Article

Evolutionary Ethics and Mate Selection

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Abstract: Moral philosophers argue that mechanisms such as reciprocal altruism and indirect reciprocity can result in the evolution of shared interests and a 'moral sense' in humans. This article discusses the need to broaden that view when considering the consequences of genetic conflict, in particular, the conflict associated with mate selection. An alternative application of evolutionary arguments to morality has been suggested by biologists such as Richard Alexander, who argue that ethical, moral and legal questions arise purely out of reproductive conflicts of interest, and that moral systems (consisting of societal rules or laws) exist to ameliorate those conflicts. Following Alexander, a novel societal rule is proposed that could lessen the negative consequences to men of reproductive conflicts with women.

Keywords: consequentialism; evolutionary ethics; indirect reciprocity; reciprocal altruism; sexual conflict; utilitarianism

Introduction

> In general, we can sum things up by saying that if we are humane, kindly, benevolent people, we want as many people as possible now and in the future to be as happy as possible (Smart 1973:33).

> Happiness, then, is an end for the individual only in the sense that it is achieved by acts leading to reproduction (Alexander 1978:265).

> For it is then inevitable that the happiness of one individual will, at some time, be directly in conflict with that of another (Kelsen 1957:2).

Many philosophers are impressed by the apparent ability of natural selection to imbue humans with evaluative and motivational mechanisms that are broadly in line with widely held beliefs about how "humane, kindly, benevolent people" *ought* to behave. For instance, Street (2008:207) writes "There is a striking coincidence between the normative judgments we human beings think are true, and the normative judgments that evolutionary forces pushed us in the direction of making." A common starting point for such speculation is the recognition by biologists that organisms have evolved to maximize the likelihood of survival of their genes (or groups of genes), copies of which may be present in other individuals (Williams 1966, 1985; Lewontin 1970; Dawkins 1976). Attitudes which appear altruistic at the behavioral level — for instance, an inclination to nurture offspring or other kin — can be selfish from a gene-centric point of view, and hence selected for, since relatives may carry the same genes that promote the nurturing behavior ('kin selection': Hamilton 1964; Maynard Smith 1964). A motivation to cooperate even with non-kin can be evolutionarily favored if the reproductive benefits to each party exceed the costs ('reciprocal altruism': Trivers 1971, 1985; Axelrod and Hamilton 1981; 'indirect reciprocity': Alexander 1974, 1979; West-Eberhard 1983). The resulting selection pressures can lead to individuals who are primed to participate, if only locally and imperfectly, in something approximating the 'greatest good to the greatest number' utilitarianism favored by many moral philosophers (e.g. Singer 2011).

But in treating individual organisms as mere vehicles for genetic replication (Dawkins 1977), evolution can be remarkably indifferent to human suffering. One example is aging, or senescence: the gradual deterioration of bodily function that occurs late in life. An individual who did not senesce would have a substantial reproductive advantage over one who does, yet natural selection seems unwilling to extend lifetimes beyond a certain limit; "individuals in most species are very short-lived compared to the longest-lived in a few species" (Alexander 1985a:786). A likely explanation is that senescence is a maladaptive consequence of other traits that *are* selected for (Medawar 1955; Williams 1957; Hamilton 1966). Genes are 'pleiotropic': every gene has more than one effect, and those effects may differ over an organism's lifetime. Genes that have beneficial effects during youth may be selected for even if they have deleterious effects later on, since some individuals will not live to suffer the negative consequences; they die prematurely due to accidents, disease, starvation etc. The result is selection for genes whose negative effects are mostly felt late in life (roughly speaking, after the onset of reproduction), and it is the accumulation of such genes over evolutionary time that is believed to be an underlying cause of senescence. In support of the hypothesis, large-sample statistical studies reveal a negative correlation between reproduction and life span (Long and Zhang 2023), and a number of human disorders have been identified for which there are strong reasons to invoke antagonistic pleiotropy as the explanation for the high frequency and persistence of the disorder (Carter and Nguyen 2011).

The genes making up a genome have a common interest in the viability of their host organism. Antagonistically pleiotropic genes are exceptions to this rule insofar as their reproductive interests conflict with the long-term viability of the organism in which they reside (Leigh 1977). Finite lifetimes are in part a consequence of this conflict.

Of course, the evolutionary mechanism just described owes nothing to human agency; people, like other senescing organisms, are simply the unfortunate victims. But there are closely related phenomena, reflecting reproductive conflicts of interest that play out at a higher (behavioral) level, which *are* driven by conscious decisions that individual humans

make and which therefore are appropriate targets of interest to moral philosophers. One example, now to be discussed, is the mechanism responsible for the shorter average lifetimes of men as compared with women.

Average female longevity exceeds that of men in almost all countries worldwide (Hutt 1972; Mealy 2000; Austad 2006), and there is evidence that this pattern has persisted at least since accurate birth records first became available in the 1700s (e.g. Tabutin 1978). The sex differential in life expectancy averages about 6-7 years in developed countries (Nathanson 1990). Male mortality[1] is greater than female mortality at all ages and this is true for virtually all primary causes of death, both internal (e.g. genetic disorders; Kraemer 2000) and external (e.g. violent death; Wilson and Daly 1985). The differences in longevity persist among 'cloistered' populations, such as monks and nuns, where both sexes share the same social, work, and eating habits (Luy 2003).

The more rapid progression of senescence in men, like senescence itself, is understood as a conflict between selective forces (Trivers 1972; Williams 1975; Hazzard 1990; Kruger and Nesse 2006). No matter how fit a man might be, his genes will find themselves in the next generation only if a woman permits him to mate with her (neglecting subversion of female choice). Both men and women can be choosy, of course, but one expects (and it has been amply confirmed) that women, like females in many species, are the more discriminating sex: "it is the female who is ultimate arbiter of *when* she mates and how often and with whom" (Hrdy 1981:18). The underlying reason for the evolved difference in choosiness is the greater obligatory cost of reproduction to females, and the correspondingly fewer opportunities that females have over their lifetimes to reproduce (Bateman 1948; Trivers 1972). A man can greatly increase his reproductive success by being indiscriminately promiscuous, even if only a fraction of his offspring survives, whereas a woman who follows the same course is unlikely to have more offspring than one who is more selective. An evolutionarily more favored strategy for her (that is, for her genes) is to partner with the man who would contribute most to the success of her children (or her non-descendant relatives): for instance, via his access to resources. The result is a selection pressure (an aspect of sexual selection; Darwin 1859, 1871), called sexually antagonistic selection (G. A. Parker 1979, 2006; Brooks 2000; Arnqvist and Rowe 2005), which acts to increase the prevalence in males of traits that promote risk-taking and competitive ability at the expense of somatic repair and disease prevention (Daly and Wilson 1983; Folstad and Karter 1992; Promislow 2003; Lessells 2006; Clutton-Brock and Isvaran 2007; Connallon, Cox and Calsbeek 2010).

The focus here will be on the attitudes that motivate women to select partners with attributes that are unfavorable to them and on the consequences that result from such choices. The cognitive algorithms in women that generate feelings of attraction to men (like those in men that generate feelings of attraction to women) were designed by evolution, of course, but no more so than the mental architectures that underlie any other human attitudes or emotions (B. J. Ellis 1992; Cosmides and Tooby 2000). When acting on such feelings, women are making decisions that are every bit as self-determined as any other decisions

[1] Mortality rate is defined as the number of deaths in a particular population, in proportion to the size of that population, per unit of time. Unlike longevity, mortality rate is a function of age.

they might make, even if the underlying cause of their feelings of attraction is the history of reproductive success of their ancestors. Women, after all, could now decide differently: they could decide to favor men whom they do *not* feel attracted to. When evaluating mate choice from the point of view of a utilitarian or consequentialist moral philosopher, one is obliged to consider not just the happiness of the women making the choices, and the well-being of their children, but also the negative consequences of those choices for men: consequences both somatic and psychological, near-term and long-term, individual and societal.

Judgments about the ethics of mate selection, like ethical judgments about any actions that humans might take, can certainly be made without enquiring into the evolutionary origins of the evaluative attitudes or decisional algorithms that motivate those actions. But there are a number of reasons why it is worthwhile bringing selectionist arguments into the discussion. (1) Treatments in the philosophical literature of 'evolutionary ethics' (e.g. Okasha 2020; Fitzpatrick 2021) typically focus exclusively on the role of natural selection in imbuing humans with a 'moral sense' — with prosocial attitudes such as altruism or a desire for cooperation. E. g. C. Wilson (2018:295): "Evolutionary ethics … treats morality as a set of dispositions and behaviors that represent transformations of the "prosocial" or "proto-moral" dispositions and behaviors of extinct human ancestors." But when there is a genetic conflict of interest between the erstwhile cooperators, as there is in the case of mate selection, evolution cannot be expected to operate in this felicitous manner, and it is important to understand the implications of that fact for theories of evolutionary ethics. (2) Insofar as the mental architectures that underlie a certain mode of behavior are a product of evolution, one expects those behaviors to be species-typical, hence widespread, hence of greater interest to a moral philosopher than they otherwise might be. (3) In analyzing any particular action from the point of view of a utilitarian or consequentialist moral philosopher, it can be important to know (or at least to speculate) about the outcomes that would result from *alternatives* to that action.[2] The following passage by Geoffrey Miller (2000:307-308) is to the point:

> If, for example, all females refused to mate with any males who ate meat, any genes predisposing individuals to vegetarianism (however indirectly) would spread like wildfire. The species would turn vegetarian no matter what survival benefits were conferred by meat-eating, as long as the sexual selection pressure against meat-eating held … Aristophanes' play Lysistrata of 411 B.C. illustrated the moral power of female sexual choice. Lysistrata convinced the other women of Athens to stop having sex with their men until the men stopped waging the Peloponnesian war. … Lysistrata's sex-strike succeeded in forcing the Athenian men to make peace with the Spartans. Her strategy would have worked equally well over evolutionary time: female sexual preferences for peace-keepers could have reduced male belligerence and aggressiveness.

To the extent that traits such as "belligerence and aggressiveness" in the human male are heritable, and have an evolutionary origin in choices made by females, it is reasonable to argue that by making different choices, women now have the ability to produce more

[2] E. g. G. R. Grice (1967:2): "Utilitarianism is the view that the reason for any moral judgement is that the action enjoined produces more good than any alternative."

favorable outcomes for men. (4) If one's goal as a moral philosopher is the creation of a happier or more humane society, understanding the evolutionary origins of bad behavior (in this case, male bad behavior) can only facilitate that goal (e.g. Gorelik and Shackelford 2014).

Patterns of Female Choice

> Mean, disdainful, cruel, offensive, and even criminal are adjectives that go hand in hand with attractive and desirable models of masculinity. Good men are often not *hot*, and the *hot* ones are hardly ever good (Ramis et al. 2013:266).
>
> The gentle, compassionate man who reads magazine surveys indicating that his qualities are the very ones that most women prefer in a mate may be the same man who is repeatedly turned down by women who seek the company of more atavistic males (Ickes 1993:83).

Consider two young men as seen through the eyes of a young woman who is seeking a sexual or romantic partner. The first is a 'nice guy':

> He cares. In terms of girls, he tries to protect those who get rejected by other boys... and he listens carefully trying to find out how to help them. In fact he's kind of simple, a nice guy; he's loyal and devoted to his family and would never lie to get something.

The second is a 'bad boy':

> He doesn't care about what people think; he knows how to get what he wants and uses every last trick to get it. Although initially you don't care, he knows at the end you will fall down in his hands and he persistently chases you till he gets you, even though he ends up being seen as a baddie, a tricky, mysterious, maybe even controlling bloke. He laughs at the girls when they try to hook up with him. Nevertheless, if you're daring and he accepts... you could be the one. Even if he makes you cry, it's worth it.

These two narratives are reproduced from the *Free Teen Desire* project questionnaire (Puigvert 2015-16). The first narrative is one of a set that describe non-sexist, compassionate males; the second is from a set describing aggressive or dominating males. The two types of profile were used by Puigvert and co-authors in their surveys of young women's preferences for young men, under two imagined scenarios: short-term 'hook-ups', or long-term, stable relationships (Puigvert et al. 2019; Ruiz-Eugenio et al. 2020; Alcantud et al. 2021).

A striking result from the *Free Teen* studies was how attractive the bad boys were judged to be. For instance, Puigvert et al. (2019) interviewed 100 secondary-school girls in the age group 13-16, in four different countries in Europe. When asked whether they would like to have a long-term relationship with a boy described by one of the aggressive profiles, the fraction of girls who responded 'yes' ranged from 13% (Spain) to 40% (Cyprus). But the researchers understood that young women might have difficulty separating their actual preferences from what society (or their conscience) tells them is acceptable — what sociologists call social desirability bias (e.g. Bernreuter 1933; Edwards 1957; Meston et al. 1998; Greenwald, McGhee and Schwartz 1998). They argued that "it could be expected that actual preferences of female participants in this type of survey are better reflected when they do not answer for themselves" and so they included two additional questions: asking whether the respondents' *female friends*, or *other girls known to them*, would prefer the aggressive personality types. The fraction of 'yes' answers increased markedly when the question was

framed in these alternative ways. The percentage of respondents who answered that *their friends* would find the 'bad boys' attractive was 25%-52%; and fully 47%-76% of survey participants judged that *other girls* would be attracted to 'bad boys'. And as high as these percentages were, all of them increased still more when the same questions were asked about partners selected for 'hook-ups' rather than for long-term relationships (Puigvert et al. 2019, Figure 2).

The *Free Teen* surveys were not the first to identify a predilection on the part of young women for 'bad boys' over 'nice guys'. For instance, Valls et al. (2008) carried out open-ended interviews with 21 girls between the ages of 14 and 17 in seven secondary schools:

> The most important result obtained from the fieldwork with these adolescents is that there is a link between attractiveness and violence … There is a general agreement among the teenagers interviewed that the "model man" to which they attribute more attractiveness is what they call a "bastard", a "macho," or a "show-off" … when this [bastard] characteristic arises, the physical appearance of a boy is considered secondary. It is more important to be a "bad guy" than to be good-looking (Valls et al. 2008:768-9).

While different studies differ in how they characterize 'nice guys' (sensitive, caring, accommodating, respectful) versus 'bad boys' (assertive, aggressive, controlling, domineering), a common finding is that young women exhibit a preference for, or at least a strong attraction to, the latter and this is particularly true when the question is framed in terms of preference for a short-term, rather than a long-term, companion (e.g. Sadalla, Kenrick and Vershure 1987; Jensen-Campbell, Graziano and West 1995; Herold and Milhausen 1999; Bukowski, Sippola and Newcomb 2000; Valls, Puigvert and Duque 2008; Carter, Campbell and Muncer 2014; Haslam and Montrose 2015; Qureshi, Harris and Atkinson 2016; Farrell and Vaillancourt 2019).

The results from the *Free Teen* studies hint that young women's stated and actual preferences might differ, in the sense that some women who report an attraction to nice guys may actually prefer bad boys. A number of other authors have found evidence for a disconnect between women's self-reports and their actual choices in men (e.g. Miller and Rivenbark 1970; Sprecher 1989; Zohar and Guttman 1989; Feingold 1990; McDaniel 2005; Wiederman and Dubois 1998; Urbaniak and Kilmann 2006). Herold and Milhausen (1999:340) write "Although many women report that nice guy characteristics are the most desired in a partner, women's actual choices do not always coincide with what they report they want in checklist studies of mate preferences".

A second potential problem with questionnaire-based studies is their artificiality: descriptions of male characteristics may not be endorsed because they are framed negatively, even though men's real-world behaviors corresponding to those descriptions are judged positively. For instance, Buss and Barnes (1986) and Burger and Cosby (1999) reported that, when asked, few women rate dominance as a desirable characteristic in a man, but in studies which showed women videos of males portraying dominant behaviors (e.g. Sadalla, Kenrick and Vershure 1987; Stone 1990; Provost, Troje and Quinsey 2008; Fink et al. 2016), or which were based on observations of men and women in real-life social interactions (e.g. Renninger, Wade and Grammer 2004), women consistently exhibited a preference for dominant men. Ahmetoglu and Swami (2012:671) note that, even in highly controlled experimental settings, "slight changes to the posture (i.e., sitting position) of a male significantly increased his level of attractiveness."

One way to circumvent such biases is to look at the real-world experiences of men — their sexual 'success' with women as it correlates with their behavior or personality. A number of studies have found that men exhibiting traits of dominance or aggression have the greatest sexual or dating success (Zuckerman 1979; W. A. Fisher et al. 1988; Gangestad and Simpson 1990; Trapnell and Meston 1996; Reise and Wright 1996; von Rueden, Gurven and

Kaplan 2011; de Bruyn, Cillessen and Weisfeld 2012; Flecha, Puigvert and Ríos 2013; Hill et al. 2013; Volk et al. 2015; Dane et al. 2017; Davis et al. 2022). The result appears to hold true both for young and for older men; for instance, de Bruyn et al. (2012:296) found that "adolescent boys who exhibited a highly aggressive profile were more sexually active than their low-status and non-aggressive male peers", and Bogaert and Fisher (1995) found that men's *lifetime* numbers of sexual partners were positively correlated with traits of dominance and hypermasculinity, while intimacy and closeness were negatively correlated.

An even more striking result, attested in numerous studies (e.g. Glueck and Glueck 1968; West et al. 1977; Palmer and Tilley 1995; Hirschi 2017), is how favorably women respond to men who engage in criminal activity, even violent criminality. Ellis and Walsh (2000:227) summarized the results of 51 studies on the relationship between number of sex partners, on the one hand, and involvement in criminal activity on the other. Fifty out of the 51 studies reported a significant positive correlation. And while the evidence is largely anecdotal, many authors have noted the remarkable, almost preternatural appeal that serial killers seem to have for many women (Fimrite and Taylor 2005; Kottler 2011; R. J. Parker 2015; Vronsky 2018; Isenberg 2021). Ogas and Gaddam (2011:98) write "It turns out that killing people is an effective way to elicit the attention of many women: virtually every serial killer, including Ted Bundy, Charles Manson, and David Berkowitz, have received love letters from large numbers of female fans".

One might wonder whether the greater success of delinquent males at getting females to 'say yes' simply reflects a greater level of effort on the men's part. Rebellon and Manasse (2004:382), in a review of the criminological literature, argue no: "[Our] results suggest that delinquency does not appear to increase dating by increasing the delinquent's desire for dates. Instead, [our results] suggest that delinquency increases dating outcomes by making the delinquent more attractive to prospective mates." And Hirschi (2017:189) notes that

> Boys who date are considerably more likely to have committed delinquent acts than boys who do not. … [This relation is] opposite to that predicted by an involvement hypothesis. Working and dating should remove opportunities to commit delinquent acts; they should, at least to some extent, have the same effect as "work and marriage" at the attainment of adulthood. They do not appear to have such an effect.

Terms such as 'aggressive' or 'dominant' can have a variety of meanings (e.g. Savin-Williams 1987:27-28). A number of researchers have attempted to put studies of female mate preference on a more objective (or at least, more reproducible) basis by characterizing male attributes in terms of standardized personality taxonomies as defined by psychologists. One widely used scale, called the five factor model (FFM) or 'Big Five' (e.g. Goldberg 1981; Digman 1990), defines five dimensions of personality: neuroticism, extraversion, openness to experience, agreeableness, and conscientiousness. Assessment of personalities according to the five-factor model are typically based on standardized, self-report questionnaires, e.g. the Revised NEO Personality Inventory, or NEO-PI-R (Costa and McCrae 1992); less often, assessment is based on reports of observed behaviors. Urbaniak and Kilmann (2006) noticed that the characteristics defining high/low agreeableness on the NEO-PIR questionnaire closely match the stereotypical characteristics of the nice guy/bad boy: individuals high in agreeableness are described as sensitive, sympathetic, gentle, cooperative while individuals low in agreeableness are tough, assertive, aggressive, cold. In a study of 191 male college students, Urbaniak and Kilmann looked at the relationship between the subjects' agreeableness as measured via the NEO-PI-R and their sexual and dating histories. They found that "a male's success in casual dating relationships and one-time sexual encounters was negatively associated with their agreeableness, meaning that those with lower agreeableness had more success". They also noted (in agreement with many of the authors cited above) that their results suggest "a discrepancy between which men women will say they prefer … and which men actually are successful".

In reviewing the literature on evolutionary ethics, one is likely to come away with a rosier picture of the attributes that women find attractive in men. For instance, Geoffrey Miller (2007:104) writes:

> People often fall in love based on positive 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 praiseworthy moral virtues by the world's most influential philosophical and religious traditions …

Miller does not distinguish here between men's and women's preferences. Nonetheless, all of the traits in Miller's list can be described as *virtuous* or *prosocial*; there is no suggestion that the men preferred by women might be (in the words of the Valls et al. study cited above) bastards, machos, or show-offs. Instead Miller (2008:211) writes: "Moral virtues are, among other things, personal traits that we are proud to display during courtship."

In developing his argument for an evolutionary origin of moral virtues, Miller (2000, 2007, 2008) leans heavily on the results of David Buss and collaborators. Starting in 1986, Buss et al. carried out a series of questionnaire-based studies of "mate selection preferences" in the United States and other countries. The results, as summarized in a number of review articles (e.g. Buss 1989; Buss et al. 2001; Easton, Goetz and Buss 2015; Buss and Schmitt 2019), are remarkably robust and consistent: both men and women are said to rank personality characteristics associated with the descriptors "pleasing disposition" and "emotional stability" as the most important (Shackelford, Schmitt and Buss 2005). A number of other authors (see, for instance, the citation list of Macfarlane 2008:112) have reported similar results based on similar methodologies.

At first blush, these results appear to be strikingly at odds with most of the other studies cited above, and it is worthwhile trying to understand why. Buss and co-authors base their methodology on that of Hill (1945) and McGinnis (1958). In the study by Hill (based on data collected in 1939, and published in the *The Journal of Home Economics*), university students were presented with a list of 18 personal characteristics and asked to rate each item as to its indispensability in a marriage partner. McGinnis (1958) repeated the Hill study seventeen years later at the same university using the same, 18-item questionnaire. The Hill/McGinnis questionnaire has been used in numerous subsequent studies of mate preference (as reviewed by Helm, Hall and Bailey 2020). Buss and collaborators have relied on the same questionnaire, sometimes in modified or augmented form, in much of their work, including the early and highly cited study of mate preferences in 37 cultures (Buss 1989, 1990) and the most recent study (Walter et al. 2020) that contains survey results from 45 countries.

The 18 personality traits that make up the Hill (1945) questionnaire are listed by McGinnis (1958) in his Table 1. The traits include "pleasing disposition" and "emotional stability" (the two traits said by Buss et al. to be most desired by both men and women) as well as "dependable character"; "education and intelligence"; "mutual attraction-love", and 13 others. As in the list by Miller cited above, all of these traits can be described as virtuous or prosocial; there are no 'bad boy' traits here. Apparently, Hill and McGinnis regarded human courtship as a dignified affair in which men and women seek only traits that are sanctioned by gentle society. In any case: by presenting the survey participants with nothing but socially desirable attributes, Hill and McGinnis guaranteed that anti-social or aggressive traits would make no appearance. As Jensen-Campbell et al. (1995:439) write, in their critique of the Buss et al. work: "Results of our present program of research suggest … that we need to

move beyond lists and categories of desirable attributes in mates" in order to better understand patterns of mate preference.[3]

Studies based on unstructured interviews, such as the Valls et al. (2008) study cited above, can generate responses that are not limited to those provided by the researcher's pre-prepared questionnaire. And it is noteworthy that many of the studies that document women's attraction to dominant or aggressive men did not have as their primary goal a survey of mate preferences. For instance, the *Free Teens Desire* Project cited above was designed to understand the persistence of (male) violence toward young women as a first step in overcoming it. Similarly, the Volk et al. (2015) and Farrell and Vaillancourt (2019) studies were aimed at understanding young men's bullying behavior; Glueck and Glueck (1968) and West et al. (1977) were concerned with the origins of male criminality, etc. Studies such as these begin from the acknowledged fact that men, particularly young men, can and often do behave badly, and from that starting point go on to investigate (among other things) the possible role of female preferences in enabling and perpetuating the bad behavior. For instance, Rebellon and Manasse (2004:363) argue that "romantic involvement that results from [male] delinquency may promote further delinquency, not only among perpetrators, but also among peer audiences."

There is another point to be made. Probably everyone knows, or knows of, men who are loving companions and fathers, on the one hand, while being brutally competitive in their interactions with other men. A female respondent in a survey of mate preferences who assigns a high rank to "pleasing disposition" means, presumably, that she prefers a partner who exhibits a pleasing disposition *toward her* (or toward her and her children), and not necessarily that she expects her partner to behave in the same way when interacting with other people (e.g. Lukaszewski and Roney 2010). Similarly, women who rate dominance as an *un*desirable trait are probably expressing a preference for men who do not dominate *them*, however they may act toward other men (e.g. Hinde 1978). Support for this interpretation comes, for instance, from examination of romance novels — a genre that has been fine-tuned over the years to be maximally appealing to its (overwhelmingly female) audience.[4] Ogas & Gaddam (2011:99), in their massive survey of the archetypical male protagonist as portrayed in the romance literature, conclude that

> when it comes to women's preferences, they don't just want a nice guy—they want an alpha [male] who learns to be nice to her. In other words, women want their romance heroes to be like coconuts: hard and tough on the outside, but soft and sweet on the inside. But the hero's sweet interior can't be available to just anyone. Only the heroine gets to crack him open. The hero is granted free rein to be a badass with everyone else, as long as he's tender and attentive with the heroine.

And Janice Radway (1984:147) writes that romances

> are exercises in the imaginative transformation of masculinity to conform with female standards. … No action on the part of the hero or, for that matter, on the part of any

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[3] For a fuller critique of the Buss et al. work, see B. J. Ellis (1992:281). Ellis characterizes the discrepancies between the findings of Buss et al. and those of other researchers as the "mate choice paradox".

[4] When the publisher Simon and Schuster made plans in 1980 to initiate a new series of romance novels, "they were not about to take any risks. They decided to design their series around a research study so they could give their readers exactly what they wanted. ... Everything ... was then tailored to their responses" (Kakutani 1980:C13).

> other character can be said to cause or explain the magic transformation of his cruelty and indifference into tender care. The abrupt transformation simply takes place.

The exclusive focus of many mate-preference surveys on favorable personality qualities betrays an even more fundamental bias: the assumption that only *intrinsic* characteristics are relevant: that attraction is independent of extrinsic factors such as a person's wealth or rank. Already in 1985, Trivers had pointed out (p. 331) that American men who marry in a given year earn roughly 50% more than men of the same age who do not marry. Evidence that this difference is driven primarily by female preference — as opposed to, say, women's economic powerlessness (e.g. Caporael 1989) — soon came in a series of studies, by Townsend and collaborators, of students in professional schools, where males and females are presumably comparable (at a given age) in terms of achievements and career prospects. In an initial study of 20 men and 20 women, Townsend (1987) found that as the students progressed through medical school, the pool of available sexual partners increased for the men and decreased for the women. Based on a larger study (170 men, 212 women), Townsend and Levy (1990:160) concluded that

> high status can equalize the acceptability of less physically attractive men and raise their acceptability to a level only inferior to that of the most physically attractive, high status man … a man therefore would have to be very handsome or very ugly for his physical attractiveness to be a decisive determinant of his attractiveness to women.

The conclusion of Townsend et al. that 'status trumps looks' calls to mind the passage quoted above from the Valls et al. (2008) study: "It is more important to be a "bad guy" than to be good-looking". It is natural to wonder whether the young women in the Valls et al. study were reacting favorably to behaviors that are predictive of *future* success (financial or social) in the young men. I revisit this question, after first discussing, in the next two sections, the likely role of sexual selection in establishing women's preferences.

Sexual Selection, Sexual Conflict, and Female Choice

> The expression 'sexual conflict' encapsulates the capacity of individuals of one sex to inflict damage on individuals of the other sex (Lessells 2006:301).

> It is reproductive access to women that drives men's quest for status (A. Campbell 2013:107).

Men and women have a shared genetic interest in the success of their children, and it is natural to suppose (e.g. Miller 2000; Nesse 2007) that 'what's good for the goose is good for the gander', reproductively speaking. But no two parents are identical, and each differs genetically from any offspring as well. The result is genetic conflict: selection will act on genes expressed in father, mother and child in different ways. An important example was first pointed out by Trivers (1972) and Parker (1979). Parents are selected to direct their time and resources so as to maximize the total number of their surviving children, each of which has the same degree of relatedness (on average) to each parent. But any particular offspring is more strongly related to itself than to any of its siblings, and so will desire a greater amount of parental investment than either parent is selected to give. This conflict at the level of the genes expresses itself in behavior, as when a child insists on being breast-fed long after the mother wants to stop, or objects to the level of attention given by a parent to a sibling (Trivers 1974). A similar conflict plays out even before birth (Haig 1993). The embryo produces hormones that enhance its growth at the expense of the mother; the mother's body counters by producing hormones that suppress the effects of the embryo's; and the evolutionary

outcome of this conflict is a reduction in the health of the mother (Stearns 1989; A. J. Wilson et al. 2005).

Parent-child conflict is a special case of a broader class of conflicts that arise between individuals who participate in sexual reproduction. The conflicts of most relevance here are between the mating pair. The cost of reproduction is different for the two adults, and "each parent's fitness [i.e. gene frequency in subsequent generations] is generally maximized if it invests less and the other parent invests more than would maximize the other parent's fitness" (Lessells 1999:75)[5]. The difference in investment is especially pronounced for mammals, and for humans in particular. The minimum, or obligate, cost imposed on the human female by reproduction includes the need to accumulate bodily reserves before and during nine months of pregnancy, placentation, lactation, the mortality risk associated with bearing and birthing a large-headed offspring, and childcare that extends some time beyond birth; while the man's investment can be as little as a brief copulatory event. As pointed out by Bateman (1948) and Trivers (1972), the greater cost to females of reproduction implies that females will be the choosier sex. Males can increase their reproductive success by mating indiscriminately, at little cost to themselves; females cannot; and the outcome is that "sexual selection acts more strongly on males, resulting in more complex or elaborate behaviors and features" (M. L. Fisher 2022:92).

Consider a gene that is expressed in both sexes but which has different fitness consequences for male and female; for instance, a gene producing a large body size. If the gene appears at the same locus in both sexes, then there is potential for 'intralocus sexual conflict': different alleles at that locus will be favored in females and in males. The result is sexually antagonistic selection; the gene's frequency in the next generation will increase as long as the typical benefit to one sex outweighs the detriment to the other. Genes that are sex-linked can spread even when their advantage to one sex is less than their benefit to the other (Rice 1984). The evolutionary outcome is that each sex holds back the adaptation of the other, as selection on one sex counteracts changes in gene frequency made in response to selection on the other sex (Lessells 1999).

Now imagine injecting an additional degree of asymmetry into the problem, by supposing that male and female differ in their typical degree of parental investment, and that some individuals have greater 'mate value' than others. Broadly speaking, sexual selection can then follow one of two pathways. Females may choose partners on the basis of *direct benefits* (Kirkpatrick 1987; Grafen 1990; Price, Schluter and Heckman 1993); that is, they may prefer males who will directly increase their reproductive success or survival, by providing parental care, access to resources, protection from other males etc. In some cases the value of the provided resource can be assessed directly by the female; more typically she must base her assessment on an 'indicator' trait, e.g., a willingness to take risks, or a record of success at hunting. Selection will then favor the female who can accurately identify

[5] It would be natural, and helpful, to include here a rigorous definition of 'sexual conflict' from the perspective of an evolutionary biologist. Unfortunately that is not possible: "the study of sexual conflict is rich in debate over concepts, assumptions, and interpretation, and much of the debate revolves around terminology" (Arnqvist and Rowe 2005:216). Those authors include a table (Table 7.1) illustrating the range of proposed definitions of sexual conflict; examples are "different evolutionary interests of the two sexes" and "sex difference in the covariance between promiscuity and offspring numbers", among eight others. The definition presented here, due to Lessels, is number two in that list.

males who will provide the maximum benefit to her, and evolution produces an equilibrium value for the (female) preference that is a compromise between the material benefit to her and the costs (if any) of the preference. Female preference in turn generates sexual selection favoring the preferred trait in males.

Sexual selection can also enhance traits in the male that provide no obvious benefit to the female. Famous examples of such traits are the peacock's elaborate tail feathers and the dimorphism of elephant seals. This *indirect selection* occurs when there is variation both in a preference on the part of females and in the preferred trait in males, and when genes for preference and trait become linked. Such 'self-reinforcing selection' was first characterized by Ronald Fisher:

> In species so situated that the reproductive success of one sex depends greatly upon winning the favor of the other … sexual selection will itself act by increasing the intensity of the preference to which it is due, with the consequence that both the feature preferred and the intensity of preference will be augmented together with ever-increasing velocity, causing a great and rapid evolution of certain conspicuous characteristics, until the process can be arrested by the direct or indirect effects of Natural Selection. (R. A. Fisher 1930:145)

Genetic linkage of preference and trait can lead to 'runaway' sexual selection in which the male trait becomes extremely exaggerated, until the disadvantages for his survival outweigh the advantage of being attractive to females (e.g. O'Donald 1967; Pomiankowski, Iwasa and Nee 1991).

In modeling the evolution of a particular trait under sexual selection, it is often difficult to separate direct from indirect mechanisms; the two are compatible and may act in combination (Andersson 1994:31). Traits that are elaborated via indirect selection may have 'gotten their start' by providing a small, *direct* benefit to male or female; for instance, in explaining evolution of "plumage character in the [pea]cock", R. A. Fisher (1930:136) postulated "an initial advantage not due to sexual preference, which advantage may be quite inconsiderable in magnitude". And even if the benefit is direct, "some degree of coevolution between courter traits and chooser preferences is all but unavoidable" (Rosenthal 2017:389). As Halliday (1983:13) writes, "we should be extremely cautious about attributing any single character exclusively to one or other form of sexual selection." But the end result of both mechanisms can be the elaboration of traits in the male that are harmful to his health or well-being. In the words of Trivers (1972:166): "if there is a tendency for females to sample the male distribution and to prefer one extreme … then selection will move the male distribution toward the favored extreme."

Importantly, "Through the decision-making processes involved in mate choice, individual behavioural mechanisms generate the evolutionary dynamics of sexual selection … sexual selection is fundamentally a behavioural process" (Bergstrom and Real 2000:493). Sexual selection, whether direct or indirect, is driven by actions that individuals, predominantly females, *choose* to make, even if (as is almost always the case) they are consciously unaware of the underlying reasons for their preferences. In fact there has been a growing appreciation in recent years of the importance of female agency[6] in evolution: of the dominant role that choices made by females play in coevolutionary interactions with males (e.g. Small 1993; Eberhard 1996; Gowaty 1997; Paul 2002; Zuk 2002; Stockley and

[6] Throughout this article I use the term 'agency' in the usual sense of a capacity to act, and not (as psychologists sometimes do) as a synonym for dominance or masculinity.

Bro-Jorgensen 2011; A. Campbell 2013). In the words of Sarah Hrdy (1981:18), "to an extraordinary degree, the predilections of the investing sex — females — potentially determines the direction in which the species will evolve".

One reason for the heightened emphasis on female preference has been the recognition that mating patterns which seem at first glance to be driven by male-male competition or male coercive tactics are often found, on closer inspection, to contain an element of female choice (Goldfoot 1982; Eberhard 1996; Wiley and Poston 1996; Stumpf and Boesch 2006, 2010). A celebrated example (Cox and Le Boeuf 1977) concerns the behavior of male elephant seals, who use their much greater size to force themselves onto females. But it turns out that female elephant seals are quite capable of influencing which males sire their offspring:

> [Elephant seal] Females frequently protest when mounted by males, and are more likely to do so if a male attempting to mount them is of low status. The effect of a female's protests is to attract the attention of another male, who attacks the mounting male and makes it impossible for him to mate successfully. In effect, female elephant seals exercise choice in favor of high-status males. What this example shows is that intense competition among members of one sex does not preclude the expression of mate choice by the other sex (Halliday 1983:11).

This example also shows how female behavior can lead to successful copulation with males having the preferred trait (in this case, status in the male hierarchy) even if there is no active discrimination on the basis of that trait. Wiley and Poston (1996:1378) argue that "It seems likely that competition for mates by one sex always depends on conditions set … by the other sex".

In the case of humans, it is sometimes argued that arranged marriage — in which parents (or other kin) select spouses for their descendants — if sufficiently widespread during our evolutionary history, could effectively have circumvented female choice (e.g. Broude 1993; C. Wilson 2018:301; Geary 2021:182). But ethnographic studies of existing societies that practice arranged marriage reveal (perhaps unsurprisingly) the wide variety of tactics that young women will use to subvert their parents' choice of marriage partner when it does not coincide with their own (Lee 1984; Wiessner 2009; Scelza 2013; Agey et al. 2019). In her ethnographic studies of the the Ju/'hoansi (!Kung) bushmen, Polly Wiessner (2009:256) found that only sixteen percent of women acquiesced peacefully with their parents' selection of spouse, whereas

> Thirty-one percent of women protested strongly, kicking, screaming, running away, or giving their husbands a very hard time … Young women would risk their lives spending the night in the bush to protest marriage.

In a review of 543 ethnographies, Agey et al. (2019) cataloged the types of action taken by young women to avoid an arranged marriage: they included committing or threatening to commit suicide, engaging in violence, and recruiting other people as mediators. And even women who find themselves in an arranged marriage can continue to exert reproductive choice by engaging in extra-marital affairs. Scelza (2011:890) found that among the Himba (Namibia) pastoralists, "Women who had choice in their marital partner were more likely to remain faithful", and that extra-pair paternity, while common, never occurred among children born into 'love match' marriages.

Indeed the fact that women so universally express strong preferences in regard to spouses suggests that such preferences *have been* selected for, even if, or *especially* if, human societies in the past constrained women's choices. Symons (1979:167, 169) argues that "selection can be expected to favor the existence of desires, though they may rarely be translated into behavior":

> In an environment in which young people have relatively little say in spouse choice, selection might favor strong adolescent emotions about members of the opposite sex, emotions that have been designed by selection specifically to function in a milieu in which an adolescent's actual behavior will be constrained by the necessity to compromise with elders

Which male traits, then, would evolution have singled out for enhancement via female choice in *homo sapiens*? A possible starting point (feasible when dealing with humans, if not with other species) is simply to ask women which traits they prefer in men. But as documented in the previous section, that approach, while useful and suggestive, is bedeviled by systematic biases and problems of interpretation. (As A. Campbell (2016:99) remarks: "human research offers an easy way (arguably *too* easy) to target sexually selected traits: self-reported preferences for mate qualities.") Alternatively, one could argue (e.g. Halliday 1983) that female preferences for certain male traits would *necessarily* evolve due to the direct benefits that accrue from choosing mates having those traits. But as Alexander (1987a:337) cautions,

> Anyone who finds it easy to assume that the first Darwinian hypothesis he thinks of is good enough should review the torturous efforts of biologists to use Darwinian theory to understand some comparatively simple attributes of life, such as sex ratios, sexuality, or outbreeding.

Perhaps for these reasons, discussions of the evolutionary influence of women's choices on men's traits often begin by noting certain behavioral similarities between humans and our nearest primate relatives (e.g. Daly and Wilson 1983, chapter 12; Archer 1988, chapter 7; Smuts 1992; Small 1993; A. Campbell 1999, 2013; Geary 2021, chapter 5). One striking similarity is the existence of male dominance, or status, hierarchies. As Robert Wright (1994:241-242) wryly notes,

> status hierarchies run in our family. … If you took a zoologist from another planet, showed him our family tree, and pointed out that the three species nearest our limb were inherently hierarchical, he would probably guess that we are too. If you then told him that hierarchy is indeed found in every human society where people have looked closely for it, and among children too young to talk, he might well consider the case [for an evolutionary origin of human status hierarchies] closed.

Dominance in primates is typically measured in terms of submissive and aggressive behaviors during agonistic interactions (e.g. Walters and Seyfarth 1987): more submissive males defer to more dominant males. So defined, primate dominance hierarchies often constitute a linear structure with one male (at least temporarily) at the 'top' and the other males behaving as if they know and recognize each others' ranks (e.g. Kummer 1982). There is considerable evidence that female primates also recognize and respond to a male's position in the hierarchy. Most importantly from the standpoint of evolutionary explanations, reproductive success has been shown to correlate with status for males in a number of non-human primate groups (Dewsbury 1982; Fedigan 1983; Cowlishaw and Dunbar 1991; L. Ellis 1995; Gerloff et al. 1999; Bradley et al. 2005; Setchell 2016). While such correlations are sometimes attributed to male-male competition or male coercive tactics, close observation often reveals a role for female choice (e.g. Caillaud et al. 2008; Surbeck et al. 2017). For instance, superficial observation of rhesus monkeys suggests that it is the male who initiates and controls copulations; but as Goldfoot (1982:417) writes, a female rhesus monkey may

> coordinate the series of mounts displayed toward her by sitting very near the male with her back toward him and at appropriate intervals making subtle staccato head, arm, or shoulder movements. … All of these postural adjustments seem to induce the male to

> attempt a mount, and when fully receptive, the female will move to the acceptance posture simultaneously with the male's initial movements toward her.

These subtle behavioral changes on the part of the female were overlooked in the early studies of rhesus monkeys. Smuts (1987:392) notes that "female refusals of male attempts to copulate have been observed in nearly all nonhuman primates".

Among wild chimpanzees, females sometimes show a preference for lower-ranked males (e.g. Stumpf & Boesch 2006). But such instances appear to be 'exceptions that prove the rule': "The [chimpanzee] females are either strangely prescient of leadership qualities or they are king makers in their own right because they mate more often than expected with young males who later go on to achieve dominant status" (A. Campbell 2013:109).

Probably few people need convincing of Wright's statement, quoted above, that status hierarchies are "found in every human society". Wright's claim that hierarchies exist "among children too young to talk" may strike some as problematic; but already at age two, boys are observed to establish dominance relations through interactions such as rough-and-tumble play (Smith and Boulton 1990; Tremblay et al. 1999; Hay, Castle and Davies 2000). By three years, male children exhibit a number of forms of dominance aggression, including verbal challenges and actual fights; by age four, boys cross-culturally express great interest in being seen as 'tough' (Omark, Omark and Edelman 1975; Charlesworth and La Freniere 1983). Weisfeld (1994) documents at least 13 ways in which "dominance behaviour in [human] children is homologous to that in other primates"; included, not surprisingly, are a higher degree of competitiveness among males and a greater tendency of males than females to exhibit non-verbal (i.e. physical) dominance.

Anthropologists have documented that in a number of preliterate/preindustrial human societies, high-status men have more wives than low-status men, sometimes far more, and that given the option, women often choose to be in polygynous marriages (e.g. Chagnon, Flinn and Melancon 1979; Flinn 1986; Betzig 1982, 1987; Cronk 1991; Irons 1993). Hence, Symons (1979:155, 157-8) argues, "clues as to how selection operated in the course of human evolutionary history may be found in ethnographic descriptions":

> It is hard to imagine that during the course of human history men failed to notice that positions of leadership were rewarded with women. … For prestige to have evolved as an autonomous human motive — which it undoubtedly has — the effort and risk that achieving high status entails must have been recompensed with reproductive success.

It would follow that male traits conducive to *achieving* positions of leadership, including a willingness to engage in violent behavior, were also likely targets of sexual selection:

> Selection probably favored political abilities, such as judgment, oratory, and persuasion, abilities to conceive and carry out complex plans, and skills in cooperative violence, including the evaluation of violent situations and the taking of calculated risks. It seems likely as well that in a milieu of complex, cooperative violence, selection would favor a male who was able to induce other males to take risks for his benefit.

While certain behaviors are undoubtedly useful in the competition for status, it is also the case that, in human societies at least, status can be 'bestowed': a person's status can increase enormously, practically overnight, if they are appointed to a high office, awarded a

prize, endowed with an inheritance etc.[7] And there is considerable, if anecdotal, evidence that women respond to such changes in male status regardless of how they are achieved. Among numerous other examples, Symons (1979:272-273) cites an interview with the American actor Henry Winkler soon after he had been promoted to the position of lead character ("Fonzie") in the popular television series *Happy Days*. In the interview, Winkler remarked "In the past, I've always done the asking and women have said yes or no. I now know what it is to be a woman" — that is: to be pursued by the opposite sex. Symons notes (p. 272) that "the magnitude of the male-female difference [in responses to status differentials] is not always understood, especially by women". A woman's attractiveness to men appears to be quite unaffected by her wealth or social standing, a fact that women sometimes seem surprised to discover.

As in the studies of non-human primates, one would like to show a robust statistical correlation between status and reproductive success for human males. It is clear that in many contemporary societies, at least, the correlation runs counter to what might be expected: the wealthy and the educated tend to have fewer children than the destitute and the poorly educated (Wrong 1958; Cochrane 1979; Potts and Selman 1979; Mueller and Short 1983; Vining 1986). But modern methods of contraception have effectively broken the link between sex and reproduction: behaviors that in the past would have resulted in many offspring, need not generate the same outcome today, and there has probably not been time enough for evolution to respond to this novel state of affairs by modifying men's or women's innate decisional rules (e.g. Tooby and Cosmides 1990:402; Symons 1992:138-139).[8]

But in a landmark study of contemporary French Canadians, Daniel Pérusse (1993) replaced 'reproductive success' with 'mating success', defining the latter in terms of "potential conceptions": computed from the number of partners a man has had and the number of sex acts that took place with each partner. (Pérusse's approach here was similar in spirit, but different in detail, from that of the studies cited in the previous section that correlated men's sexual or dating success with their personality or behavior.) He found a strong correlation of mating success with social status, which he defined using three traditional indicators: level of education, occupation, and income. Social status was found to account for *most* of the variance in men's mating success; furthermore the correlation was strengthened by excluding married men, who "may not be in a position to translate socioeconomic advantages into mating success as freely as uninvolved men" (p. 275).

Pérusse (p. 281) emphasized the likely importance of female choice in maintaining the observed correlation between social status and potential conceptions:

> the present findings support the existence of diverging reproductive strategies in men and women and clearly point to female choice as the main causal factor in the relationship found here between male social status and male mating success.

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[7] Archaeologists distinguish 'achieved' and 'ascribed' status; the latter includes, for instance, status assigned at birth. See e.g. Renfrew and Bahn (2015:199).

[8] Symons (1992:148, 154) argues further that "the statement that a particular form of behavior is an adaptation to a particular environment does not imply the current existence of beneficial effects on survival and reproduction ... In fact, since the adaptations that underpin human behavior were designed by selection to function in specific environments, there is a principled Darwinian argument for assuming that behavior in evolutionarily novel environments will often be *mal*adaptive." And Ghiselin (1997:292) writes "There is no problem with particular organisms failing to reproduce in spite of their propensity to do so."

Pérusse presented this conclusion only after considering, and rejecting, possible explanations that are *not* dependent on female choice. He began by pointing out that men tend to exploit mating opportunities irrespective of their own social status, hence "the source of the [observed] correlation between male status and mating success is likely to come from females." He noted that in modern human societies (unlike, say, a community of chimpanzees or elephant seals) "female choice is unlikely to be absent from any mating occurrence except rape" due to the general absence of female claustration, arranged marriages, female defense polygyny, or other male coercive tactics. He found implausible the argument that high-status men might simply be dating females with a greater willingness to copulate (for reasons unrelated to the men's status): if such a tendency existed in females, he argued, one would expect low-status men to exploit it.

Pérusse's suggestion for the evolved form of the female preference was as follows: that women are "motivated to confer mating privileges differentially according to male status" with preference given to high-status men. For the corresponding, sexually-selected male trait, he suggested "striving to elevate oneself in the social hierarchy". But Pérusse was careful to acknowledge that his study, by targeting only *attained* status, did not directly test any particular hypothesis about the form of the adaptation(s) that would motivate men to *achieve* status; rather, in his study, "the hypothesized tendency for self-elevation in the social hierarchy was *operationalized* as achieved position in that hierarchy." As emphasized by Margo Wilson (1993:311) in her commentary on the Pérusse work,

> Achieved status, however, is an abstract construct used to describe the relative position of an individual with respect to things such as income, prestige, and power within a delimited population of individuals. How can such an abstract construct, describing the compromise outcome of various parties' behaviors, have been the target of selection?

Since the focus of the present article is on the consequences for men of women's choices, I consider in the next section one male behavioral trait that is implicated in the competition for status and which is widely acknowledged to have a basis in sexual selection.

Female Choice and Male Aggression

> Competition for mates is the defining aspect of all forms of sexual selection, including that based on mate choice (Andersson 1994:12).

> Male–male competition and female choice are, in some respects, different sides of the same coin (Geary 2021:216).

There exists something approaching a consensus among evolutionary biologists that human male aggression — or rather, that the species-typical *differences* between men's and women's aggressive behaviors (differences in magnitude, expression, development etc.) — are a consequence of antagonistic sexual selection. Male aggression is seen as part of a sexually-selected complex of traits which contribute positively to men's reproductive success — that is to say, to their inclusive fitness — by directly or indirectly increasing their appeal to women, while at the same time impacting negatively on men's health, longevity and (one expects) their lifetime happiness (e.g. Daly and Wilson 1988, 1994; Archer 1988, 2009, 2013; Rowe 2002, chapter 3; A. Campbell 2006; Geary 2006, 2021; Kanazawa 2009; Stanyon and Bignoni 2014; Puts 2016; Gorelik 2021).

It must be stated at the outset that explanations for human male aggression that invoke sexual selection, while widely accepted, are difficult to prove: "Speculation about sexual selection of various human traits are [sic] common but often difficult to test rigorously"

(Andersson 1994:19). And, of course, there are dissenters from the consensus view, most prominently those who would interpret male aggression (like essentially all human behavior) as reflecting arbitrary, socially imposed 'roles' (e.g. Goldstein 1986; Wood and Eagly 2002; Hyde 2005; Butler 2006).

Discussions of sexual selection often adopt as a starting point the definition provided by Charles Darwin: "the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction" (Darwin 1871:256). In the *absence* of sexual selection as just defined, one might expect males in a given population to leave similar numbers of offspring. Variance in male reproductive success[9] is therefore often taken as *prima facie* evidence that sexual selection is, or has been, active; e.g. Puts (2016:29): "Sexual selection tends to be strongest where reproductive variance is greatest, and where reproductive differences depend most strongly on mating success." In practice, the variance in male reproductive success is usually operationalized as the relative variance in male and female reproductive success ('effective polygyny'; e.g. Daly and Wilson 1983:152; Low 1988). A number of studies of contemporary, but pre-industrial, societies find a male-to-female variance ratio in the range of ~2 to ~5 (Chagnon 1979; Hewlett 1988; Brown, Laland and Borgerhoff Mulder 2009). Using the latest techniques, one can do better, and make inferences about the *cumulative* effects of differential reproduction over humans' evolutionary history. Based on DNA samples from three (Khoisan, Mongolian, Papua New Guinean) contemporary populations, Wilder, Mobasher and Hammer (2004) concluded that roughly twice as many women as men contributed to the current human population. Men, evidently, are (or have been) far more likely than women to perish without producing any offspring.

What would be the link, then, between men's greater reproductive variance, on the one hand, and an evolved capacity for aggression on the other? The argument here is an indirect, but reasonably compelling, one. E.g. Browne (1995):

> The greater reproductive variance of males means that the stakes of the mating game are higher for males than females. Therefore, evolutionary theory predicts that males, in order to enhance their reproductive success, should exhibit greater risk-taking behavior (particularly in resource and mate acquisition), greater aggressiveness, and greater promiscuity.

Or Frederick, Reynolds, and Fisher (2013:309):

[9] We may seem to be covering similar ground here as in the previous section, but there is a subtle distinction. Studies such as that of Pérusse target the correlation between (some measure of) status and (some measure of) reproductive success (RS). If such a correlation exists and is 'steep', some men will have much greater RS than others, and the distribution of RS over the entire sample will be broad: there will be a large variance (that is, dispersion) about the mean value for all the men considered together. This dispersion about the mean is what is referred to in this section as the 'reproductive variance' and it is the quantity that is relevant to establishing effective polygyny. Confusion may sometimes arise when authors (quite properly) use 'variance' to describe the dispersion about the mean value of the RS for some sub-sample; for instance, at some fixed value of status (as does Pérusse (1993) in his discussion of his Figure 7). See Low (1988:191) for a fuller discussion.

> The choosiness of females forces males to engage in intense intrasexual competition. Males compete with each other to develop traits that are attractive to females or that enable them to successfully bully other males.

And Daly and Wilson (1988:145):

> Fitness variance is a measure of the intensity of competition, and the more intense that competition — that is to say, the more disparate the outcomes — then the more likely it becomes that selection will favor a psychology prone to *risky* competitive tactics, including escalated fighting even to the point of death.

In other words (or so the argument goes): female choosiness, as reflected in men's more variable reproductive success, causes selection for men who have the particular qualities that cause them to be chosen as mates, and among those qualities will be a disposition to use risky and/or aggressive tactics to compete with other men for limited mating opportunities.

Based on this argument, *support* for the sexual selection theory of men's aggression is typically presented, not in terms of women's preference for aggressive men *per se*, but rather by arguing that observed patterns of male aggression are consistent with those of an adaptation that evolved to facilitate intrasexual (male-male) competition.

Here then are some of the data and arguments that have been adduced in support of the hypothesis.

— Both men and women can (and do) behave aggressively, but since the causal arrow of sexual selection points predominantly from female to male, one expects men to be more aggressive (on average) than women. That this is so, apparently in all cultures and (as near as can be determined) throughout all of recorded history, is well documented (e.g. Eagly and Steffen 1986; Sutherland, Cressey and Luckenbill 1992; Bettencourt and Miller 1996; Byrnes, Miller and Schafer 1999; Knight et al. 2002; Archer 2004, 2009; Ellis et al. 2008). The male-female difference exists for all types of aggression, from verbal to violent, but the more dangerous and risky the behavior, the larger the sex difference (Cairns and Cairns 1994; A. Campbell 2006; Archer 2013).

— The vast majority of homicides are murders of men by other men: "There is no known human society in which the level of lethal violence among women even begins to approach that among men" (Daly and Wilson 1988:146). A man is about twenty times more likely to be killed by another man than a woman is to be killed by another woman.[10] Homicides committed by women are much more likely than those committed by men to be killing of children; when the victim is an adult male, the woman's motivation is often defensive (Daly and Wilson 1988). These differences are as expected if the ultimate purpose of men's aggressive behavior is to facilitate intrasexual competition.

— Male homicides often result from escalation of seemingly trivial altercations (Wolfgang 1958; Wilson and Daly 1985). The fact that men are much more willing than women to risk physical damage or death in such encounters is consistent with an evolutionary cost-benefit analysis (Daly and Wilson 1988:164 – 65). For men, "successful reproduction may only be possible if they challenge other men and risk injury in escalated encounters" (Archer 2009:251); the alternative, for them, may be to produce no offspring. For women, it is argued

[10] This statistic does not include war killings, which occur almost entirely at the hands of men; e.g. Adams (1983).

(e.g. A. Campbell 1999), the possible loss of reproductive potential due to physical injury is the more important factor, implying that women will be less liable than men to place themselves into situations involving risk — as observed.

— Men often involve themselves, seemingly voluntarily, in behaviors or occupations that involve risk, even in contexts that are not obviously related to reproductive success. For instance, in spite of a trend toward less gender segregation in the workplace, men continue to be overrepresented in high-risk industries such as construction, mining and fire-fighting, and the vast majority of workplace fatalities continue to occur among men (Knestaut 1996; Bureau of Labor Statistics 2022). But as G. C. Williams (1966:217) notes, such behavior is not necessarily inconsistent with a sexual selection origin for male aggression:, "A bull may have a seasonal cycle of behavior, but he retains a part of his belligerent nature at all seasons." A. Campbell (1995:205) argues that earlier death among males results both from "the dangers of male – male competition and from the generalised risky behaviour of young men".

— Crimes involving little physical danger, such as financial fraud or petty theft, exhibit the smallest degree of male-female difference; whereas robbery, which combines theft and violence, is a characteristically male crime (Walsh 2009:257-285). A. Campbell (1999:210) argues that "Women aggress and they steal but they rarely do both at the same time because the equation of resources and status reflects a particularly masculine logic" and (2009:123) "To demonstrate that one poses a credible threat to others it is necessary to demonstrate a reckless disregard for personal safety".

— The tendency among men to commit serious interpersonal crimes exhibits an apparently universal dependence on age (Hirschi and Gottfredson 1983, 1985; Greenberg 1985; Steffensmeier et al. 1989; Eisner 2003). The crime rate peaks in the late teenage years following a rapid rise during adolescence; it then decreases rapidly in the early twenties and remains low during the remainder of a man's life. One consequence is that *young* men commit the overwhelming majority of violent crimes in every society. The universality of this 'age-crime curve' has a natural explanation in terms of sexual selection (Rowe 1996; Kanazawa and Still 2000; Archer and Côté 2005). The reproductive benefits of violent competition first manifest after the onset of puberty: "The teenage boy needs to quickly establish his reputation and to acquire the material things that make him attractive to the opposite sex" (Rowe 2002:54). The ratio of costs to benefits shifts after a young man acquires a mate and/or a child; he is then better off, reproductively speaking, by redirecting his efforts from mating competition to parenting.

— As discussed earlier (e.g. Betzig 1987; Irons 1993; Pérusse 1993), there is evidence for a correlation between men's status, as measured in terms of resource acquisition or other indices of social success, and their (actual or potential) reproductive success. Certainly in our evolutionary past, and to some degree in modern industrialized societies as well, ascending the male status hierarchy has been facilitated by a capacity for aggressive and/or risky behavior.

—- Human male aggression co-exists with a number of other traits which, together, are characteristic of polygynous species in which sexual competition is more intense among males than among females (Puts 2010; Archer 2013; Wilson, Miller and Crouse 2017; Gorelik 2021). Humans are sexually dimorphic: men are 40% heavier than women in terms of fat-free mass and have 60% more lean muscle mass (Mayhew and Salm 1990; Lassek and Gaulin 2009) — a difference that is comparable to that of gorillas (Zihlman & MacFarland,

2000).[11] While men's size and strength may be selected for other reasons — resource acquisition, or success at hunting — large, strong males in almost all species employ their strength and size in fights for females; and anyway it has been argued that men's ability to hunt (and women's preference for successful hunters) is itself an example of sexual selection (e.g. Kaplan et al. 2000). Men also reach sexual maturity about two years later than women, a trait that is attributed (in humans as in other species) to a need to delay risky encounters with older males until they are large enough effectively to compete with them (Andersson 1994).

— As noted above, aggressive behavior manifests itself at a very early age in human children. While evolutionary arguments do not make definite predictions about the age at which aggression should develop, or when the sex differences should first appear, some features of aggressive behavior by male children suggest that it serves the purpose of preparation for conflicts with other males during later life (Bjorklund and Pellegrini 2002; Archer and Côté 2005). Most children become less aggressive between pre-school age and adolescence; this trend is argued to be inconsistent with a gradual process such as 'socialization', and more consistent with an evolutionary perspective, which suggests that humans (like many other animals) are primed to learn cues that indicate when it is preferable *not* to fight (Archer 1994; Tremblay et al. 1999). Boys exhibit more physical aggression than girls from a very young age (Baillargeon et al. 2007; Campbell, Shirley, and Caygill 2002), also suggestive of an evolved pattern of behavior that develops early in life, irrespective of social influences.

Now, arguing (as many of these authors do) that human male aggression is a consequence of sexually-antagonistic selection is not *quite* the same as arguing that *female choice* is ultimately responsible for men's more aggressive behavior. And in fact, in discussions of the evolutionary origins of male aggression, female choice is sometimes not mentioned; or if it is, its importance is minimized (e.g. Archer 2009; Kordsmeyer et al. 2018). In part, this attitude can be justified: "What is important in terms of the possible evolutionary consequences of mate choice is not whether a true preference is involved, but whether variations in the behavior of members of one sex are correlated with variations in their mating success" (Halliday 1983:3). So, for instance, the discovery by Zerjal et al. (2003) of a high frequency of a particular Y-chromosome lineage in 16 populations currently inhabiting northern China and Mongolia could be explained by the fact that Genghis Khan and his male relatives killed the men and raped the women after invading the area a millennium ago; but much the same outcome could result if the women of that time and place found themselves attracted to men with the behavioral characteristics, or the material resources, of Khan's marauders.

In the case of the Mongol invasions, there are good reasons to believe (e.g. Morgan 1986) that male coercive behavior was the decisive factor. But it must be said that evolutionary psychologists and biologists sometimes seem to present human reproductive history as *nothing but* a series of male coercive acts; women and their preferences are, at least rhetorically, erased from the picture. For instance, Daly and Wilson (1994:271) write "The competent use of violent skills contributes quite directly to male fitness: both successful

[11] These statistics may seem surprising given the much smaller male-female differences in stature and total weight. However human females are unique among primates in having copious fat stores (Pond and Mattacks 1987). It is, presumably, muscle mass that is most relevant to the capacity for aggressive behavior.

warriors and successful game hunters have converted their successes into sexual, marital and reproductive success". Now, the only "direct" route from male competitive success to reproduction would be rape, or some other atypical behavior.[12] In more typical liaisons, a woman's cooperation is essential: she can decide how, or whether, to respond to a man's success. Bjorklund and Pellegrini (2002:222) are careful to underscore this point:

> High-status or otherwise successful males do not simply "take" females as mates; rather, by competing successfully with other males, they possess traits that females, over evolutionary time, have come to prefer. To a large extent females select successful males, rather than successful, stronger males forcing smaller females into submission.

When evaluating the suitability of a competitively-successful male as a sexual partner, women in the past (as at present) could choose to reject him out of disgust at the aggressive tactics that he used to succeed; or she might grant her favors to the 'loser' out of empathy with his plight; or she could decide that "successful warriors" should never be rewarded with sex, regardless of how attractive she found them, on the ground that the delights of partnering with such a man are outweighed by the negative consequences to society of encouraging aggressive behavior.

The point here is not that one should make ethical judgments about women's choices in the distant past. As Buss (1996:308**)** aptly puts it, "we are all the end products of a long causal process that involved the coevolution of women's preferences and men's intrasexual competition tactics." Rather (as motivated in the Introduction) the interest here lies in understanding whether the species-typical mate preferences currently exhibited by women have an evolutionary origin, and what those preferences are. To the extent that that evolution was driven by men's coercive acts, and not female preference, there would be less reason to expect women in current societies to exhibit an evolved predilection for aggressive, or risk-tolerant, or competitively successful men.

Recall Pérusse's argument, in his study of mating success in a contemporary society, that "female choice [is] the main causal factor in the relationship found here between male social status and male mating success." Pérusse reached this conclusion after considering, and rejecting, the possibility that subversion of women's choices was widespread. For instance, arranged marriages were rare among his study participants. But not all of Pérusse's arguments apply with equal force to societies in the distant past. As in the example of the depredatory Mongols cited above, history contains numerous examples of men acting collectively to capture or coerce women — instances which probably had evolutionary consequences but were probably not examplars of female choice.

At the same time, it is not hard to find historical examples of women's ability to choose, *even in* societies where female coercion was widely practiced. Here are four examples, culled, unsystematically, from the author's modest private library; no doubt a competent historian could identify more. (1) Herodotus (*Histories* 5.6) relates that (in 5th century BCE) Thracian parents arrange marriages for their daughters, but prior to marriage, "allow them to have intercourse with any man they want". (2) In Hadrian's (2nd century) Rome, we are told (Carcopino 1941:83), a father would not have dreamed of forcing a daughter to marry against her will. (3) In 14th century England, marriage was often arranged when children were very young, but even adolescent children "could, if they wished, formally dissent from it, and a

[12] For instance, the behavior of the physician who allegedly used his own sperm to impregnate multiple women without their consent (Lukpat 2022).

number of such cases of repudiations can be collected from bishops' registers and other sources" (Power 1975:40). (4) In colonial New England, young women who objected to their parents' choice of husband would often force the issue by becoming pregnant with their preferred partner before marriage (Smith and Hindus:1975).

Perhaps the essential point here is one made by Symons (1979:270): "With respect to those areas of life in which intense reproductive competition has occurred in ancestral populations … it was the difficulty of "getting" that led to selection for "wanting"." The fact that a woman's choice of partner has such strong consequences for her reproductive success implies (Symons would argue) that women's mate preferences *should be* subject to selection, even in societal contexts in which she faces opposition to her choice of a marriage partner.

If one accepts, then, that female choice was largely responsible for the sex differences in human aggression (a possibility that is acknowledged even by some authors — e.g. Puts (2010) —who seem anxious to minimize the importance of female choice), one is still left with uncertainty about the particular, evolved mental algorithms that led women to favor aggressive men, and that, presumably, still guide women's choices. As discussed above, Pérusse made a strong case that women prefer high-status men. But it is reasonable also to give at least some credence to the results of the mate-preference studies that were outlined in a preceding section. Perhaps the most robust of the results presented there was the correlation of male criminal behavior with number of sexual partners — suggesting that women are primed to prefer, not just high-status men, but also men who exhibit behavioral traits that are (or were, in the past) indicative of an ability to ascend the male status hierarchy. That possibility is very much in line with selectionist arguments. For instance, Rosenthal (2017:403) argues, on general grounds, that "selection should favor preferences for indicator traits that are reliable predictors of subsequent courter behavior", and Symons (1979:201) that "visible signs of success in intrasexual competition are also likely to be important determinants of male attractiveness to females". And as a number of authors (e.g. Simpson 1993:306) have pointed out, human females in the past must commonly have found themselves in social environments where variations in male status were small. For instance, a cohort of young men just entering puberty are likely to be nearly indistinguishable in terms of their access to resources. Emergence of an adaptation that prompts women to prefer high-status men in contexts where status differentials exist, and to prefer young men who exhibit 'bad boy' attributes (such as aggression) that are predictive of high status in the future (as in the *Free Teen* surveys), would not be surprising.

In their interviews of young women in seven secondary schools, Valls et al. (2008:769) explored the possible consequences of the girls' preference for 'bad boys':

> … according to Anna [a 16-year-old girl who stated that she was going out with a "bastard"], boys also perceive that [their] attractiveness is associated with domination, so they decide to act in accordance with this model. She explained how this process shapes some boys' behaviors:
>
> > So more and more . . . the other guys say, "Christ! Look at what this bastard gets up to and they all wanna be [like] him," so then they are like, "well I'll be a bastard too."

One can imagine how demoralizing it must be for a sensitive young man — after having cultivated the virtues of compassion and selflessness, in response to urging by his parents, his teachers, his clergy — to discover, soon after entering puberty, that young women have eyes only for the bastards; and, a few years later, to realize that his chances of attracting a desirable marriage partner depend more on his career trajectory than on the content of his character.

The scenario that 'Anna' describes should be of interest to consequentialist moral philosophers, if not to a wider audience. But perhaps even more challenging of the

philosopher's attention is the contrast between the evolutionary consequences of sexually antagonistic selection, as presented here, and the dynamics of 'evolutionary ethics', as summarized by Street (2008:207) at the start of this paper ("There is a striking coincidence between the normative judgments we human beings think are true, and the normative judgments that evolutionary forces pushed us in the direction of making"). The fact that sexual selection leads females to make judgments, and males to behave, in ways that are so clearly at odds with the way that (to quote again from Smart 1973) "humane, kindly, benevolent people" *ought* to act is a consequence of genetic conflict — in this case, conflict between the reproductive interests of male and female, of men and women. This circumstance suggests a different application of evolutionary arguments to moral philosophy than the usual one, and that will be the topic of the next section.

A Biologist's View of Morality

> Ethical, moral and legal questions arise out of conflicts of interest among human individuals and groups (Alexander 1982:389).
>
> A moral system is essentially a society with rules (Alexander 1985b:3).

Kin selection, reciprocal altruism, and indirect reciprocity are believed by biologists to have imbued humans with mental algorithms that, at least in the environment of evolutionary adaptation, tended to maximize an individual's inclusive fitness through encouraging certain forms of cooperative or altruistic behavior — for instance, providing assistance to kin, or engaging in mutually beneficial interactions with non-kin. In discussing 'evolutionary ethics' or the 'evolution of morality', moral philosophers often focus on the evolved 'moral sense' that is presumed to underlie such behavior. For instance, in their chapter "Evolution of Morality," Edouard Machery and Ron Mallon (2010:27) write

> Prominent researchers, including [Robert] Trivers himself, have proposed that while originally developed to explain altruism in a large range of species … reciprocal altruism and indirect reciprocity also explain the evolution of morality in humans. [Richard] Alexander puts it succinctly (1987:77): ''Moral systems are systems of indirect reciprocity.''

In the concluding paragraph of her chapter "Evolution and Ethics: An Overview", Catherine Wilson (2018:295) writes "Evolutionary ethics … treats morality as a set of dispositions and behaviors that represent transformations of the "prosocial" or "proto-moral" dispositions and behaviors of extinct human ancestors." Michael Vlerick (2017:227) writes "On the whole, however, the general consensus is that the central "function" of our moral sense is to promote cooperation within groups". And Michael Tomasello (2016:137) writes:

> The set of approaches grouped under the general rubric of evolutionary ethics focus on theoretical principles of cooperation in evolution and how they might apply to the human case. The foundational work from this perspective is Alexander's *The Biology of Moral Systems* (1987), which emphasizes processes of reciprocity, and especially, in the human case, indirect reciprocity.

While these summary statements, and many similar ones that could be quoted, are not strictly incorrect, they give a sometimes misleading view of what is perhaps the more nuanced understanding among many biologists of the relevance of evolutionary arguments to questions of morality and ethics. The views of biologist Richard Alexander, in particular, are often cited and often mis-represented. As biologist David Lahti (2013:315) cautions,

> perhaps most who discuss the biology of prosocial behavior leave us with the idea that niceness is the norm and the rare Machiavellians are the exceptions to explain and avoid. … If [biologist Richard] Alexander and others (Batson et al. 1999; Trivers 2000) are correct, in terms of our adherence to the ideals of the moral point of view the goodies are the exception, if they exist at all.

In this section I review the arguments made by Richard Alexander in his attempts to apply evolutionary theory to the study of ethical questions. Alexander is (with the possible exception of Robert Trivers) perhaps the most highly regarded and most frequently cited of the biologists who have written on this topic. A thorough reading of Alexander's two influential monographs (1979, 1987b), as well as the many other review articles and essays by him and co-authors (e.g. Alexander 1974, 1975, 1978, 1980, 1981, 1985b, 1989, 1993, 2005; Alexander and Borgia 1978; Flinn and Alexander 2007), reveals two recurrent, and essential, themes that are often overlooked or poorly represented in discussions of his work as presented in the philosophical literature. These are, in brief: (1) Morality is *purely a response to conflicts of interest*; in the absence of such conflicts there would be no reason to speak of ethics or morality. (2) Far from embodying evolved capacities, moral or ethical systems consist of *sets of rules* that are *deliberately designed by humans* to deal with conflicts that arise in group living.

That species-typical mental algorithms promoting cooperative or prosocial behavior exist and have evolved via natural selection is not contested by Alexander (or by most other evolutionary biologists); indeed Alexander (together with West-Eberhard) is credited with having elaborated one of the most important of such mechanisms, indirect reciprocity (or, as Alexander often called it, 'social reciprocity'). However, in agreement with many natural scientists (e.g. D. T. Campbell 1972, 1979; Trivers 1985; Richards 1986; Williams 1988; Kanazawa 2009), Alexander does not identify such evolved propensities with morality or a 'moral sense'. In a society consisting of individuals whose interests align perfectly, there would never arise a situation (these scientists argue) in which one person's goals conflict with any other person's goals, and the question "How should I behave?" would never have an ethical dimension.[13]

Alexander's focus on conflicts of interest makes his ideas uniquely well suited to the present study. Hence the importance of clarifying his arguments here before continuing.

In slightly more detail, then, Alexander's view of morality and its relation to evolution can be summarized as follows:

1. Individuals are primed to pursue their own interests, that is, to behave in a way that (in the environments of evolutionary adaptation, if not currently) would have led to proliferation of their genes, whether or not they are consciously aware of this fact (and typically they are not). E. g. Alexander (1978:253-4): "Background explanations for all activities of life, including our own behavior, will eventually be found in generalizations deriving from the cumulative effects of an inevitable and continuing process of differential reproduction of [genomic] variants." *Conscious* understanding of one's own motivations and desires can only be

[13] Hardly anyone aside from a moral philosopher would describe the affection of a mother for her child, or of a husband for his wife, as reflecting a 'moral sense'. Questions of morality would arise in most people's minds (one expects) only if the mother pursued her own interests to the detriment of the child, the husband neglected his wife to pursue other women etc. In any case, this is Alexander's view.

expected to arise in the case that such knowledge serves reproductive interests; Alexander (e.g. 1989) argues that in many cases, evolution would go in the direction of suppressing conscious awareness of the underlying motivations, even to the extent of instilling self-deception so as to produce (in the words of D. T. Campbell 1975) a more "sincere hypocrisy".

2. Conflicts of interest are inevitable in group interactions. They arise out of a history of genetic individuality, the latter a consequence of sexual reproduction. E.g. Alexander (1985b:6): "individuals may be expected to behave so as to serve their own (genetic, reproductive) interests rather than the interests of others or of the whole group whenever the interests of others or the group conflict with those of the individual." Importantly, this is true even with respect to behaviors that are presumptively cooperative or prosocial. E.g. in reciprocal altruism, each individual can benefit by cheating; a woman can deceive her partner with respect to the paternity of her child; the reproductive interests of the mother conflict with those of the fetus etc. Extraordinary degrees of cooperativeness are only expected (in sexually reproducing species) where identity or near-identity of genetic interests is achieved; for instance, in the members of large social insect colonies (ants, termites, honeybees). Such has never been the case for humans (e.g. Alexander 1974).

3. *Without conflicts of interest there would be no need for a concept of morality*. E.g. Alexander (1980:131): "Ethical questions, and the study of morality or concepts of justice and right and wrong, derive solely from the existence of conflicts of interest." Alexander (1982:389) notes that "Although this assertion seems to be accepted universally [by non-philosophers], those who write on ethics, morality and law rarely emphasize it":

> It is my impression that many moral philosophers do not approach the problem of morality and ethics as if it arose as an effort to resolve conflicts of interests. Their involvement in conflicts of interest seems to come about obliquely through discussions of individuals' views with respect to moral behavior, or their proximate feelings about morality — almost as if questions about conflicts of interest arise only because we operate under moral systems, rather than vice versa (Alexander 1987b:89).[14]

Alexander (1982:389) does provide a short list of non-biologist writers who share his view of the importance of conflicts of interest: Roscoe Pound (1941), Ralph Perry (1954) and Hans Kelsen (1957).

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[14] A recent example that illustrates Alexander's point is Michael Tomasello's (2016) *A Natural History of Human Morality*. In his book, Tomasello discusses conflicts almost exclusively in terms of moral dilemmas that arise from attempts by individuals to adhere to conflicting societal norms, rather than in terms of (reproductive) conflicts *between* individuals. E.g. "solving moral dilemmas involving conflicting norms requires a personal weighing of values in a manner that often conforms to no conventional pattern" (Tomasello 2016:115); "The outcome for contemporary individuals is a complex and variegated sense of morality in which different social norms often conflict with one another" (p. 127-8); "natural morality is embedded in a cultural morality of social norms, and these have been crafted at different historical periods for different recurrent situations, so they sometimes conflict" (p. 160). Tomasello gives Alexander due credit, calling his 1987 *The Biology of Moral Systems* a "foundational work", but he does not mention (at least in this book) Alexander's key idea that morality arises out of a need to resolve conflicts of reproductive interest that arise within groups.

4. The ethical rules that make up what Alexander calls "moral systems" are *societal responses to conflicts of interest*: they consist of "restraints on particular methods of seeking self-interests, specifically on activities that affect deleteriously the efforts of others to seek their own interests" (Alexander 1987b:81). Moral systems consist of "rule-dominated patterns of social reciprocity", "agreed-upon rules about how far any of us can go in serving our own interests within the social group" (Alexander 2005:322). Again: "restraints on individuals and subgroups serving their own interests occur solely because of the likelihood of prohibitive costs being imposed by some part of the rest of society; this is precisely the definition of moral systems I am developing here" (Alexander 1987b:88). Such rules and laws can be, and often clearly are, deliberately created and enforced: sometimes by those in positions of authority, sometimes collectively by groups. Examples are rules that limit reproductive striving by imposing monogamy, laws that limit the accumulation of wealth via progressive taxation, or laws forbidding nepotism or rape. Alexander distinguishes, carefully and consistently, between moral *systems* (which are societal artifacts) and moral *sentiments* (which may, or may not, have evolved via natural selection):

> Nothing about the human phenotype involving morality either has been identified or need be identified as innate, instinctive, inherited, or unchangeable … one need not argue (and I never have argued) that any particular ethical or moral rules will ever be discovered to follow naturally or inevitably or at all from evolutionary facts (Alexander 1993:174, 176-7).

5. By reducing opportunities for selfish behavior, moral *systems* can have the effect (intended or not) of aligning individual and group interests: they can lead to societies in which each individual can most easily increase their reproductive success by increasing the efficiency and productivity of the whole group. In this sense, they can transcend the more limited degree of cooperative behavior that might be attributed to natural selection alone. Alexander (1975, 1989) and Alexander and Borgia (1978) have argued that the 'leveling' effect of societal rules or laws, by repressing reproductive competition and conflict within groups, has been an important factor in the ability of humans to form large and complex societies.[15]

6. Arguments from evolution have nothing whatsoever to say about *normative* ethics: about what people *ought* to be doing. E. g.

> Because morality involves conflicts of interest, it cannot easily be generalized into a universal despite virtually continual efforts by utilitarian philosophers to do that; morality does not derive its meaning from sets of universals or undeniable facts (Alexander 1987a:321).

Whence, then, the strikingly different opinions that many philosophers attribute to biologists such as Alexander? Perhaps one explanation is that terse, summary statements such as "Moral systems are systems of indirect reciprocity" can be found scattered throughout Alexander's work, often as the opening line of an abstract or book chapter. But Alexander is always careful to clarify in the immediately following text that by "*systems* of

[15] Here Alexander might, or might not, be arguing for a kind of 'group selection' (e.g. D. S. Wilson 1999; Nesse 1994; Dennett 1994, 2002). My reading of this and similar passages is that Alexander is careful never to commit himself to such a position, nor to rule it out.

indirect reciprocity" (as opposed to "indirect reciprocity" *tout court*) he means *societal rules* that are a *response to conflicts of interest*. For instance:

> Moral systems are systems of indirect reciprocity. They exist because of conflicts of interest, and arise as an outcome of the complexity of social interactions in groups of long-lived individuals with (a) varying conflicts and confluences of interest, (b) indefinitely iterated social interactions, and (c) multiple alternate interactants (Alexander 1987b:142).

But probably a more fundamental reason for the moral philosophers' perennial misreading of Alexander is their insistence that ethical behavior *ought to* reflect a (sincere) moral sense and that moral truths *ought to be* universals.[16] For instance, philosopher Geoffrey Warnock (1971:62, 68), in critiquing 'rule utilitarianism', writes

> For surely, if I am sensibly to accept a rule 'Never X', I must have some reason for accepting it - for accepting a rule at all, and specifically that rule; but - if the rule is to be said to be a moral rule - what could that reason possibly be except the view that to X is, actually, morally wrong? … whatever may be the proper criterion by which to assess the merits of systems of rules, I do not see how the claim could be substantiated that morality ought to be essentially such a system.

Alexander, for his part, recognized the superficial resemblance of his concept of moral systems to rule utilitarianism (1980:128; 1987b:120) but he (characteristically) focused on conflict: on the opportunity that 'moral rules' afford for the advancement of one's self-interests at the expense of others:

> A rule utilitarian is said to be one who supposedly always asks himself about each act, "What if everyone did this?" "What if there were a rule that this act is permissible?"… it would be beneficial to parade one's self as an adherent to rule utilitarianism because of the implication of altruism (doing what is best for the group as a whole) and the effect of that implication on potential interactants (Alexander 1987b:120).

(Elsewhere Alexander wrote: "individuals are expected to parade the ideas of much altruism and of indiscriminate altruism as beneficial, so as to encourage people in general to engage in increasing amounts of social investment whether or not it is beneficial to their interests" (1985b:12) and "biologists realize that the conflicts of interests that exist because of histories of genetic difference imply instead that nearly all communicative signals, human or otherwise, should be expected to involve significant deceit" (1987b:73).)

As an exemplar of societal rules designed to deal with reproductive conflicts of interest, Alexander (1974, 1975, 1981, 1987b:71-73) and Alexander et al. (1979) highlight socially imposed monogamy.[17] In societies practicing harem polygyny, a few men can monopolize

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[16] The difficulty of reconciling these two assumptions with evolutionary theory has been characterized by Street (2006) as the "Darwinian dilemma". No such dilemma occurs under Alexander's interpretation of moral systems, since Alexander posits neither innate moral faculties, nor the existence of universally valid moral propositions.

[17] Alexander et al. (1979) distinguish between "ecologically imposed monogamy" and "socially imposed monogamy". The former means that "monogamy is universal or prevalent apparently because, owing to the ecological situation, individual men are typically unable to gain by attempting to provide for offspring of more than one wife" (pp. 418-9).

large numbers of women, reducing (sometimes to zero) the reproductive opportunities of other men. Alexander argued that in societies that are resource-rich enough to allow extreme differentials in men's ability to accumulate resources and status, enforced *monogamy* could result from the

> collective power of males forced to be either monogamous or mateless in the polygynous system. … Socially imposed monogamy, in relatively affluent societies as opposed to ecologically imposed monogamy in marginal habitats, may represent a sort of ultimate example of the effectiveness of coalitions against the relatively few males who could, if it were permitted, succeed at polygyny. The few potentially polygynous males would be opposed as individuals, unlikely to form even a coalition with other potentially polygynous males (Alexander 1975:96).

Alexander (1987b:71) notes that "Young men at the age of maximal sexual competition are the most divisive and competitive class of individuals in human social groups" and he argues that socially imposed monogamy can have the side-benefit of reducing the motivation for violent conflict between men.[18] He also (Alexander 1981:516) suggests that "Monogamy, from whatever source, also creates bonds between spouses, rooted in their common interest in a brood of offspring, and the history of such common interest; as far as adults are concerned, this bond may otherwise be without parallel in all of human history". Alexander's views present an interesting contrast with those of Geoffrey Miller, who argues (2000, 2007, 2008) that virtues such as kindness and marital fidelity are evolutionary consequences of sexual selection via mate choice. Alexander, by contrast, emphasizes the inherent conflicts of interest that exist between male and female and sees "moral" behavior arising from the pair bond as an indirect (not evolved) consequence of attempts to resolve those conflicts.

A Modest Proposal

> There is not a more perilous or immoral habit of mind than the sanctifying of success (Dalberg-Acton 1906/1956:204).

The conflicts between men that are addressed by societal rules enforcing monogamy may have their origins in men's and women's different patterns of reproductive investment, as Alexander and others have argued, but proximate motivations for instituting society-wide monogamy need have nothing to do with knowledge of such things. Rather: men in societies that practice harem polygamy are *unhappy* that their sexual access to women is so limited, and they perceive (correctly) that the proximate cause of that unhappiness is the ability of certain men to monopolize the limited supply.

Indeed Alexander argues that happiness in general is nothing more nor less than an evolved response to successful reproduction, or to behavior that in the past led to successful reproduction:

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[18] Wright (1994:98): "Few things are more anxiety-producing for an elite governing class than bogs of sex-starved and childless men with at least a modicum of political power." Wright also notes that monogamy is not necessarily a plus for women: given a choice between living in poverty with one man, or as one among multiple wives of a rich and high-status man, a woman might prefer the latter. The wide- spread preference for monogamy among democratic societies, he argues, probably reflects a history of dominance of the legislative process by men.

> Now we can suggest that what humans have evolved to strive for is to reproduce and to reproduce maximally — indeed, to *out*-reproduce others. Happiness, then, is an end for the individual only in the sense that it is achieved by acts leading to reproduction. Happiness is a means to reproduction. … the striving of organisms can be generalized on solid grounds, and it is not hedonistic at all but reproductive; in historical terms hedonism is itself reproductive, and when it is not we expect it to eventually be abandoned (Alexander 1978:265).

It would follow that societal laws that limit the negative consequences of reproductive competition should lead to increased happiness for men, at least in an average sense — that is: they should have the effect of moving society closer to the utilitarian ideal of maximal happiness. So, for instance, in the case of competition for status, Alexander (1980:136) argues that

> unhappiness as a consequence of unlikely or irrational personal goals is likely to be most prevalent in societies that are hierarchically structured, so that lofty goals may be developed from observations of the success of others, and yet so constituted as to generate severe inequalities of opportunity so that the perceived goals are inaccessible for what are logically interpreted as unjust reasons.

There is a large and growing literature that documents the link between men's loss of status, on the one hand, and their likelihood of contemplating or committing suicide on the other (e.g. Breed 1963; Maris 1967; Lewis and Sloggett 1998; Andreeva et al. 2015; Dombrovski et al. 2018; Walther et al. 2023).[19] These studies document that men are much more severely impacted psychologically by status loss than women, and that it is the *change* in status, rather than low status per se, that leads men to suicide. Of course, suicide can hardly be called an adaptive behavior; but natural selection moulds mental architectures, not behaviors per se, and negative emotions can have an adaptive function (e.g. Nesse 1990; Cosmides and Tooby 2000). The feelings of low self-esteem or depression that accompany a man's loss of status may generally serve as a warning that his attractiveness to women has lessened, even if such feelings may sometimes become so strong that they motivate maladaptive behaviors such as suicide (Wright 1994:389).

As Alexander noted, success is only measurable in relative terms. An individual's loss in status can result equally from a competitive failure, or from another's competitive success; from loss of a job, or from a colleague's promotion. And when a single individual achieves a substantial gain in status, the status of many other people suffers, excepting those few whose interests (Alexander would say: whose *reproductive* interests) align with those of the winner. William the Conqueror's victory at the battle of Hastings resulted in an enormous increase in his status, the status of some close relatives, and of the cadre of banditti who accompanied him, but the status of everyone who was anyone in pre-conquest England dropped precipitously (Douglas 1967:265-6). And the awarding of a Nobel Prize in science is likely to be experienced as a boon by the prize-winner, the laureate's spouse and children, and any students who stand to benefit from the winning scientist's letters of recommendation, but to

[19] Based on their metasynthesis of 78 studies carried out over the last twenty years, Bennett et al. (2023) state "In 76% of studies, we found evidence to suggest that failing to meet norms of male success was associated with increased psychological pain and suicide risk … In 46% of studies, from lower, middle and upper income settings, a profound sense of personal failure, of not meeting social expectations for men, and experiencing an unbearable loss of status and social value were described as proximal drivers of suicidal behaviors in men."

the great majority of scientists the event represents an irremediable loss of status, and it would be understandable if their emotional reaction was one of distress or despair.

The realization that status hierarchies primarily benefit those at the top is hardly a novel one; in the words of Peter Singer (1999:58), "there is little connection between status and the benefits one brings to others". As a way of ameliorating the negative consequences of concentrating wealth in a few, high-status individuals, Singer proposed a re-distribution of wealth via a tax on spending. But Singer's proposal would do little to address the (in Alexander's words) "unhappiness as a consequence of … observations of the success of others": that is, the relentless psychological toll on the majority of men who are forced to operate within status hierarchies and who never quite manage to reach the top.

The fact is that societies are constantly creating new instruments for status distinction that do little more than create new hierarchies, or reify existing ones. There is no function of a newspaper that requires the existence of the Pulitzer Prize; no aspect of scientific research that is enabled by the Nobel Prize committee; no sense in which the annual awards of the Academy of Motion Picture Arts and Sciences are necessary to the production of films. Indeed principled arguments can be made that the status distinctions bestowed by these organizations are detrimental to the very professions they claim to promote.[20] But by creating new ways to augment the status of a few individuals, they inevitably create new avenues of failure, hence new opportunities for psychological distress, for a great many others.

The thesis advanced here — that an evolutionary perspective leads one to question the morality of bestowing (or accepting, or praising the recipients of) prizes and awards — is likely to be contested. As a number of authors (including Charles Darwin) have pointed out, humans seem instinctively to equate high status with goodness (the *Britannica Dictionary* defines 'noble' both as "belonging to the highest social class" and "having personal qualities that people admire".) Once a status hierarchy exists, expressions of admiration directed toward a high-status individual are likely to yield reproductive dividends, and the most convincing way to express admiration is to actually feel it, in a deep, unquestioning way (Alexander 1979:134; Hartung 1988). "Of course he won the prize!" people are apt to say. "He deserved it. He must have!" And so a proposal to rid the social world of unnecessary status distinctions — all of which, after all, are creations of human beings, not features of the natural world — seems, paradoxically, unnatural.

References

Agey E., Morris A., Chandy M., Gaulin S. J. C. 2019. Arranged marriage often subverts offspring mate choice: an HRAF-based study. *American Anthropologist* 123(4):861-878.

Ahmetoglu G., Swami V. 2012. Do women prefer "nice guys"? The effect of male dominance behavior on women's ratings of sexual attractiveness. *Social Behavior and Personality* 40(4): 667- 672.

Alcantud P. M., Puigvert L., Rios O., Duque E. 2021. Language of desire: a methodological contribution to overcoming gender violence. *International Journal of Qualitative Methods* 20:1–8.

Alexander R. D. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics* 5:325-383.

[20] For the Pulitzer Prize, see Shafer 2015; the Nobel Prize, McKie 2018; the Academy Award, Orr 2018.

Alexander R. D. 1975. The search for a general theory of behavior. *Behavioral Science* 20: 77-100.

Alexander R. D. 1978. Natural selection and societal laws. Pages 249-290 in *Morals, Science, and Sociality*, *The Foundations of Ethics and Its Relationship to Science, Volume III,* edited by H. T. Engelhardt Jr. and D. Callahan. Hastings-on Hudson (NY): Hastings Center.

Alexander R. D. 1979. *Darwinism and Human Affairs*. Seattle: University of Washington Press.

Alexander R. D. 1980. Evolution, social behavior, and ethics. Pages 124-149 in *Knowing and Valuing: The Search for Common Roots. The Foundations of Ethics and Its Relationship to Science, Volume IV*, edited by H. T. Engelhardt Jr. and D. Callahan. Hastings-on-Hudson (NY): Hastings Center.

Alexander R. D. 1981. Evolution, culture, and human behavior: Some general considerations. Pages 509-520 in *Natural Selection and Social Behavior: Recent Research and New Theory,* edited by R. D. Alexander and D. W. Tinkle. New York: Chiron Press.

Alexander R. D. 1982. Biology and the moral paradoxes. *Journal of Social and Biological Structures* 5:389-395.

Alexander R. D. 1985a. Genes, consciousness, and behavior theory. Pages 783-802 in *A Century of Psychology as Science*, edited by S. Koch and D. E. Leary. American Psychological Association.

Alexander R. D. 1985b. A biological interpretation of moral systems. *Zygon* 20(1):3-20.

Alexander R. D. 1987a. Evolutionary approaches to human behavior: What does the future hold? Pages 317-341 in *Human Reproductive Behavior: A Darwinian Perspective*, edited by L. Betzig, M. Borgerhoff Mulder and P. Turke. Cambridge (UK): Cambridge University Press.

Alexander R. D. 1987b. *The Biology of Moral Systems*. Hawthorne (NY): Aldine De Gruyter.

Alexander R. D. 1989. Evolution of the human psyche. Pages 455-513 in *The Human Revolution*, edited by P. Mellars and C. Stringer. Edinburgh: Edinburgh University Press.

Alexander R. D. 1993. Biological considerations in the analysis of morality. Pages 163-196 in *Evolutionary Ethics*, edited by M. H. Nitecki and D. V. Nitecki. Albany: State University of New York Press.

Alexander R. D. 2005. Evolutionary selection and the nature of humanity. Pages 301-348 in *Darwinism & Philosophy*, edited by V. Hoisle and C. Illies Notre Dame: University of Notre Dame Press.

Alexander R. D., Borgia G. 1978. Group selection, altruism, and the levels of organization of life. *Annual Review of Ecology and Systematics* 9:449-474.

Alexander R. D., Hoogland J. L., Howard R. D., Noonan K. M., Sherman P. W. 1979. Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates, and humans. Pages 402-435 in *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, edited by N. A. Chagnon and W. Irons. William North Scituate (MA): Duxbury Press.

Andersson M. 1994. *Sexual Selection*. Princeton: Princeton University Press.

Andreeva E., Magnusson Hanson L. L., Westerlund H., Theorell T., Brenner M. H. 2015. Depressive symptoms as a cause and effect of job loss in men and women: Evidence in the context of organisational downsizing from the Swedish Longitudinal Occupational Survey of Health. *BMC Public Health* 15:1045.

Archer J. 1988. *The Behavioural Biology of Aggression*. Cambridge (UK): Cambridge University Press.

Archer J. 1994. Violence between men. Pages 121-140 in *Male Violence*, edited by J. Archer. London: Routledge.

Archer J. 2004. Sex differences in aggression in real-world settings: a meta-analytic review. *Review of General Psychology* 8:291-322.

Archer J. 2009. Does sexual selection explain human sex differences in aggression? *Behavioral and Brain Sciences* 32:249–311.

Archer J. 2013. Human sex differences in aggression from the perspective of sexual selection. Pages 101-120 in *Aggression in Humans and Other Primates: Biology, Psychology, Sociology,* edited by H.-H. Kortüm Hans-Henning and J. Heinze. Berlin: Walter de Gruyter.

Archer J., Côté S. 2005. Sex differences in aggressive behavior: a developmental and evolutionary perspective. Pages 425-446 in *Developmental Origins of Aggression*, edited by R. E. Tremblay, W. W. Hartup and J. Archer. New York: Guilford Press.

Arnqvist G., Rowe L. 2005. *Sexual Conflict*. Princeton: Princeton University Press.

Austad S. N. 2006. Why women live longer than men: sex differences in longevity. *Gender Medicine* 3(2): 79-92.

Axelrod R., Hamilton W. D. 1981. The evolution of cooperation. *Science* 211:1390-1396.

Baillargeon R. H., Zoccolillo M., Keenan K., Côté S., Pérusse D., Wu H.-X., Boivin M., Tremblay R. E. 2007. Gender differences in physical aggression: A prospective population-based survey of children before and after 2 years of age. *Developmental Psychology* 43(1):13–26.

Bateman A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2:349-368.

Bennett S., Robb K. A., Zortea T. C., Dickson A., Richardson C., O'Connor R. C. 2023. Male suicide risk and recovery factors: A systematic review and qualitative metasynthesis of two decades of research. *Psychological* Bulletin 149(7-8), 371–417.

Bergstrom C. T., Real L. A. 2000. Towards a theory of mutual mate choice: lessons from two-sided matching. *Evolutionary Ecology Research* 2:493–508.

Bernreuter R. G. 1933. Validity of the personality inventory. *Personnel Journal* 11:383–386.

Bettencourt B. A., Miller N. 1996. Gender differences in aggression as a function of provocation: a meta-analysis. *Psychological Bulletin* 119:422-447.

Betzig L. L. 1982. Despotism and differential reproduction: a cross-cultural correlation of conflict asymmetry, hierarchy, and degree of polygyny. *Ethology and Sociobiology* 3:209-221.

Betzig L. L. 1987. Mating and parenting in Darwinian perspective. Pages 3-20 in *Human Reproductive Behavior: A Darwinian Perspective*, edited by L. L. Betzig, M. Borgerhoff Mulder, and P. Turke. Cambridge (UK): Cambridge University Press.

Bjorklund D. F., Pellegrini A. D. 2002. *The Origins of Human Nature: Evolutionary Developmental Psychology*. Washington (DC): American Psychological Association.

Bogaert A. F., Fisher W. A. 1995. Predictors of university men's number of sexual partners. *The Journal of Sex Research* 32(2):119-130.

Bradley B. J., Robbins M. M., Williamson E. A., Steklis H. D., Steklis N. G., Eckhardt N., Boesch C., Vigilant L. 2005. Mountain gorilla tug-of-war: Silverbacks have limited control over reproduction in multimale groups. *Proceedings of the National Academy of Sciences of the United States of America* 102:9418–23.

Breed W. 1963. Occupational mobility and suicide among white males. *American Sociological Review* 28(2):179-188.

Brooks R. 2000. Negative genetic correlation between male sexual attractiveness and survival. *Nature* 406(6791):67-70.

Broude G. 1993. Attractive single gatherer wishes to meet rich, powerful hunter for good time under mongongo tree. *Behavioral and Brain Sciences* 16:287-289.

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

Browne K. R. 1995. Sex and temperament in modern society: a Darwinian view of the "glass ceiling" and the "gender gap" in compensation. 37 *Arizona Law Review* 971.

Bukowski W. M., Sippola L. K., Newcomb A. F. 2000. Variations in patterns of attraction of same- and other-sex peers during early adolescence. *Developmental Psychology* 36(2):147–154.

Bureau of Labor Statistics 2022. *Census of Fatal Occupational Injuries Summary, 2021*. USDL-22-2309.

Burger J. M., Cosby M. 1999. Do women prefer dominant men? The case of the missing control condition. *Journal of Research in Personality* 33:358–368

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

Buss D. M. et al. 1990. International preferences in selecting mates - a study of 37 cultures. *Journal of Cross-Cultural Psychology* 21(1):5-47.

Buss D. M. 1996. Sexual conflict: evolutionary insights into feminism and the "battle of the sexes". Pages 296-319 in *Sex, Power, Conflict: Evolutionary and Feminist Perspectives*, edited by D. M. Buss and N. M. Malamuth. New York: Oxford University Press.

Buss D. M., Barnes M. 1986. Preferences in human mate selection. *Journal of Personality and Social Psychology* 50(3): 559-570.

Buss D. M., Schmitt D. P. 2019. Mate preferences and their behavioral manifestations. *Annual Review of Psychology* 70:77–110.

Buss D. M., Shackelford T. K., Kirkpatrick L. A., Larsen R. J. 2001. A half-century of mate preferences: the cultural evolution of values. *Journal of Marriage and Family* 63: 491-503.

Butler, J. 2006. *Gender Trouble: Feminism and the Subversion of Identity*. New York: Routledge.

Byrnes J. P., Miller D. C., Schafer W. D. 1999. Gender differences in risk taking: A meta-analysis. *Psychological Bulletin* 125(3), 367-383.

Caillaud D., Levréro F., Gatti S., Ménard N., Raymond M. 2008. Influence of male morphology on male mating status and behavior during interunit encounters in western lowland gorillas. *American Journal of Physical Anthropology* 135(4):379–388.

Cairns R. B., Cairns B. D. 1994. *Lifelines and Risks: Pathways of Youth In Our Time*. Cambridge (UK): Cambridge University Press.

Campbell A. 1995. A few good men: evolutionary psychology and female adolescent aggression. *Ethology and Sociobiology* 16:99-123.

Campbell A. 1999. Staying alive: Evolution, culture, and women's intrasexual aggression. *Behavioral and Brain Sciences* 22:203–252.

Campbell A. 2006. Sex differences in direct aggression: What are the psychological mediators? *Aggression and Violent Behavior* 11(3):237-264.

Campbell A. 2009. Gender and crime: an evolutionary perspective. Pages 117-136 in *Biosocial Criminology: New Directions in Theory and Research*, edited by A. Walsh and K. M. Beaver. New York: Routledge.

Campbell, A. 2013. *A Mind of Her Own: The Evolutionary Psychology of Women*, 2nd edition. Oxford (UK): Oxford University Press.

Campbell A. 2016. Review of David C. Geary's *Evolution of Vulnerability: Implications for Sex Differences in Health and Development*. *Human Nature* 27:98–103.

Campbell A., Shirley L., Caygill L. 2002. Sex-typed preferences in three domains: Do two-year-olds need cognitive variables? *British Journal of Psychology* 93:203– 217.

Campbell D. T. 1972. On the genetics of altruism and the counter-hedonic components in human culture. *Journal of Social Issues* 28(3):21-37.

Campbell D. T. 1975. On the conflicts between biological and social evolution and between psychology and moral tradition. *American Psychologist* 30:1103-1126.

Campbell D. T. 1979. Comments on the sociobiology of ethics and moralizing. *Behavioral Science* 24:37-45.

Caporael L. R. 1989. Mechanisms matter: the difference between sociobiology and evolutionary psychology. *Behavioral and Brain Sciences* 12(1):17-18.

Carcopino J. 1941. *Daily Life in Ancient Rome*. London: G. Routledge & Sons.

Carter G. L., Campbell A. C., Muncer S. M. 2014. The Dark Triad personality: attractiveness to women. *Personality and Individual Differences* 56:57–61.

Carter A. J., Nguyen A. Q. 2011. Antagonistic pleiotropy as a widespread mechanism for the maintenance of polymorphic disease alleles. *BMC Medical Genetics* 12:160.

Chagnon N. A. 1979. Is reproductive success equal in egalitarian societies? Pages 374-401 in *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, edited by N. A. Chagnon and W. Irons. William North Scituate (MA): Duxbury Press.

Chagnon N. A., Flinn M. V., Melancon T. F. 1979 Sex-ratio variation among the Yanomamö Indians. Pages 290-320 in *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective,* edited by N. A. Chagnon and W. Irons. North Scituate (MA): Duxbury Press.

Charlesworth W. R., La Freniere P. 1983. Dominance, friendship, and resource utilization in preschool children's groups. *Ethology and Sociobiology* 4(3):175–186.

Clutton-Brock T. H., Isvaran K. 2007. Sex differences in ageing in natural populations of vertebrates. *Proceedings of the Royal Society B* 274:3097–3104.

Cochrane S. H. 1979. *Fertility and Education: What Do We Really Know?* Baltimore: The Johns Hopkins University Press.

Connallon T., Cox R. M., Calsbeek R. 2010. Fitness consequences of sex-specific selection. *Evolution* 64(6):1671-1682.

Cosmides L., Tooby J. 2000. Evolutionary psychology and the emotions. Pages 91-115 in *Handbook of Emotions*, second edition, edited by M. Lewis and J. M. Haviland-Jones. New York: The Guilford Press.

Costa P. T., Jr., McCrae R. R. 1992. *Revised NEO Personality Inventory and NEO Five-Factor Inventory (NEO-FFI)*. Odessa (FL): Psychological Assessment Resources.

Cowlishaw G., Dunbar R. I. 1991. Dominance rank and mating success in male primates. *Animal Behaviour* 41:1045–1056.

Cox C. R., Le Boeuf B. J. 1977. Female incitation of male competition: a mechanism in sexual selection. *The American Naturalist* 111(978):317-335.

Cronk L. 1991. Wealth, status, and reproductive success among the Mukogodo of Kenya. *American Anthropologist* 93:345–60.

Dalberg-Acton J. E. E. (Lord Acton) 1956/1906. *Lectures on Modern History*. Edited with an introduction by John Neville Figgis and Reginald Vere Laurence. London: Macmillan & Co. Ltd.

Daly M., Wilson M. 1983. *Sex, Evolution, and Behavior*, second edition. Belmont (CA): Wadsworth Publishing Company.

Daly M., Wilson M. 1988. *Homicide*. New York: Aldine De Gruyter.

Daly M., Wilson M. 1994. Evolutionary psychology of male violence. Pages 253-288 in *Male Violence*, edited by J. Archer. London: Routledge.

Dane A. V., Marini Z. A., Volk A. A., Vaillancourt T. 2017. Physical and relational bullying and victimization: differential relations with adolescent dating and sexual behavior. *Aggressive Behavior* 43:111–122.

Davis A. C., Brittain H., Arnocky S., Vaillancourt T. 2022. Longitudinal associations between primary and secondary psychopathic traits, delinquency, and current dating status in adolescence. *Evolutionary Psychology* 20(1):1–17.

Darwin C. 1859. *On the Origin of Species by Means of Natural Selection, or, the Preservation of Favoured Races in the Struggle for Life*. London: John Murray.

Darwin C. 1871. *The Descent of Man: and Selection in Relation to Sex*. London: John Murray.

Dawkins R. 1976. *The Selfish Gene*. New York: Oxford University Press.

Dawkins R. 1977. Replicator selection and the extended phenotype. *Zeitschrift fiir Tierpsychologie* 47:61-76.

de Bruyn E. H., Cillessen A. H. N., Weisfeld G. E. 2012. Dominance-popularity status, behavior, and the emergence of sexual activity in young adolescents. *Evolutionary Psychology* 10(2):296-319.

Dewsbury D. A. 1982. Dominance rank, copulatory behavior, and differential reproduction. *The Quarterly Review of Biology* 57(2): 135-159

Digman J. M. 1990. Personality structure: emergence of the five-factor model. *Annual Review of Psychology* 41(1):417-440.

Dombrovski A. Y., Aslinger E., Wright A. G. C., Szanto K. 2018. Losing the battle: Perceived status loss and contemplated or attempted suicide in older adults. *International Journal of Geriatric Psychiatry* 33:907–914.

Douglas D. C. 1967. *William the Conqueror*. Berkeley (CA): The University of California Press.

Eagly A. H., Steffen V. J. 1986. Gender and aggressive behavior: a meta-analytic review of the social psychological literature. *Psychological Bulletin* 100:309-330.

Easton J. A., Goetz C. D., Buss D. M. 2015. Human mate choice, evolution of. Pages 340-347 in the *International Encyclopedia of the Social & Behavioral Sciences*, 2nd edition, Volume 11.

Eberhard W. G. 1996. *Female Control: Sexual Selection by Cryptic Female Choice*. Princeton: Princeton University Press.

Edwards A. L. 1957. *The Social Desirability Variable in Personality Assessment and Research*. New York: The Dryden Press.

Eisner M. 2003. Long-term historical trends in violent crime. *Crime and Justice: A Review of Research* 30:83-142.

Ellis B. J. 1992. The evolution of sexual attraction: evaluative mechanisms in women. Pages 267-288 in *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, edited by J. H. Barkow, L. Cosmides and J. Tooby. New York: Oxford University Press.

Ellis L. 1995. Dominance and reproductive success among nonhuman animals: A cross-species comparison. *Ethology and Sociobiology* 16:257-333.

Ellis L., Walsh A. 2000. *Criminology: A Global Perspective*. Boston: Allyn and Bacon.

Ellis L., Hershberger S., Field E., Wersinger S., Pellis S., Geary D., Palmer C., Hoyenga K., Hetsroni A., Karadi K. 2008. *Sex Differences: Summarizing More Than a Century of Scientific Research*. New York: Psychology Press.

Farrell A. H., Vaillancourt T. 2019. Temperament, bullying, and dating aggression: longitudinal associations for adolescents in a romantic relationship. *Evolutionary Psychology* 17(2):1–13.

Fedigan L. M. 1983. Dominance and reproductive success in primates. *Yearbook of Physical Anthropology* 26:91-129.

Feingold A. 1990. Gender differences in effects of physical attractiveness on romantic attraction: A comparison across five research paradigms. *Journal of Personality and Social Psychology* 59:981–993.

Feingold A. 1992. Gender differences in mate selection preferences: A test of the parental investment model. *Psychological Bulletin* 112:125-39.

Fimrite P., Taylor M. 2005. No shortage of women who dream of snaring a husband on death row. *San Francisco Chronicle*, March 27, 2005.

Fink B., André S., Mines J. S., Weege B., Shackelford T. K., Butovskaya M. L. 2016. Sex difference in attractiveness perceptions of strong and weak male walkers. *American Journal of Human Biology* 28:913-917.

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

Fisher M. L. 2022. Female intrasexual competition. Pages 91-117 in volume 3 of *The Cambridge Handbook of Evolutionary Perspectives on Sexual Psychology*, edited by T. K. Shackelford. Cambridge (UK): Cambridge University Press.

Fisher W. A., White L. A., Byrne D., Kelly K. 1988. Erotophobia-erotophilia as a dimension of personality. *The Journal of Sex Research* 25(1):123-151.

FitzPatrick W. 2021. Morality and evolutionary biology. From the Spring 2021 Edition of the *Stanford Encyclopedia of Philosophy*.

Flecha R., Puigvert L., Ríos O. 2013. The new masculinities and the overcoming of gender violence. *International and Multidisciplinary Journal of Social Sciences* 2(1):88-113.

Flinn M. V. 1986. Correlates of reproductive success in a Caribbean village. *Human Ecology* 14:225-243.

Flinn M. V., Alexander R. 2007. Runaway social selection in human evolution. Pages 249-255 in *The Evolution of Mind: Fundamental Questions and Controversies*, edited by Steven W. Gangestad, Jeffry A. Simpson. New York: The Guilford Press.

Folstad I., Karter A. J. 1992. Parasites, bright males, and the immunocompetence handicap. *American Naturalist* 139: 603–22.

Frederick D. A., Reynolds T. A., Fisher M. L. 2013. The importance of female choice: Evolutionary perspectives on constraints, expressions, and variations in female mating strategies. Pages 304-329 in *Evolution's Empress: Darwinian Perspectives on the Nature of Women*, edited by M. L. Fisher, J. R. Garcia, and R. Sokol Chang. Oxford: Oxford University Press).

Gangestad S. W., Simpson J. A. 1990. Toward an evolutionary history of female sociosexual variation. *Journal of Personality* 58(1):69-96.

Geary D. C. 2006. Sexual selection and the evolution of human sex differences. *Psychological Topics* 15(2):203-238.

Geary D. C. 2021. *Male, Female: The Evolution Of Human Sex Differences*, 3rd edition. Washington, DC: American Psychological Association.

Gerloff U., Hartung B., Fruth B., Hohmann G., Tautz D. 1999. Intracommunity relationships, dispersal pattern and paternity success in a wild living community of Bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 266(1424):1189–1195.

Glueck S., Glueck E. T. 1968. *Delinquents and Nondelinquents in Perspective*. Cambridge (MA): Harvard University Press.

Goldberg L. R. 1981. Language and individual differences: The search for universals in personality lexicons. Pages 141-165 in *Review of Personality and Social Psychology*, Vol. 2, edited by L. Wheeler. Beverly Hills (CA): Sage.

Goldfoot D. A. 1982. Multiple channels of sexual communication in rhesus monkeys: Role of olfactory cues. Pages 413-428 in *Primate Communication*, edited by C. T. Snowdon, C. H. Brown and M. R. Petersen. Cambridge (UK): Cambridge University Press.

Goldstein J. H. 1986. *Aggression and Crimes of Violence*. Oxford: Oxford University Press.

Gorelik G. 2021. Domains of female choice in human evolution. *Evolutionary Behavioral Sciences*. Advance online publication. https://doi.org/10.1037/ebs0000276 .

Gorelik G., Shackelford T. K. 2014. Evolutionary awareness. *Evolutionary Psychology* 12(4): 783-813.

Gowaty P. A. (editor) 1997. *Feminism and Evolutionary Biology: Boundaries, Intersection, and Frontiers*. New York: Chapman & Hall.

Grafen A. 1990. Sexual selection unhandicapped by the Fisher process. *Journal of Theoretical Biology* 144:473–516.

Greenberg D. F. 1985. Age, crime, and social explanation. *American Journal of Sociology* 91:1-21.

Greenwald A., McGhee D., Schwartz J. 1998. Measuring individual differences in implicit cognition: the implicit association test. *Journal of Personality and Social Psychology* 74(6):1464–1480.

Haig D. 1993. Genetic conflicts in human pregnancy. *Quarterly Review of Biology* 68:495-532.

Halliday T. R. 1983. The study of mate choice. Pages 3-32 in *Mate Choice*, edited by P. Bateson. Cambridge (UK): Cambridge University Press.

Hamilton W. D. 1964. The genetical evolution of social behavior. Parts I, II. *Journal of Theoretical Biology* 7(1): 1–52.

Hamilton W. D. 1966. The moulding of senescence by natural selection. *Journal of Theoretical Biology* 12:12-45.

Hartung J. 1988. Deceiving down: Conjectures on the management of subordinate status. Pages 170-185 in *Self-Deception: An Adaptive Mechanism?* edited by J. S. Lockard and D. L. Paulhus. Englewood Cliffs (NJ): Prentice Hall.

Haslam C., Montrose V. T. 2015. Should have known better: The impact of mating experience and the desire for marriage upon attraction to the narcissistic personality. *Personality and Individual Differences* 82:188–192.

Hay D. F., Castle J., Davies L. 2000. Toddlers' use of force against familiar peers: A precursor of serious aggression? *Child Development* 71:457–467.

Hazzard W. R. 1990. The sex differential in longevity. Pages 37-47 in *Principles of Geriatric Medicine and Gerontology,* second edition, edited by W. Hazzard, R. Endres, E. Bierman and J. Blass. New York: McGraw Hill.

Helm H. W. Jr., Hall A., Bailey K. G. D. 2020. Generational gender differences in mate selection. *North American Journal of Psychology* 22 (1):111-123.

Herold, E. S., Milhausen R. R. 1999. Dating preferences of university women: An analysis of the nice guy stereotype. *Journal of Sex and Marital Therapy* 25(4):333-343.

Herodotus 1996. *The Histories*. New York: Penguin Books.

Hewlett B. S. 1988. Sexual selection and parental investment among Aka pygmies. Pages 263-276 in *Human Reproductive Behavior: A Darwinian Perspective*, edited by L. L. Betzig, M. Borgerhoff Mulder and P. Turke. Cambridge (UK): Cambridge University Press.

Hill A. K., Hunt J., Welling L. L. M., Cárdenas R. A., Rotella M. A., Wheatley J. R., Dawood K., Shriver M. D., Puts D. A. 2013. Quantifying the strength and form of sexual selection on men's traits. *Evolution and Human Behavior* 34:334–341.

Hill R. 1945. Campus values in mate selection. *Journal of Home Economics* 37:554-558.

Hinde R. A. 1978. Dominance and role — two concepts with dual meanings. *Journal of Social and Biological Structures* 1:27-38.

Hirschi T. 2017. *Causes of Delinquency*. Oxon (UK): Routledge.

Hirschi T., Gottfredson M. 1983. Age and the explanation of crime. *American Journal of Sociology* 89(3):552-584.

Hirschi T., Gottfredson M. 1985. Age and crime, logic and scholarship: comment on Greenberg. *American Journal of Sociology* 91:22-27.

Hrdy S. B. 1981. *The Woman that Never Evolved*. Cambridge (MA): Harvard University Press.

Hutt C. 1972. *Males and Females*. Harmondsworth, Middlesex: Penguin Books.

Hyde J. S. 2005. The gender similarities hypothesis. *American Psychologist* 60(6):581-592

Ickes W. 1993. Traditional gender roles: do they make, and then break, our relationships? *Journal of Social Issues* 49(3): 71-85.

Irons W. 1993. Monogamy, contraception and the cultural and reproductive success hypothesis. *Behavioral and Brain Sciences* 16:267-322.

Isenberg S. 2021. *Women Who Love Men Who Kill: 35 Stories of Prison Passion*. New York: Diversion Books.

Jensen-Campell L. A., Graziano W. G., West S. G. 1995. Dominance, prosocial orientation, and female preferences — Do nice guys really finish last? *Journal of Personality and Social Psychology* 68(3):427-440.

Kanazawa S. 2009. Evolutionary psychology and crime. Pages 90-110 in *Biosocial Criminology: New Directions in Theory and Research*, edited by A. Walsh and K. M. Beaver. New York: Routledge.

Kanazawa S., Still M. C. 2000. Why men commit crimes (and why they desist). *Sociological Theory* 18(3): 434-447.

Kaplan, Hillard, Hill, Kim, Lancaster, Jane and Hurtado, A. Magdalena (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology* 9, 156–185.

Kelsen H. 1957. *What is Justice? Justice, Law and Politics in the Mirror of Science: Collected Essays*. Berkeley (CA): University of California Press.

Kirkpatrick M. 1987. Sexual selection by female choice in polygynous animals. *Annual Review of Ecology and Systematics* 18:43–70.

Knestaut A.1996. Fewer women than men die of work-related injuries, data show. *Compensation and Working Conditions*, June 1996.

Knight G. P., Guthrie I. K., Page M. C., Fabes R. A. 2002. Emotional arousal and gender differences in aggression: a meta-analysis. *Aggressive Behavior* 28:366- 393.

Kordsmeyer T. L., Hunt J., Puts D. A., Ostnerd J., Penke L. 2018. The relative importance of intra- and intersexual selection on human male sexually dimorphic traits. *Evolution and Human Behavior* 39:424–436.

Kottler J. A. 2011. *The Lust for Blood: Why We Are Fascinated by Death, Murder, Horror, and Violence*. Amherst (MA): Prometheus Books.

Kraemer S. 2000. The fragile male. *British Medical Journal* 321(7276): 1609-1612.

Kruger D. J., Nesse R. M. 2006. An evolutionary life-history framework for understanding sex differences in human mortality rates. *Human Nature* 17(1):74-97.

Kummer H. 1982. Social knowledge in free-ranging primates. Pages 307-324 in *Animal Mind — Human Mind, Life Sciences Research Reports, volume 21*, edited by D. R. Griffin. Berlin: Springer.

Lahti D. C. 2013. Twelve (more) things about the evolution of morality make people nauseous. Pages 307-324 in *Human Social Evolution: The Foundational Works of Richard D. Alexander*, edited by K. Summers and B. Crespi. Oxford (UK): Oxford University Press.

Lassek W. D., Gaulin S. J. C. 2022. Substantial but misunderstood human sexual dimorphism results mainly from sexual selection on males and natural selection on females. *Frontiers in Psychology* 13:859931.

Lee R. B. 1984. *The Dobe !Kung*. New York: Holt, Rinehart and Winston.

Leigh E. G. Jr. 1977. How does selection reconcile individual advantage with the good of the group? *Proceedings of the National Academy of Sciences USA* 74(10): 4542-4546.

Lessells C. M. 1999. Sexual conflict in animals. Pages 75-99 in *Levels of Selection in Evolution*, edited by L. Keller. Princeton: Princeton University Press.

Lessells C. M. 2006. The evolutionary outcome of sexual conflict. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 361:301–317.

Lewis G., Sloggett A. 1998. Suicide, deprivation, and unemployment: record linkage study. *The BMJ* 317:1283–6.

Lewontin R. C. 1970. The units of selection. *Annual Review of Ecology and Systematics* 52:1-18.

Low B. S. 1988. Measures of polygyny in humans. *Current Anthropology* 29 (1):189-194.

Lukaszewski A. W., Roney J. R. 2010. Kind toward whom? Mate preferences for personality traits are target specific. *Evolution and Human Behavior* 31(1):29-38.

Lukpat A. 2022. Fertility doctor accused of using his own sperm is ordered to pay millions. *New York Times*, April 28, 2022.

Luy M. 2003. Causes of male excess mortality: insights from cloistered populations. *Population and Development Review* 29(4):647-676.

Macfarlane R. 2008. Women's Understanding of the Nice-Guy Paradox: A Phenomenological Study. Masters thesis, University of Johannesburg.

Machery E., Mallon R. 2010. Evolution of morality. Pages 3-46 in *The Moral Psychology Handbook*, edited by J. M. Doris. Oxford (UK): Oxford University Press.

Maris M. 1967. Suicide, status, and mobility in Chicago. *Social Forces* 46(2):246-256.

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

Maynard Smith J. 1964. Group selection and kin selection. *Nature* 201:1145-1147.

McDaniel A. K. 2005. Young women's dating behavior: Why/Why not date a nice guy? *Sex Roles* 53(5-6):347-359.

McGinnis R. 1958. Campus values in mate selection - a repeat study. *Social Forces* 35:368-373.

McKie R. 2018. Why Nobel prizes fail 21st-century science. *The Guardian*: September 30 2018. https://www.theguardian.com/science/2018/sep/30/nobel-prize-fails-modern-science

Mealey L. 2000. *Sex Differences: Development and Evolutionary Strategies*. San Diego: Academic Press.

Medawar P. B. 1955. The definition and measurement of senescence. *Ciba Foundation Colloquium on Aging* 1:4-15.

Meston C. M., Heiman J. R., Trapnell P. D., Paulhus D. L. 1998. Socially desirable responding and sexuality self-reports. *The Journal of Sex Research* 35(2):148-157.

Miller G. 2000. *The Mating Mind: How Sexual Choice Shaped the Evolution of Human Nature*. London: Doubleday.

Miller G. 2007. Sexual selection for moral virtues. *The Quarterly Review of Biology* 82(2): 97-125.

Miller G. 2008. Kindness, fidelity, and other sexually selected virtues. Pages 209-244 in *Moral Psychology, Volume 1: The Evolution of Morality: Adaptations and Innateness*, edited by W. Sinnott-Armstrong. Cambridge (MA): MIT Press.

Miller H. L., Rivenbark W. H. 1970. Sexual differences in physical attractiveness as a determinant of heterosexual liking. Psychological Reports 27(3):701-702.

Morgan D. 1986. *The Mongols*. Oxford (UK): B. Blackwell.

Mueller E., Short K. 1983. Effects of income and wealth on the demand for children. Pages 590-642 in *Determinants of Fertility in Developing Countries*, Vol. 1, edited by R. A. Bulatao and R. D. Lee. New York: Academic Press.

Nathanson C. A. 1990. The gender-mortality differential in developed countries: demographic and sociocultural dimensions. Pages 3-24 in *Gender, Health, and Longevity: Multidisciplinary Perspectives*, edited by M. G. Ory and H. R. Warner. New York: Springer Publishing Company.

Nesse R. M. 1990. Evolutionary explanations of emotions. *Human Nature* 1(3):261-289.

Nesse R. M. 2007. Runaway social selection for displays of partner value and altruism. *Biological Theory* 2(2):143–155

O'Donald P. 1967. A general model of sexual and natural selection. *Heredity* 22:499–518.

Ogas O., Gaddam S. 2011. *A Billion Wicked Thoughts: What the World's Largest Experiment Reveals About Human Desire*. New York: Dutton.

Okasha S. 2020. Biological altruism. From the Summer 2020 Edition of the *Stanford Encyclopedia of Philosophy*.

Omark D. R., Omark M., Edelman M. 1975. Formation of dominance hierarchies in young children. Pages 289-316 in *Psychological Anthropology*, edited by T. Williams. The Hague: Mouton.

Orr C. 2018. Yet another reason the new 'popular film 'Oscar is a terrible idea. *The Atlantic*: August 11, 2018. https://www.theatlantic.com/entertainment/archive/2018/08/yet-another-reason-the-new-popular-film-oscar-is-a-terrible-idea/567257/

Palmer C. T., Tilley C. F. 1995. Sexual access to females as a motivation for joining gangs: An evolutionary approach. *Journal of Sex Research* 32(3):213-217.

Parker G. A. 1979. Sexual selection and sexual conflict. Pages 123-166 in *Sexual Selection and Reproductive Competition in Insects,* edited by M. S. Blum and N. A. Blum. New York: Academic Press.

Parker G. A. 2006. Sexual conflict over mating and fertilization: an overview. *Philosophical Transactions of the Royal Society of London*. *Series B, Biological Sciences* 361:235–259.

Parker R. J. 2015. *Serial Killer Groupies*. United States of America: RJ Parker Publishing, Inc.

Paul A. 2002. Sexual selection and mate choice. *International Journal of Primatology* 23(4):877-904.

Perry R. B. 1954. *Realms of Value: A Critique of Human Civilization*. Cambridge (MA): Harvard University Press.

Pérusse D. 1993. Cultural and reproductive success in industrial societies: Testing the relationship at the proximate and ultimate levels. *Behavioral and Brain Sciences* 16(2):267-322.

Pomiankowski A., Iwasa Y., Nee S. 1991. The evolution of costly mate preferences. 1. Fisher and biased mutation. *Evolution* 45:1422–1430.

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

Potts M., Selman P. 1979. *Society and Fertility*. Estover (UK): Macdonald and Evans.

Pound, R. 1941. *My Philosophy of Law. Credos of Sixteen American Scholars*. Boston:Boston Law Book Co.

Power E. 1975. The lady. Pages 35-52 in *Medieval Women*, edited by M. M. Postman. Cambridge (UK): Cambridge University Press.

Price T., Schluter D., Heckman N. E. 1993. Sexual selection when the female directly benefits. *Biological Journal of the Linnean Society* 48:187-211.

Promislow D. 2003. Mate choice, sexual conflict, and evolution of senescence. *Behavior Genetics* 33(2):191-201.

Provost M. P., Troje N. F., Quinsey V. L. 2008. Short-term mating strategies and attraction to masculinity in point-light walkers. *Evolution and Human Behavior* 29:65-69.

Puigvert L. 2015-16. *Free Teen Desire* Project. Marie Sklodowska-Curie, EU Horizon 2020 Research and Innovation Programme. Grant agreement No. 659299.

Puigvert L., Gelsthorpe L., Soler-Gallart M., Flecha R. 2019. Girls 'perceptions of boys with violent attitudes and behaviours, and of sexual attraction. *Palgrave Communications* 5:56.

Puts D. 2010. Beauty and the beast: mechanisms of sexual selection in humans. *Evolution and Human Behavior* 31:157–175.

Puts D. 2016. Human sexual selection. *Current Opinion in Psychology* 7:28–32.

Qureshi C., Harris E., Atkinson B. E. 2016. Relationships between age of females and attraction to the Dark Triad personality. *Personality and Individual Differences* 95:200–203.

Radway J. A. 1984. *Reading the Romance: Women, Patriarchy, and Popular Literature*. Chapel Hill (NC): The University of North Carolina Press.

Ramis M., Alonso M. J., Siles G. 2013. Communicative methodology of research in the preventive socialization of gender violence. *International Review of Qualitative Research* 6(2): 266- 276.

Rebellon C. J., Manasse M. 2004. Do "bad boys" really get the girls? Delinquency as a cause and consequence of dating behavior among adolescents. *Justice Quarterly* 21:2:355-389.

Reise S. P., Wright T. M. 1996. Personality traits, cluster B personality disorders, and sociosexuality. *Journal of Research in Personality* 30(1):128-136.

Renninger L. A., Wade T. J., Grammer K. 2004. Getting that female glance: Patterns and consequences of male nonverbal behavior in courtship contexts. *Evolution and Human Behavior* 25(6): 416-431.

Rice W. R. 1984. Sex chromosomes and the evolution of sexual dimorphism. *Evolution* 38(4):735–742.

Richards R. 1986. A defense of evolutionary ethic. *Biology and Philosophy* 1:265-93.

Rosenthal G. G. 2017. *Mate Choice: The Evolution of Sexual Decision Making from Microbes To Humans*. Princeton: Princeton University Press.

Rowe D. C. 1996. An adaptive strategy theory of crime. Pages 268-314 in *Delinquency and Crime: Current Theories,* edited by J. David Hawkins. Cambridge (UK): Cambridge University Press.

Rowe D. C. 2002. *Biology and Crime*. Los Angeles: Roxbury Publishing Company.

Ruiz-Eugenio L., Racionero-Plaza S., Duque E., Puigvert L. 2020. Female university students ' preferences for different types of sexual relationships: implications for gender-based violence prevention programs and policies. *BMC Women's Health* 20:266.

Sadalla E. K., Kenrick D. T., Vershure B. 1987. Dominance and heterosexual attraction. *Journal of Personality and Social Psychology* 52(4): 730-738.

Savin-Williams R. C. 1987. *Adolescence: An Ethological Perspective*. Springer-Verlag: New York.

Scelza B. A. 2011. Female choice and extra-pair paternity in a traditional human population. *Biology Letters* 7:889–891.

Scelza B. A. 2013. Choosy but not chaste: multiple mating in human females. *Evolutionary Anthropology* 22:259–269.

Setchell J. M. 2016. Sexual selection and the differences between the sexes in Mandrills (Mandrillus sphinx). *American Journal of Physical Anthropology* 159:105-129.

Shackelford T. K., Schmitt D. P., Buss D. M. 2005. Universal dimensions of human mate preferences. *Personality and Individual Differences* 39(2):447-458.

Shafer J. 2015. The Pulitzer Prize scam. *Politico*: April 20, 2015. https://www.politico.com/magazine/story/2015/04/2015-pulitzer-prizes-jack-shafer-column-117151/

Simpson J. A. 1993. Male reproductive success as a function of social status: Some unanswered evolutionary questions. *Behavioral and Brain Sciences* 16(2):306.

Singer P. 2011. *Practical Ethics.* Third edition. Cambridge (UK): Cambridge University Press.

Singer, P. 1999. *A Darwinian Left*. New Haven (CT): Yale University Press.

Small M. F. 1993. *Female Choices: Sexual Behavior of Female Primates*. Ithaca (NY): Cornell University Press.

Smart J. J. C. 1973. An outline of a system of utilitarian ethics. Pages 3-74 in *Utilitarianism: For and Against*, edited by J. J. C. Smart and Bernard Williams. Cambridge (UK): Cambridge University Press.

Smith D. S., Hindus M. S. 1975. Premarital pregnancy in America 1640-1971: An overview and interpretation. *The Journal of Interdisciplinary History* 5(4):537-570.

Smith P. K., Boulton M. 1990. Rough-and-tumble play, aggression and dominance: perception and behaviour in children's encounters. *Human Development* 33(4/5):271-282.

Smuts B. B. 1987. Sexual competition and mate choice. Pages 385-399 in *Primate Societies*, edited by B. B. Smuts. Chicago: University of Chicago Press.

Smuts B. B. 1992. Male aggression against women: an evolutionary perspective. *Human Nature* 3:1-44.

Sprecher S. 1989. The importance to males and females of physical attractiveness, earning potential, and expressiveness in initial attraction. *Sex Roles* 21:591–607.

Stanyon R., Bignoni F. 2014. Sexual selection and the evolution of behavior, morphology, neuroanatomy and genes in humans and other primates. *Neuroscience and Biobehavioral Reviews* 46:579–590.

Stearns S. C. 1989. Trade-offs in life-history evolution. *Functional Ecology* 3(3):259-268.

Steffensmeier D. J., Allan E. A. Harer M. D., Streifel C. 1989. Age and the distribution of crime. *American Journal of Sociology* 94: 803-831.

Stockley P., Bro-Jorgensen J. 2011. Female competition and its evolutionary consequences in mammals. *Biological Reviews* 86:341–366.

Stone V. E. 1990. *Perception of Status: An Evolutionary Analysis of Nonverbal Status Cues*. Doctoral dissertation, Stanford University.

Street S. 2006. A Darwinian dilemma for realist theories of value. *Philosophical Studies* 127:109-166.

Street S. 2008. Reply to Copp: naturalism, normativity, and the varieties of realism worth worrying about. *Philosophical Issues* 18:207-228.

Stumpf R. M., Boesch C. 2006. The efficacy of female choice in chimpanzees of the Taï Forest, Côte d'Ivoire. *Behavioral Ecology and Sociobiology* 60:749–765.

Stumpf R. M., Boesch C. 2010. Male aggression and sexual coercion in wild West African chimpanzees, *Pan troglodytes verus*. *Animal Behaviour* 79(2):333–342.

Surbeck M., Langergraber K. E., Fruth B., Vigilant L., Hohmann G. 2017. Male reproductive skew is higher in bonobos than chimpanzees. *Current Biology* 27(13):R640–R641.

Sutherland E. H., Cressey D. R., Luckenbill D. 1992. *Principles of Criminology*. Dix Hills (NY): General Hall.

Symons D. 1979. *The Evolution of Human Sexuality*. Oxford: Oxford University Press.

Symons D. 1992. On the use and misuse of Darwinism in the study of human behavior. Pages 137-162 in *The Adapted Mind: Evolutionary Psychology and the Generation of Culture,* edited by J. H. Barkow, L. Cosmides, J. Tooby. New York: Oxford University Press.

Tabutin D. 1978. La surmortalité féminine en Europe avant 1940. *Population* 33(1):121-148.

Tomasello M. 2016. *A Natural History of Human Morality*. Cambridge (MA): Harvard University Press.

Tooby J., Cosmides L. 1990. The past explains the present: emotional adaptations and the structure of ancestral environments. *Ethology and Sociobiology* 11:375-424.

Townsend J. M. 1987. Sex differences in sexuality among medical students: effects of increasing socioeconomic status. *Archives of Sexual Behavior* 16:425-441.

Townsend J. M., Levy G. D. 1990. Effects of potential partners' physical attractiveness and socioeconomic status on sexuality and partner selection. *Archives of Sexual Behavior* 19(2):149-164.

Trapnell P. D., Meston C. M. 1996. Sex and the big five: nice guys finish last. Poster presented at the 104th Annual Convention of the American Psychological Association, Toronto, ON, Canada.

Tremblay R. E., Japel C., Pérusse D., Mcduff P., Boivin M., Zoccolillo M., Montplaisir J. 1999. The search for the age of 'onset' of physical aggression: Rousseau and Bandura revisted. *Criminal Behavior and Mental Health* 9:8–23.

Trivers R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35-57.

Trivers R. L. 1972. Parental investment and sexual selection. Pages 136–179 in *Sexual Selection and the Descent of Man 1871–1971*, edited by B. G. Campbell. Chicago (IL): Aldine Publishing Company.

Trivers R. L. 1974. Parent-offspring conflict. *Integrative and comparative biology* 14(1):249-264.

Trivers R. L. 1985. *Social Evolution*. Menlo Park (CA): Benjamin/Cummings.

Urbaniak, G. C., Kilmann P. R. 2006. Niceness and dating success: A further test of the Nice Guy stereotype. *Sex Roles* 55:209–224.

Valls R., Puigvert L., Duque E. 2008. Gender violence among teenagers: socialization and prevention. *Violence Against Women*14(7):759-785.

Vining D. R. 1986. Social versus reproductive success: The central theoretical problem of human sociobiology. *The Behavioral and Brain Sciences* 9(1):167-187.

Vlerick M. 2017. Better than our nature? Evolution and moral realism, justification and progress. Pages 226-239 in *The Cambridge Handbook of Evolutionary Ethics*, edited by M. Ruse and R. J. Richards. Cambridge (UK): Cambridge University Press.

Volk A. A., Dane A. V., Marinit Z. A., Vaillancourt T. 2015. Adolescent bullying, dating, and mating: testing an evolutionary hypothesis. *Evolutionary Psychology* 13(4):1–11.

Von Rueden C., Gurven M., Kaplan H. 2011. Why do men seek status? Fitness payoffs to dominance and prestige. *Proceedings of the Royal Society B* 278:2223–2232.

Vronsky P. 2018. *Sons of Cain: A History of Serial Killers from the Stone Age to the Present*. New York: Berkley.

Walsh A. 2009. *Biology and Criminology: The Biosocial Synthesis.* Routledge Advances in Criminology, volume 7. New York: Routledge.

Walter, K. V. et al. 2020. Sex differences in mate preferences across 45 countries: a large-scale replication. *Psychological Science* 31(4):408-423.

Walters J. R., Seyfarth R. M. 1987. Conflict and cooperation. Pages 306-317 in *Primate Societies,* edited by B. B. Smuts. Chicago: University of Chicago Press.

Walther A. et al. 2023. Status loss due to COVID-19, traditional masculinity, and their association with recent suicide attempts and suicidal ideation. *Psychology of Men & Masculinities* 24(1):47–62.

Warnock G. J. 1971. *The Object of Morality*. London: Methuen & Company Limited.

Weisfeld G. 1994. Aggression and dominance in the social world of boys. Pages 42-69 in *Male Violence,* edited by J. Archer. London: Routledge.

West D. J., Farrington D. P., Gundry G., Knight B. J., Osborn S. G. 1977. *The Delinquent Way of Life: Third Report of the Cambridge Study in Delinquent Development*. London: Heinemann.

West-Eberhard M. J. 1983. Sexual selection, social competition, and speciation. *Quarterly Review of Biology* 58(2):155–183.

Wiederman M. W., Dubois S. L. 1998. Evolution and sex differences in preferences for short-term mates: Results from a policy capturing study. *Evolution and Human Behavior* 19:153–170.

Wiessner, P. 2009. Parent-offspring conflict in marriage: Implications for social evolution and material culture among the Ju/'hoansi bushmen. Pages 251-264 in *Pattern and Process in Cultural Evolution*, edited by S. Shennan. Berkely (CA): University of California Press.

Wilder J. A., Mobasher Z., Hammer M. F. 2004. Genetic evidence for unequal effective population sizes of human females and males. *Molecular Biology and Evolution* 21(11):2047-2057.

Wiley R. H., Poston J. 1996. Indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution* 50:1371–1381.

Williams G. C. 1957. Pleiotropy, natural selection, and the evolution of senescence. *Evolution* 11(4):398-411.

Williams G. C. 1966. *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton (NJ): Princeton University Press.

Williams G. C. 1975. *Sex and Evolution*. Princeton (NJ): Princeton University Press.

Williams G. C. 1988. Huxley's evolution and ethics in sociobiological perspective. *Zygon* 23(4):383-407.

Williams G. C. 1985. In defense of reductionism in evolution. *Oxford Surveys in Biology* 2:1-27.

Wilson A. J., Pilkington J. G., Pemberton J. M., Coltman D. W., Overall A. D. J., Byrne K. A., Kruuk L. E. B. 2005. Selection on mothers and offspring: Whose phenotype is it and does it matter? *Evolution* 59(2):451-463.

Wilson C. 2018. Evolution and ethics: an overview. Pages 295-308 in *The Routledge Handbook of Evolution and Philosophy*, edited by R. Joyce. New York: Routledge.

Wilson, M. 1993. What is the adaptation: Status striving, status itself or parental teaching biases?

Behavioral and Brain Sciences 16(2), 311-311.

Wilson M., Daly M. 1985. Competitiveness, risk taking, and violence: the young male syndrome. *Ethology and Sociobiology* 6:59-73.

Wilson, M. L., Miller C. M., Crouse K. N. 2017. Humans as a model species for sexual selection research. *Proceedings of the Royal Society B* 284(1866):20171320.

Wolfgang M. E. 1958. *Patterns in Criminal Homicide*. Philadelphia: University of Pennsylvania Press.

Wood W., Eagly A. H. 2002. A cross-cultural analysis of the behavior of women and men: implications for the origins of sex differences. *Psychological Bulletin* 128(5):699–727.

Wright R. 1994. *The Moral Animal*. New York: Random House.

Wrong, D. H. 1958. Trends in class fertility in western nations. *The Canadian Journal of Economics and Political Science* 24(2):216-229.

Zerjal T., Xue Y., Bertorelle G., Wells R. S., Bao W., Zhu S. et al. 2003. The genetic legacy of the Mongols. *American Journal of Human Genetics* 72:717-721.

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

Zohar A., Guttman R. 1989. Mate preference is not mate selection. *Behavioral and Brain Sciences* 12(1):38-39.

Zuckerman M. 1979. *Sensation Seeking: Beyond the Optimal Level of Arousal*. Hillsdale (NJ): Erlbaum.

Zuk M. 2002. *Sexual Selections: What We Can and Can't Learn about Sex from Animals*. Berkeley (CA): University of California Press.