attractiveness (Avila et al., 2001; Haukka et al., 2003). The only exception seems to prove the rule: the manic phase of bipolar disorder (‘manic-depression’) often leads to increased magnaminity, heroism, gift-giving, and moral crusading, and also leads to new love affairs, infidelities, promiscuity, and babies (Jamison, 1993; Wilson, 1998).

### Religiosity

In most hierarchical, large-scale societies throughout history, religion has provided a cultural framework for the display and evaluation of moral virtues. Yet in all societies, there are conspicuous individual differences in public religiosity (e.g. frequencies of church-going, tithe-giving, public prayer) and in private faith. Psychology of religion research has shown that, although cultural and family environments determine specific religious affiliations, beliefs, and rituals, religiosity as an individual-differences trait shows moderate heritability that increases through adolescence to adulthood (D’Onofrio et al., 1999; Koenig et al., 2005). Religiosity also shows mild positive correlations with agreeableness, conscientiousness, and extraversion (Saroglou, 2002). It positively predicts moral conservatism, traditionalism, benevolence, and conformity, and negatively predicts hedonism, status-striving, and universalism (Saroglou et al., 2004). There is strong assortative mating not only for specific religious affiliation, but also for religiosity (Feng & Baker, 1994; Kalmijn, 1998).

### Other Psychological Traits

There are many other traits that show both sexual attractiveness and a quasi-moral status, at least in a substantial proportion of societies. These include the capacities for:

* Creativity (Haselton & Miller, in press; Kanazawa, 2000; Miller, 1997, 1999),
* Artistic virtuosity (Boas, 1955; Kohn & Mithen, 1999; Miller, 2001),
* Achieving social status through merit (Ellis, 2001; Pérusse, 1993), and
* Acquiring wealth through merit (Conniff, 2002; Frank, 1999; Veblen, 1899).

Even if some critics insist on a narrower list of “true” moral virtues, these core virtues may still be explained by this sexual selection model. Kindness, for example, would surely be on any reasonable list of the core virtues, and it appears to fit the standard pattern of sexually-selected traits given mutual mate choice: reliability as a stable personality trait, validity as a good genes and good parent indicator, heritability, sexual attractiveness in long-term relationships, and conspicuous display in courtship. Thus, for purposes of assessing this sexual selection mode, it may not matter much exactly where we draw the line between moral and non-moral virtues.

### Are These Traits Really Judged as Moral Virtues or Vices?

In what sense do these cognitive, personality, and psychopathology traits have a ‘quasi-moral status’? There are at least four reasons to think they do – three from social psychology, and one from theology. First, most people show a ‘just world belief’ (Lerner, 1980) that creativity, beauty, status, and wealth are merited by those who enjoy them, as both causes and consequences of moral virtue. Second, there is a powerful ‘halo effect’ around such traits, so they are judged as boosting the likely moral virtues of judged individuals (Nisbett & Wilson, 1977). For example, defendants in criminal cases who are more physically attractive, high in occupational status, and wealthy are more likely to be acquitted or given lighter sentences by juries of their (often lower-status) peers (McKelvie & Coley, 1993). Some halo effects may reflect accurate inferences about genuinely correlated traits (‘true halo’), rather than perceiver bias (‘halo error’) (Solomonson & Lance, 1997). Third, research using the Implicit Association Test shows that many dimensions judged in person perception are highly evaluative, and load on a common good/bad dimension that confounds moral goodness, likeability, pleasantness, status, racial similarity, and physical attractiveness (Fazio & Olson, 2003; Greenwald et al., 2002).

Finally, the theological reason: religious people often attribute these quasi-moral traits in hypertrophied form to deities as a reason for valuing their goodness, as when they feel gratitude to a God credited with creating the world in all its beauty, out of a magnanimous generosity to mortals (Boyer, 2001: Roes & Raymond, 2003). Believers typically credit benevolent deities with supernatural levels of the quasi-moral personality traits (intelligence, conscientiousness, agreeableness, and emotional stability), as well as the standard sexually-selected fitness indicators (size, strength, status, beauty, longevity). In monotheistic religions, these traits are bundled together; in polytheistic religions (e.g. ancient Egyptian, Greek, Roman, Norse, and Aztec pantheons; Hinduism, Confucianism), different super-normal traits are attributed to different deities. Contemporary comic books and fantasy films show the standard polytheistic pattern, with different super-normal quasi-moral traits attributed to different super-heroes (e.g. the Marvel comics X-Men pantheon of Professor X, Wolverine, Cyclops, and Storm; the Tolkien pantheon of Gandalf, Aragorn, Legolas, and Frodo).

Ever since Socrates, philosophy has tried to develop precise distinctions between theoretical constructs that are often empirically correlated. Most philosophers think in terms of necessary and sufficient conditions, not in terms of factor analysis. Thus, moral philosophers may balk at such flagrantly irrational conflations of moral goodness, social reputation, economic power, and sexual attractiveness. Indeed, they may be tempted to quote a cautionary verse from Ogden Nash: “It’s always tempting to impute / Unlikely virtues to the cute.” But moral philosophers did not drive the genetic evolution of human virtues; ordinary folks did. If we are seeking a descriptive explanation for human morality, we should attend to the person-perception judgments that may have causally driven moral evolution in our species. Ultimately, it is an empirical psychological question whether ordinary folks judge these traits to have a moral or quasi-moral status, especially in making social and sexual judgments about others.

### Virtue Ethics, Virtue Epistemology, and Virtue Aesthetics

One reason for accepting the quasi-moral status of individual differences traits such as intelligence and physical attractiveness is the recent convergence between virtue ethics, virtue epistemology, and virtue aesthetics. Philosophers are once again considering the relationships between goodness, truth, and beauty.

For example, there is clear overlap between virtue ethics and virtue epistemology, which is the study of cognitive and intellectual virtues (DePaul & Zagzebski, 2003). Traditional epistemology focuses on evaluating the truth of particular concepts and conceptual systems through consistency and coherence criteria. By contrast, virtue epistemology tries to understand the normative properties of beliefs in terms of the normative properties of cognitive agents. For example, Aristotle named intuition, wisdom, prudence, and science as intellectual virtues. For the virtue epistemologist then, true beliefs arise out of acts of intellectual virtue – acts typical of intelligent, rational, cognitively complex agents (Zagzebski, 1996) who show impartiality, epistemic responsibility, and intellectual courage (Code, 1987; Montmarquet, 1993). In virtue epistemology as in virtue ethics, the favored level of description is the whole individual as a cognitive/moral agent, not the isolated belief or moral act. This naturally leads to an emphasis on individual differences in epistemological virtue – differences that intelligence researchers have already succeeded in measuring with unparalleled reliability and validity for over a century.

Virtue epistemology and virtue ethics also strive for a unified theory of value across moral and cognitive domains (Brady & Pritchard, 2003). For Montmarquet (1993) the key intellectual virtue of ‘epistemic conscientiousness’ resembles a moral personality trait more than a cognitive ability, and it seems closely related to the ‘Big Five’ traits of openness and conscientiousness. Kvanvig (1992) views intellectual virtues as cognitive ideals valued by people in social groups, thus relating virtue epistemology to person perception research. Zagzebski (1996) has gone furthest in viewing the intellectual virtues as a sub-set of the moral virtues. Thus, if truth, knowledge, and accuracy are epistemological virtues, perhaps they are moral virtues as well. As with moral virtues, there is a strong distinction in virtue epistemology between getting things right accidentally versus intentionally: praiseworthy beliefs are those that are due to an individual’s own abilities, efforts, actions, and skills, rather than dumb luck or blind chance (Greco, 2000; Lehrer, 2000). In summary, virtue epistemology would see mate choice for intelligence as mate choice for a cardinal moral virtue.

Likewise, there is an evolutionarily deep relationship between moral goodness and aesthetic beauty, as reflected in the overlap between virtue ethics and the recent revival of Darwinian aesthetics (Grammer et al., 2003; Miller, 2001; Thornhill, 1998). This has intellectual roots in late 19th century evolutionary biology, when mate choice for sexual ornaments was seen as the central evolutionary process that creates organic beauty (Darwin, 1871; Grosse, 1897; Spencer, 1887). Darwinian aesthetics is a virtue aesthics insofar as it views beauty prototypically as an agent-level property of living organisms, as they are perceived by other members of the same species.

Beauty is thus an emergent property of co-evolution between a signalling system (the beauty cues displayed by some individuals) and a receiver system (the aesthetic judgment system in other individuals). It is partly in the objective genetic quality and phenotypic condition of the beautiful individual, and partly in the perceptual adaptations of the beholder (Senior, 2003; Symons, 1995). Darwinian aesthetics has successfully analyzed human facial and bodily attractiveness in costly signaling terms as a set of good genes and good phenotype indicators (e.g. Fink & Penton-Voak, 2002; Grammer et al., 2003; Langlois et al., 2000).

Darwinian aesthetics extends well beyond an animal’s physical attractiveness. Art, music, and performances produced by animals (e.g. bowerbird nests, nightingale songs, hominid hand-axes, Cindy Sherman’s self-portraits) can all be viewed as part of the organism’s ‘extended phenotype’ (Borgia, 1995; Dawkins, 1982; Kohn & Mithen, 1999). Such aesthetic behavioral products may be assessed by somewhat different perceptual adaptations than physical attractiveness, but they obey the same basic principles of costly signaling theory, such as conspicuous cost and conspicuous precision (Boas, 1955; Miller, 2001).

The question remains: is there any substantive overlap between virtue ethics and virtue aesthetics, such that beauty in the Darwinian-aesthetic sense could be construed as a genuine moral virtue? There are a few examples of beauty serving as a reliable cue of altruism. First, some sexually-selected beauty advertises ability and willingness to invest resources in mates and offspring – i.e. to perform acts of unselfish altruism in the interests of one’s family (Iwasa & Pomiankowski, 1999; Kokko, 1998). This good-parent sexual selection process favors the bright red plumage of male cardinals (Linville et al., 1998), the dark chest-badges of male house sparrows (Voltura et al., 2002), and the aesthetically conspicuous resource-displays of humans (Conniff, 2002; Miller, 2001). Second, some recent research confirms 19th century criminologist Cesare Lombroso’s view that convicted felons (i.e. individuals low in virtue) tend to be less physically attractive than average. For example, adult felons, violent juvenile delinquents, and anti-social children show increased ‘minor physical anomalies’, cranio-facial abnormalities, and neurodevelopmental abnormalities, and decreased body symmetry, ‘developmental stability’, and overall attractiveness (e.g. Arsenault et al., 2000; Harris et al., 2001; Lalumiere et al., 2001). Finally, some recent philosophical work considers the intersection of aesthetics and ethics (Eaton, 1992; Levinson, 1998). For example, McGinn’s (1997) ‘aesthetic theory of virtue’ argues that virtue coincides with ‘beauty of the soul’, and vice with ugliness of the soul.

The good, the true, and the beautiful are closely related -- not because they share some conceptual overlap of necessary and sufficient conditions, but because, in the real world, each tends to be disrupted by the same kinds of genetic mutations, developmental errors, and neuropsychological abnormalities. The result is that human moral virtues, cognitive abilities, and sexually attractive traits tend to positively correlate with each other across individuals.

How Sexual Selection May Have Interacted with

Other Selection Pressures to Shape Human Moral Virtues

Many forms of social selection probably shaped human morality, including:

* kin selection (Hamilton, 1964; Daly, Salmon, & Wilson, 1997),
* reciprocal altruism (Trivers, 1971; Sugiyama, Tooby, & Cosmides, 2002),
* commitment mechanisms (Frank, 1988; Nesse, 2001),
* risk-sharing mechanisms (Boone, 1998; Sugiyama & Sugiyama, 2003),
* social norm and punishment mechanisms (Fehr & Fischbacher, 2004; Henrich & Boyd, 2001),
* group selection (Boehm, 1996; Wilson et al., 2004), and
* equilibrium selection among alternative evolutionary strategies (Alvard & Nolin, 2002; Boyd & Richerson, 1990).

In each case, sexual selection would tend to anticipate, sharpen, and amplify the social selection pressure to produce a more extreme, more costly, more pro-social version of the moral virtue than social selection could achieve alone. The reason is that non-sexual forms of social selection can shape morality only insofar as they confer fairly concrete survival benefits (e.g. shared food, protection from predators) on the morally virtuous. Mate choice can shape morality much more powerfully and broadly, because it demands only that moral behaviors carry some signaling value about a potential mate’s good genes and/or good parenting abilities. In general, sexual selection can ‘super-charge’ other evolutionary processes by adding just the sort of positive-feedback dynamics that tend to trigger evolutionary innovation and speciation (Crespi, 2004; Miller & Todd, 1995).

An especially interesting, powerful, and neglected interaction may be that between sexual selection and group-level equilibrium selection (not to be confused with standard group selection – see Miller, 2000a). Many evolutionary games have multiple ‘Nash equilibria’: states where each player is maximizing their individual payoffs given the strategies already played by others. For example, male cetacean mating strategies have at least two equilibria: peacefully attracting females through long, loud songs (as in the humpback whales), or aggressively herding and raping females (as in the bottlenose dolphins – Connor et al., 1992). Some equilibria are better for everybody (they bring net positive payoffs to everyone; they are ‘Pareto-dominant’); some equilibria are worse for everybody (‘Pareto-inferior’), but cannot be escaped easily because individuals who deviate from the equilibrium do even worse. A virtuous bottlenose dolphin could not opt out of his species’ coercion-based mating system, without negating his reproductive success.

Normally, natural selection alone is not very good at escaping from such Pareto-inferior equilibria to reach Pareto-dominant equilibria (Boyd & Richerson, 1990). Sexual selection may help, by conferring reproductive benefits on individuals who deviate from selfish, anti-social equilibria (Miller, 2000a). This sexual payoff for virtue is functionally similar to the social-reputation payoffs for virtue modelled by other researchers (e.g. Barclay, 2004; Milinski et al., 2002). However, standard social-reputation models create a second-order ‘free rider’ problem (Gintis, 2000): who will altruistically take the trouble to punish the wicked and reward the virtuous? As research from behavioral game theory (e.g. on the Ultimatum Game) shows, most humans are emotionally compelled to impose this sort of ‘altruistic punishment’ of others who act selfishly (Fehr & Gächter, 2002); the question is why? Most explanations make somewhat vague appeals to cultural evolution or social norms (e.g. Boyd et al., 2003), without identifying any plausible individual fitness payoffs for punishing the wicked. By contrast, this sexual payoff model solves it by identifying selfish mate-choice incentives (e.g. good dad and good gene payoffs) for ‘rewarding’ the virtuous with sexual relationships.

Most contemporary theories of moral evolution accept the importance of multi-level selection across the genetic, individual, and group levels – either implicitly or explicitly (Wilson et al., 2004). Generally, group-level selection for prosocial behvior is what ‘breaks the symmetry’ between alternative equilibria in evolutionary games, to allow the evolution of genuine empathy and altruism (Lahti & Weinstein, 2005). This model of sexual selection interacting with group-level equilibrium selection is a potent way that pro-social virtues can establish a genetic beach-head in an otherwise selfish population, long before group-level equilibrium selection can favor morally unified groups.

## Predictions of the Sexual Selection Model for Moral Virtues

This sexual selection model makes a large number of testable predictions. These often take an unusual form, since costly signalling adaptations have very different phenotypic and genetic features compared to other types of adaptations. In particular, many of these predictions concern individual differences in virtues – not a common research topic in evolutionary psychology or moral philosophy, which tend to focus on species-typical moral judgments and behaviors. For more detail on the rationale behind these predictions, see Miller (2000a,b,c; 2001).

To test most of these predictions, it would be necessary to develop reliable, valid measurement scales that can identify stable individual differences in particular kinds of moral virtues. Such scales should ideally show the psychometric properties desired of any intelligence test or personality assessment: internal consistency reliability, parallel-forms reliability, test-retest reliability, inter-rater reliability, face validity, construct validity, predictive validity, concurrent validity, convergent validity, discriminant validity, and ecological validity (Anastasi & Urbina, 1997). To discriminate between rival theories concerning the evolutionary origins and adaptive functions of specific human virtues, we need to assess the adaptive design features of each putative virtue in reliably quantitative ways. This will require much more psychometrically sophisticated approaches to virtue ethics – not just asking people to give answers to a few multiple-choice ‘trolley problems’ from moral philosophy.

Generally, sexually-selected virtues as quantified in this way should show most of the following 20 features:

*Genetic Features*:

1. positive heritability: if virtues are good genes indicators, they should prove genetically heritable in twin and adoption studies, or using other behavior-genetic methods. If virtues are costly and evolved under sexual selection, the genes underlying virtues should become more expressed only after sexual maturity, perhaps in response to sex hormones. This should lead to higher virtue heritability in adults than in children, as has been found with intelligence (Plomin et al., 2001).
2. negative correlations with mutation load (number of harmful genetic mutations): heritable variation in virtues should reflect variation in overall mutation load, as intelligence may do (Prokosch et al., 2005). For example, since mutation load in sperm increases dramatically as men age (Crow, 2000), younger fathers should, all else being equal, sire more virtuous children.
3. genetic inbreeding effects: if virtues are good-genes indicators, the offspring of sibling or cousin marriages should show reduced virtue levels, due to the increased expression of harmful homozygous mutations.
4. molecular genetic features: specific virtue-reducing alleles should be mostly of fairly recent evolutionary origin that have not yet been eliminated by sexual selection in particular breeding populations; thus, despite the heritability of virtue, it will be extremely difficult to find specific “virtue genes” that replicate across human groups (see Shaner et al., 2004).
5. positive genetic correlations between trait and preference: if mate choice was shaping virtues over recent evolutionary history, we should expect to see a positive genetic correlation between virtues themselves and choosiness about virtues. Such genetic correlations can be assessed with standard multivariate genetic modeling, based on the cross-trait, cross-twin correlations in identical versus fraternal twin pairs.

*Phenotypic Features*:

1. stable phenotypic variance: virtues should vary significantly between individuals in the species, and the differences should be fairly consistent across situations (cf. Harman, 1999). Without variance there is no way for mate choice to use the trait as an indicator; without stability, there is no way to generalize the trait from one situation to another.
2. condition-dependent costs: virtues should incur a significant cost to produce, in energy, time, risk, or nutritional resources. Individuals with higher genetic fitness or better phenotypic conditions should be better able to bear these costs.
3. positive correlation with other objective fitness indicators: variation in virtues should correlate positively with other well-established fitness indicators, such as physical health, mental health, longevity, fertility, body size, body symmetry, and intelligence (e.g. Gangestad & Thornhill, 1999; Prokosch et al., 2005)
4. comorbidity among vices, and between vices and brain abnormalities: if different virtue-deficits (vices) reflect harmful pleiotropic mutations with partly overlapping effects, then vices should show positive genetic correlations (genetic comorbidity) with each other, especially as vices become more serious and extreme. Also, if vices reflect harmful mutations that impair normal neurodevelopment, then they should be associated with various standard brain abnormalities widely observed for other fitness-reducing behavioral traits such as mental illness and mental retardation: smaller cortical volume, larger ventricles, abnormal cortical lateralization, atypical localization of processing as observed in fMRI studies, etc.
5. higher trait variance in males: in species that evolved with some degree of polygyny and some frequency of extra-pair copulation, the higher male variance and skew in reproductive success should favor a risk-seeking pattern of trait expression, such that male virtue levels show higher variance than female trait values (see Archer & Mehdikhani, 2003). That is, there should be more super-virtuous males but also more virtue-deficient males.
6. strategic investment in trait based on self-assessed talent: in species such as humans that have several different kinds of behavioral courtship displays, there are different sexual/status niches (Ellis, 2001; Weisfeld, 1999). Juveniles should assess their relative virtues and invest time and effort in sharpening virtue-display skills preferentially in their highest-virtue areas.

*Social and Sexual Features*:

1. perceivability: variation in virtues should be perceivable, directly or indirectly, consciously or unconsciously, by the opposite sex, in a way that could potentially influence mate choice;
2. positive correlations with other subjectively desired traits, such as physical attractiveness, social status, charisma, etc.; these correlations should be genuine, not just steretyped ‘halo effects’ (cf. Nisbett & Wilson, 1977)
3. positively valued in mate choice: all else being equal, virtues should be favored in mate choice. Virtues as good genes indicators may be favored more often by males, in short-term relationships, and by women at peak fertility near ovulation. Virtues as good parent indicators may be favored more often by females, in long-term relationships, and by women at lower fertility in the cycle. During peak mating effort, virtues may be favored more in the opposite sex than in one’s own sex, and more in potential mates of appropriate age than in younger or older individuals.
4. conspicuous courtship display: during courtship, individuals should conspicuously (if unconsciously) display virtues to the opposite sex. This could be measured across different time-scales, comparing courtship to non-courtship situations across ovulation cycle stages, relationship stages, and social contexts.
5. young-adult peak in trait expression: for sexually selected behavioral traits, conspicuous virtue-displays should peak in young adulthood, at the peak of mating effort. They should be low before puberty, should increase rapidly thereafter, and should decline gradually as individuals shift their time and energy from courtship to parenting.
6. alternative mating strategies: individuals lacking the sexually-attractive virtues should more often pursue alternative mating strategies that try to circumvent mate choice by the opposite sex, including increased use of sexual harassment and sexual coercion (Gangestad & Simpson, 2000; Thornhill & Palmer, 2000).
7. positive assortative mating: in species with social monogamy such as ours, individuals should assortatively mate with respect to virtues, because the competitive mating market should ensure that high-virtue individuals prefer each other, leaving lower-virtue individuals no choice but to settle for each other (see Todd & Miller, 1999).
8. derogation of trait quality in sexual competitors: if virtues are valued in courtship, same-sex rivals should selectively derogate each other with respect to virtue deficits (see Buss & Dedden, 1990).
9. gossip about trait values: in social species such as ours with collective mate-choice that takes into account the views of family and friends, gossip about potential mates should focus some attention on virtues as fitness indicators, with high virtue recognized and praised.

### Example: Sexual Fidelity as a Moral Virtue

For example, suppose a researcher hypothesizes that sexual fidelity evolved by sexual selection through mutual mate choice (rather than through kin selection, reciprocal altruism, or group selection). A first step might be to investigate fidelity’s socio-sexual features. Do surveys, interviews, and experiments show that people prefer sexually faithful mates, all else being equal? Yes: jealousy research shows that men and women across cultures react very negatively to sexual infidelity, yet are highly motivated to discover it (Buss, 2000; Shackelford & Buss, 1997). Do people verbally derogate their sexual rivals for being unfaithful, using technical moral-philosophy terms such as: bimbo, floozy, skank, slut, tart, tramp, trollop, whore (for females), or bastard, bum, cad, cheat, creep, dog, knave, lecher, rat, rogue, scoundrel, sleazeball, slimebucket, snake (for males). Do people gossip about other people’s sexual infidelities, especially to friends and family? (Indeed, if there is an infidelity to gossip about, do we ever gossip about anything else?) Do people conspicuously display their likely future fidelity in courtship, e.g. by making impassioned, adaptively self-deceptive declarations of infinite, eternal, exclusive love?

If the answers are generally yes, then the researcher might progress to phenotypic studies of sexual fidelity as an individual-differences dimension. Are there stable individual differences in the likelihood of fidelity versus infidelity, or is infidelity driven entirely by chance and opportunity? Research on the opposite of fidelity, the personality construct of ‘sociosexuality’ (interest in promiscuous, short-term, or extra-pair mating), confirms there are stable individual differences in this trait dimension (Gangestad & Simpson, 2000). Is fidelity positively correlated with other desirable moral virtues and fitness-related traits, such as kindness, conscientiousness, agreeableness, mental health, longevity, and intelligence? (This question becomes complicated, since individual of higher mate value will be sought more often for short-term, extra-pair copulations, so will be tempted by more opportunities for infidelity – Gangestad & Simpson, 2000. Mate value and infidelity opportunities would have to be carefully statistically controlled in studies of fidelity’s correlations with other moral virtues.)

The genetic studies of infidelity would be the hardest to perform, but often the most informative. Would twin and adoption studies show that the propensity to infidelity vs. relationship stability is heritable? (actually, they do already: Bailey et al., 2000; Cherkas et al., 2004). Would genetic inbreeding (e.g. offspring of first-cousin matings) reduce fidelity, suggesting a role for partially recessive harmful mutations in driving infidelity? Would one find positive genetic correlations between the tendency to fidelity, and the mate preference for fidelity, as might be expected if there has been sexual selection for the trait?

Clearly, the sexual selection hypothesis for moral virtues is eminently testable. However, it requires new ways of thinking about costly-signalling adaptations (Miller, 2000b,c). These cannot be assessed using the standard adaptationist criteria for naturally-selected traits (e.g. low cost, high efficiency, high modularity, low phenotypic variance, low heritability, and reliable development across all individuals) that are more familiar to evolutionary theorists (e.g. Andrews et al., 2003; Tooby & Cosmides, 1992). For naturalistic moral philosophy to benefit maximally from contemporary scientific insights, it must not only increase its appreciation of sexual selection’s power, but also expand its understanding of how to analyze costly-signalling adaptations.

## Implications for Normative Ethics

Normative ethics is supposed to help us distinguish right from wrong and good from evil. It tries to achieve a ‘reflective equilibrium’ between (1) possible universal moral principles, (2) derived moral implications that would apply in particular situations, and (3) human moral intuitions that react to those principles, implications, and situations (Rawls, 1971; Daniels, 1996). The hope is that normative ethicists can articulate a set of universal, coherent, consistent moral principles that yield intuitively acceptable moral implications across all possible situations, and that thereby embody a rational distillation of human moral sensibility. Almost all moral philosophers accept that this is the legitimate goal of normative ethics, though debates still rage between consequentialists and deontologists, between act ethicists and virtue ethicists, etc. However, if moral virtues rose through sexual selection, this reflective-equilibrium approach to normative ethics is likely to fail for at least three reasons.

First, suppose human moral intuitions evolved as part of our person-perception system for inferring stable, morally valenced, mating-relevant personality traits from observable behaviors. If so, we are trying to do ethical alchemy: trying to refine unconscious, domain-specific, species-specific, person-perception adaptations (the base metal) into verbally articulated, domain-general, universal moral principles (the gold). This is likely to be an uphill battle. One reason it is difficult to make our moral intuitions consistent and coherent is that moral intuitions usually precede reasoned moral judgments (Haidt, 2001), and are often driven by morally judgmental emotions that figure prominently in sexual relationships, such as anger (Ellis & Malamuth, 2000), disgust (Rozin et al., 1999), jealousy (Buss, 2000), embarrassment (Keltner & Buswell,1997), shame (Tangney, 1999), and gratitude (McCullough et al., 2001).

Second, if our person-perception system relies on social-inference heuristics that are fast, frugal, and pragmatic, then our moral judgments will often violate procedural norms of rationality derived from logic, statistics, and rational choice theory, such as consistency, transitivity, and completeness (Gigerenzer & Todd, 1999). There are deep decision-theoretic reasons why it may be impossible to derive a set of consistent, coherent moral preferences from the operation of such social-inference heuristics. To know whether this is a fatal objection to the reflective equilibrium approach to normative ethics, we need to learn a lot more about moral judgment heuristics in the context of person perception research (e.g. Funder, 2004; Haselton & Funder, in press).

Third, human moral intuitions evolved to assess people’s stable moral virtues in ancestrally typical, fitness-relevant situations, and to guide ancestrally feasible forms of social response such as forming friendships or mateships, gossiping about liars, punishing cheaters, or ostracizing psychopaths. There is no reason to expect our moral intuitions to show consistent, logically defensible reactions to evolutionarily novel moral dilemmas that involve isolated, hypothetical, behavioral acts by unknown strangers who cannot be rewarded or punished through any normal social primate channels.

For example, we often seem cognitively paralyzed by many current debates in reproductive bioethics (Petrinovich, 1995). How should we feel about abortion, sperm donation, egg donation, surrogate pregnancy, human cloning, genetic testing, or genetic enhancement? Different framings of these issues will activate different, domain-specific moral intuitions (Haidt, 2001). This is precisely why rhetorical metaphors are effective in such moral debates. For example, ‘genetic enhancement’ may seem pernicious fascism if we view it as a limited resource that will be appropriated by the powerful for their nefarious ends, or it may seem democratically liberating if we view it as a natural extension of good genes mate choice, for those whose own sub-optimal mate value precludes getting good genes from a willing partner (Miller, 2000a). Is there any neutral, rational position from which we can judge such issues, without assimilating them to one or another of our domain-specific moral intuitions? Probably not: rational decision-making depends upon subjective utility functions that must be supplied either by the genetic imitation of ancestral utilities (‘gut instinct’), or the social imitation of peer utilities (‘learning’, ‘social norms’). Gut moral instincts will be mute or misleading guides to moral dilemmas raised by new technology, and moral conformity to peer opinion will be biased by vested political, corporate, and media interests that define the current ‘ethical issues’ in their own interests.

These three evolutionary psychology problems resemble some philosophical problems with the reflective equilibrium method (Brandt, 1990). Basically, there is no compelling logical reason to think that our moral intuitions have any true normative credibility as guides to genuinely moral behavior, and a coherently systematized set of these subjective moral fictions will remain fictional. Of course, there may be evolutionary reasons to expect that species-typical human moral intuitions would tend to maximize inclusive fitness under ancestral conditions. However, that is quite different from claiming that they are normatively justifiable in any broader sense. For example, Peter Singer (1990, 1994) has made some compelling but counter-intuitive arguments concerning animals rights, euthanasia, and infanticide; in such cases, it seems impossible to reach a reflective equilibrium between our gut moral instincts and our scientifically informed normative judgments.

In the light of these moral-psychological problems, consider two different forms of a typical normative-ethics question. Abstract form: Is it morally right to assassinate a genocidal war criminal? (Perhaps – many have praised the attempted assassination of Adolf Hitler by Colonel Claus von Stauffenberg on July 20, 1944). Personal form: Suppose there is a 21st century head of state who ordered his country into a fraudulent and illegal war that resulted in thousands of needless civilian casualties, but who is almost certain to avoid accountability to the International Criminal Court in The Hague. Would it be moral to feel sexually attracted to a man who succeeded in killing the wicked head of state, with a single head-shot from a Barrett M82A1 .50-caliber semi-automatic sniper rifle at 800 meters on a windy day? The personal form is much more specific about the identities of the moral judgment-maker, the morally-judged individual, the civilian victims, the nature of the assassination, and the fitness-relevant, socio-sexual implications of the moral judgment. These details should and do matter in making adaptive mate-choice judgments about the moral virtues of snipers. A woman who knows her ordnance might admire the sniper’s good genes indicators, such as his resourcefulness (the M82A1 costs $7,775 retail), his physical condition (the rifle is five feet long and weighs 34 pounds), and his marksmanship (the 800-meter head shot was near the rifle’s maximum effective anti-personnel range of 1000 meters). Yet she may equally worry about his good dad indicators: his vigilante action may reveal psychopathy, paranoid schizophrenia, bipolar disorder, impulsiveness, fame-seeking narcissism, or high-risk sensation-seeking (Fein & Vossekuil, 1999; Meloy et al., 2004). She can only tell be gathering further information about his virtues, both moral and non-moral – which is the function of prolonged human courtship.

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