Citation: Gorelik, G. (2021). Domains of female choice in human evolution. *Evolutionary Behavioral Sciences*.

Domains of Female Choice in Human Evolution

Gregory Gorelik

Cedar Park, TX

Abstract

The present article advances the view that women's mate preferences can be grouped into at least two overarching domains: competitiveness and fatherhood. Theoretical and empirical considerations suggest that female mate preferences evolve in contexts of male competitiveness and often amplify the effects of male-male competition. Evidence for the importance of male-male competition and female choice for competitiveness in humans is reviewed. Evidence is likewise offered for the importance of human fatherhood as an additional domain of female choice outside of male competitiveness. Implications of more inclusive mate preferences for the evolution of cognitive architecture are discussed.

Keywords: sexual selection, female choice, male-male competition, fatherhood, paternal investment

Summary Statement

Researchers in evolutionary psychology typically believe that people evolved numerous and specific mate preferences. Instead, I make the case that most mate preferences can be grouped into a few overarching domains. I discuss women's preferences for men's competitiveness and fatherhood as two examples of such overarching domains.

Domains of Female Choice in Human Evolution

In the current article, I reassess the psychological level at which women's mate preferences have been designed by sexual selection. Early advances in evolutionary psychology gave rise to ongoing debates and controversies that stem from an unnecessary focus on overly specific traits and preferences in the study of human mating (see, e.g., Chawla, 2017). This granular focus may have been partly responsible for some lack of generalization across ecological and cultural contexts and occasional replication failures (Lehmann & Calin-Jageman, 2017; see also Penton-Voak, Jacobson, & Trivers, 2004, for evidence of pathogen prevalence increasing women's preference for masculine faces and evidence from Marcinkowska et al., 2019, showing the opposite effect). The study of female choice in humans would benefit from a focus on a limited set of overarching preferences that subsume more specific preferences that are less stable due to their dependence on unique ecological, cultural, and individual contexts. I focus on male competitiveness and fatherhood as two such overarching preferences. Although it is possible for more specific preferences to evolve, it is likely that a research focus on more inclusive preferences is more parsimonious and will lead to more fruitful explorations of the evolved human mind.

The Dual Role of Most Sexually Selected Traits

Sexual selection encompasses two mechanisms: intrasexual competition and intersexual selection. Among humans, as among most mammals, intrasexual competition is most frequent and intense between males (male-male competition) whereas intersexual selection is marked by more discerning mate choice by females (female choice). Both mechanisms were proposed by Darwin and continue to inform our understanding of evolutionary processes and trends.

Nevertheless, the extent to which each mechanism has left its mark on extant species, including humans, is debated.

Traits and behaviors under sexual selection often show no clear sign of whether their evolutionary origin and maintenance is predominantly due to intrasexual competition or mate choice. Darwin noticed such functional ambiguity with respect to the intricately branched antlers and curved horns of male deer and antelopes and speculated that “if ... the horns, like the splendid accoutrements of the knights of old, add to the noble appearance of stags and antelopes, they may have been modified partly for this purpose, though mainly for actual service in battle” (Darwin, 2006/1871, p. 1164). Evolutionary scholars since Darwin have likewise commented on the dual roles served by most sexually selected traits. Berglund and colleagues (1996), for example, surveyed a collection of studies on multiple types of sexually selected signals, including visual, acoustic, chemical, and electric, among almost 50 different species of insects, fish, amphibians, reptiles, birds, and mammals. Most of the signals, they found, serve a dual competition and mate choice function. And when a signal serves a single sexually selected function, it is usually associated with competition (only two out of the 48 species surveyed brandished signals that served solely as mate choice ornaments).

Berglund and colleagues (1996) suggest that male-male competition selects for armaments and threat displays that are particularly hard to fake in that their function is tested in actual combat. And it is not that female choice plays no role in the evolution of such traits. Rather, females use the outcomes of male-male competition as cues to efficiently select prospective mates. Per Berglund and colleagues:

Given that males already possess conspicuous, honest, quality-signalling traits used in male-male competition, what would prevent females from exploiting this existing source

of information rather than selecting arbitrary or other traits? Parsimonious females that directly utilize a reliable source of information are bound to benefit compared to females that use other or no cues in their choice process... (p. 393)

Berglund and colleagues suggest that sexually selected traits evolve initially under male-male competition and are subsequently elaborated by female choice (though never in the direction of sabotaging the trait's initial competitive function). Trivers (1972) made a similar observation in his landmark paper on parental investment:

Reproductive success, independent of ability to survive is easier for the female to gauge because she can directly observe differences in reproductive success before she chooses ... Female choice then greatly augments the effects of male-male competition. (p. 169)

In the current article, I argue that female choice in humans is likewise mostly dictated by the constraints of male-male competition and provide evidence to support this contention. This does not mean that female choice is unimportant or is somehow obstructed by male-male competition. It does mean, however, that female choice is more subtle and opportunistic than is suggested by simpler accounts that depict it as reflecting decisions without the influence of male competitiveness. Nevertheless, there are probably domains of female choice for male traits and behaviors that may be orthogonal to, or somewhat divorced from, male-male competition. In the current article, I discuss the role of human fatherhood as one example.

The Importance of Male-Male Competition in Human Evolution

Male-male competition has been a potent force in human evolution. There are at least five lines of evidence supporting this claim:

1. Human sexual dimorphism.
2. Men's competitiveness in modern and traditional societies.

3. Genetic evidence.
4. Evidence from phylogenetic/comparative studies.
5. Evidence from psychophysiological function.

Evidence from Sexual Dimorphism

Sexual dimorphism refers to all physical, behavioral, and psychological differences between males and females. In humans, men are typically taller, physically stronger, and more behaviorally competitive than women (Balish, Deaner, Rainham, & Blanchard, 2016; Lippa, 2009; von Rueden, Alami, Kaplan, & Gurven, 2018). In 1996, the average human height around the globe was 171.28 cm for men and 159.49 cm for women (Roser, Appel, & Ritchie, 2013). This sex difference in height has been consistently maintained since the beginning of data collection, even as the average height of both sexes increased into the 20th century. An additional difference, and one that is particularly relevant to male-male competition, is found in muscle mass and bone density. Men have higher levels of lean muscle mass and bone density in their arms than women (i.e., women's lean muscle mass is ~91% of men's and women's bone density is ~83% of men's; Nindl, Scoville, Sheehan, Leone, & Mello, 2002), which is what would be expected if men's evolution depended on physical struggles over reproductive opportunities with other men. Sexual dimorphism in human psychological traits is likewise evident from surveys showing greater competitiveness and interest in competitive milieus (e.g., individual and group sports) among men than among women (competitiveness marginal effects for women range from -0.26 to -.14; OR = 1.98 for men citing competitiveness as their primary reason to play sports or games; Buser, Niederle, & Oosterbeek, 2014; Balish, Deaner, & Rainham, 2016). Furthermore, sex differences in competitive interests and behavior are evident even in childhood, with boys engaging in roughhousing and non-violent aggressive play to a greater extent than girls

(LaFreniere, 2011). Girls, on the other hand, are more likely to exhibit indirect, or relational aggression (e.g., social exclusion of disliked peers), than boys (Kraft & Mayeux, 2018).

Evidence from Modern and Traditional Societies

In modern societies, evidence for greater levels of male-male (vs. female-female) competition comes from the rates of violent criminality among men. Men comprise more than 90% of all perpetrators and 80% of all victims of homicide worldwide (UNODC, 2019). Men also comprise 94% of all convicts serving prison sentences for violent crime. This pattern is consistent across widely differing ecological and cultural contexts, and likely represents a greater biological propensity for reproductive aggressiveness among men. This sex difference in proneness to violent competition is mirrored in traditional hunter-gatherer and horticultural societies, where men are overwhelmingly more likely to be the instigators of violent individual and group conflict. Indeed, observations of traditional societies from the Amazon (e.g., Yanomamö, Ache) to the highlands of New Guinea and the Australian outback reveal that (1) violent conflict between individual men and between all-male rival coalitions is common and (2) the single greatest motivation for such conflict is access to women (Chagnon, 2013, pp. 214-278; Fortune, 1939; Henrich, 2020, p. 60; Hill & Hurtado, 2017, pp. 46-47).

Evidence from Genetics

Genetic evidence suggests greater evolutionary and historical rates of competition among men than among women (though some of this evidence may be indicative of mate choice and other mechanisms). All men inherit a Y-chromosome from their fathers. Because the Y-chromosome is transmitted from father to son, it is possible to examine its genetic variability to answer questions about men's evolution. One set of findings that is relevant to the present discussion shows that the Y-chromosome is much smaller than other chromosomes and is less

genetically diverse than mitochondrial DNA—i.e., the cellular mechanism of energy production whose genetic record is inherited from the mother (Gusmão, Brión, & Gomes, 2008; Kayser et al., 2003; Sayres, Lohmueller, & Nielsen, 2014). These findings suggest that fewer men than women contributed to the human gene pool—that is, some ancestral men mated with multiple women whereas other men did not mate at all. However, greater Y-chromosome homogeneity may be evidence of either ancestral male-male competition or female choice, as both mechanisms exclude some males from reproduction.

Genetic evidence from more recent human history suggests that male-male competition may be a likely cause of lower Y-chromosome genetic diversity. The genetic record suggests that some men were able to sire more offspring than other men throughout periods of intense male violence and subjugation. A genetic sequence on the Y-chromosome of 8% of Asian men, for example, can be traced to the 13th-century conquests of Genghis Khan and his sons (Derenko et al., 2007). Similarly, 21.5% of northwest Irish and 16.7% of west-central Scottish men carry the Y-chromosome signature of the late antiquity Irish warlord “Niall of the Nine Hostages” (Moore, McEvoy, Cape, Simms, & Bradley, 2006). Admittedly, ancestral claims can be debated and, again, the mechanisms of selection may include those that are not competition-based. A more recent genome-wide association study, for example, found that men’s, but not women’s, propensity for childlessness was higher in the presence of harmful autosomal mutations (Gardner et al., 2020). These mutations were correlated with lower intelligence and higher incidence of mental illness, and their association with childlessness remained when physiological explanations (e.g., infertility) were ruled out. This led the authors to suggest that the mutations are lowering men’s fertility via their effects on men’s behavior—specifically, behavior that is under women’s mate choice. To support this explanation, the

authors reported an association between mutation load and not having a romantic partner at the time of data sampling. Nevertheless, it can be argued that lower intelligence and mental illness can reduce a man's competitive ability, and so the obstructive effects of these mutations on men's reproductive success may be mediated by competitive failure.

Evidence from Phylogenetic/Comparative Studies

Another line of evidence for the importance of male-male competition in human sexual selection comes from comparative studies of humans and other animals, particularly other primates. In virtually all species marked by greater female investment in reproduction (including, though not limited to, the production of high-nutrient gametes, costly and risky gestation and childbirth, energy- and mobility-limiting lactation, and the overwhelming burdens of caregiving and childrearing), males must compete for access to mates (Trivers, 1972). Competition, in turn, leads to the emergence of sex differences. At the extreme, the sex difference reaches as high as a quadrupling of the weight of male elephant seal bulls relative to female cows (Stoffel et al., 2020). Such sex differences are best explained by intense male-male competition as the primary influence on reproduction, as only the biggest and strongest males can defeat their reproductive rivals and sire the next generation of males. The direct influence of male-male competition on reproductive outcomes in elephant seals does not exclude female choice, however. Indeed, both mechanisms often work in tandem, as when females instigate brawls between males and subsequently mate with the winner (Cox & Le Boeuf, 1977).

Among the great apes, males are often larger, stronger, and more aggressive than females (De Waal & Hoekstra, 1980; Thompson et al., 2020; Watts, Muller, Amsler, Mbabazi, & Mitani, 2006; Zihlman, Stahl, & Boesch, 2008). Adult male orangutans possess enlarged cheek flanges and are larger than females and subadult males (Fox, 2002; Mitani, Gros-Louis, & Richards,

1996). Male gorillas are likewise much bigger and are twice the weight of female gorillas (Taylor, 1997). This is to be expected as typically the strongest, largest, and most crested male gorillas can monopolize access to a group of females (Caillaud, Levréro, Gatti, Menard, & Raymond, 2008). Both male-male competition and female choice are important mechanisms of sexual selection among gorillas, where females favor dominant males with access to feeding territories who are capable of protecting them and their offspring (Caillaud, Levréro, Gatti, Menard, & Raymond, 2008; Jeffery, Abernethy, Tutin, Anthony, & Bruford, 2007). Among our closest relatives, the chimpanzees, males are more likely to engage in direct aggression and dominance displays—especially in the presence of estrous females—and often engage in coalitional aggression against neighboring groups (Muller, 2002; Watts, Muller, Amsler, Mbabazi, & Mitani, 2006; Wrangham & Peterson, 1996). Even among the more peaceful and female-dominated bonobos, dominance rank is correlated with male reproductive success (Gerloff, Harung, Fruth, Hohmann, & Tautz, 1999) to an even greater extent than among the relatively more chauvinistic chimpanzees (though this may be due to female choice as much as to male-male competition; Surbeck, Langergraber, Fruth, Vigilant, & Hohmann, 2017). Among all great apes, including humans, males have larger skulls and the sex difference in human skull size exceeds even that of chimpanzees and bonobos (Schaefer, Mitteroecker, Gunz, Bernhard, & Bookstein, 2004). Together with the previously discussed evidence for greater size, strength, and aggressiveness among men, the overwhelming conclusion is that our species is not an exception to the primate pattern of frequent male-male competition.

Evidence from Psychophysiological Function

The psychophysiological effects of competition on men offer an additional line of evidence for the role of male-male competition in human evolution. What distinguishes this

category of evidence from the preceding categories is that, in addition to furnishing evidence for the pervasiveness of male-male competition in humans, it speaks to its adaptive function. Specifically, the role of testosterone in men's competitive behavior corresponds with evolutionary considerations and, likewise, comports with predictions derived from animals as diverse as cichlid fish, anolis lizards, and seasonal birds (Hattori & Wilczynski, 2014; Parikh, Clement, & Fernald, 2006; White, Nguyen, & Fernald, 2002; Wingfield, Hegner, Dufty Jr, & Ball, 1990). According to the challenge hypothesis (Wingfield et al., 1990), males are expected to upregulate their levels of testosterone in anticipation of reproductive contests with other males. In addition to its role in the development of male primary and secondary sexual anatomy, testosterone motivates male competitiveness specifically in contexts of male-male competition over direct access to females or to feeding territories where females congregate. Wingfield and colleagues' study of the phenomenon revealed that testosterone had no effect on male birds' overall aggression—increases in testosterone did not co-occur with aggressive encounters outside of the breeding season. Rather, testosterone's role in male aggression was limited to dominance contests with reproductive competitors. Related inquiry into the "winner effect" showed that male winners are more likely to experience a testosterone boost than male losers and that this boost increases the probability of winning again (or motivates further competitiveness as a functional response to the winner's demonstrable dominance) (Fuxjager, Oyegbile, & Marler, 2011; Mesterson-Gibbons, 1999; though see Dijkstra, Schaafsma, Hofmann, & Groothuis, 2012, for evidence of a link between androgens and competitiveness regardless of winning status).

Research on the winner effect in humans confirms its presence in competitive contexts ranging from sports to board games to randomly assigned computer game outcomes (Booth, Shelley, Mazur, Tharp, & Kittok, 1989; Carré, Campbell, Lozoya, Goetz, & Welker, 2013;

Gladue, Boechler, & McCaul, 1989; Mazur, Booth, & Dabbs Jr, 1992). Even vicarious competitive outcomes experienced by sports fans and voters in an election are associated with testosterone changes (Bernhardt, Dabbs, Fielden, & Lutter, 1998; Stanton, Beehner, Saini, Kuhn, & LaBar, 2009; though see Burk, Mayer, & Wiese, 2019, for evidence of outcome-neutral testosterone increases during vicarious competition). The winner effect is somewhat misnamed, however, in that it is not winning *per se* that precedes a testosterone boost; rather, showcasing dominance over potential reproductive rivals seems to be the main cause. Being a mediocre player on a winning basketball team, for example, may not lead to a testosterone increase (Gonzalez-Bono, Salvador, Serrano, & Ricarte, 1999). That the winner effect is primarily active in men's competitive contexts is suggested by the findings of a meta-analysis showing weak winner effects in women (Geniole, Bird, Ruddick, & Carré, 2017). Although testosterone's hypothesized role in motivating men to not quit competing when they are ahead seems to be the primary driver of the winner effect, research on the effect of winning on men's sexual interest suggests that testosterone may likewise be upregulating men's sex drive in anticipation of greater reproductive opportunities (Gorelik & Bjorklund, 2015; Markey & Markey, 2011; Markey & Markey, 2010). Additional research is needed to clarify whether winners do experience an increase in reproductive opportunities and, if so, whether the increase results from the effect of winning on intimidating rivals or increased attractiveness to potential mates. It is also possible that the effects of competition on rivals and prospective mates co-occur.

Women's Mate Choice Amplifies Men's Competitiveness

Since the latter years of the 20th-century, women's mate choice has been a focal area of investigation within the field of evolutionary psychology. Foundational research by Buss and colleagues (e.g., Buss, 1989; Buss et al., 1990; Shackelford, Schmitt, & Buss, 2005) revealed

that women value socioeconomic status, education, and other traits associated with social dominance in romantic partners, whereas men value physical attractiveness (this sex difference in mate preferences has now been replicated in a sample of more than 14,000 participants from 45 countries—Walter et al., 2020). Subsequent research added physical strength and the bodily components associated with it, such as upper-body musculature, to the growing list of women's preferences for men's competitiveness (Garza, Pazhoohi, & Byrd-Craven, 2021; Gallup & Fink, 2018; Sell, Lukazsweski, & Townsley, 2017). This is not to say that women do not value attractiveness, but they do not put as high a premium on good looks as men do when choosing mates.

Women's unique mate preferences evolved because they allowed ancestral women to maximize access to resources for themselves and their dependent offspring (Bjorklund & Shackelford, 1999). Humans, like other slowly developing mammals such as elephants and whales, rely on parental care for childhood survival. Humans, in particular, require an extended juvenile period for the development of cognitive abilities necessary for social and cultural living—abilities that are reflected in the human brain's much greater size relative to that of even other large-brained primates (Kaplan, 1997; Scalise Sugiyama, 2011). Because women's physiology sets a limit on their expected maximum number of offspring, their reproductive success is best served by investing heavily in only a few children rather than in conceiving as often as possible. This makes the availability of resources for investment a limiting factor. Under such selection pressures, women evolved to prefer mates who have the ability and are willing to provide them with resources. Access to resources for men necessitated competition over resources with other men, which, in turn, led to the evolution of male competitive traits such as aggressiveness, industriousness, and ambition.

But the need to acquire resources was probably not the only evolutionary origin of male competitiveness. Male competitiveness itself, aside from whatever resources the male might provide to a mate and her offspring, likely signals physical and genetic health (in line with handicap and other “good genes” models; Candolin, 2000; Hodges-Simeon, Gurven, & Gaulin, 2015). A mate preference for competitiveness may likewise evolve in an environment in which most members of the population already prefer competitiveness in a mate (in line with Fisherian runaway and “sexy son” models of mate choice; Prokop, Michalczyk, Drobnik, Herdegen, & Radwan, 2012). It would therefore sometimes benefit a woman to mate with a successful competitor even if he is likely to desert her following conception. It must be said, of course, that much of human reproductive behavior is sensitive to ecological and demographic factors. For example, whereas it might serve a woman’s reproductive interests to mate with a man who is unable or unwilling to provide her with resources in an environment where resources can be easily obtained elsewhere, a woman living in a scarce environment might better serve her reproductive interests by securing a dependable supply of resources from her mate. Similarly, in an environment in which the sex ratio is skewed toward men, a woman is in a better position to demand resources from prospective mates in exchange for sexual access (Schmitt, 2005). But no matter whether a woman is mating for the short- or long-term, or whether she is directly seeking resources from her mate, women’s preference for motivational and skilled competitiveness is a mate-preference category that subsumes more specific preferences for traits and qualities such as education or income. Addressing the importance of men’s underlying competitiveness over more superficial markers of status, Jonason, Li, and Madson (2012), for example, showed that women prefer short- and long-term mates who had earned their income over those who had inherited it, embezzled it, or acquired it by chance.

A female preference for competitiveness in prospective mates speaks to the substantial impact of female choice on human evolution. This is despite the fact that much of human reproduction in traditional societies is dictated by a young person's parents. Arranged marriage and bride price are found in traditional societies the world over (Apostolou, 2008; Apostolou, 2007). Patrilineal elders in these societies make use of these practices to secure cross-clan alliances and to extract resources for themselves and their kin (Henrich, 2020, p. 107), which often benefits parental reproductive interests more than it does the reproductive interests of offspring (Trivers, 1974). These practices, and the institutions they give rise to, constrain girls' autonomy to make their own reproductive decisions, thereby limiting the effects of female choice. Nevertheless, girls in these societies continue to have their own mate preferences and, to a greater or lesser extent, have some influence over their reproductive lives (Apostolou, 2017; Apostolou, 2010; Scelza, 2011). And, despite differences between children and parents in how highly they value good economic prospects (a trait that tracks someone's competitive ability) in a prospective mate or in-law, a daughter and her parents value good economic prospects in a husband more than a son and his parents do in a bride (Apostolou, 2015).

Male-Male Competition in the Post-Industrial World

It is reasonable to expect that the influence of male-male competition on men's reproductive success would be lessened in modern, post-industrial societies (so-called WEIRD cultures—i.e., Western, Educated, Industrialized, Rich, and Democratic; see Henrich, 2020), where men are less likely to engage in overt individual or coalitional aggression and women's mating decisions are less constrained by men's competitive outcomes. Whereas men in traditional societies must prove themselves in often violent formal and informal contests over mating access, women in modern societies are free to mate with men who would not otherwise

be able to physically defeat their reproductive rivals. Reasonable though this expectation is, there is little evidence for it. Several studies speak to the continuing importance of competitiveness for men's reproductive outcomes in modern, Western societies. In one study, Hill and colleagues (2013) tracked U.S. college men's mating success (measured as the number of sex partners they had in the past year) as a function of traits associated with either dominance or physical attractiveness. One of the central findings was that men whose traits were rated as more dominant (e.g., voice of lower timbre and pitch, body of greater girth) had more sex partners than men whose traits were rated as more attractive (e.g., tall men and men with attractive faces; height, somewhat surprisingly, was not associated with dominance and did not predict more sex partners).

Hill and colleagues (2013) discuss the possibility that female choice, although important, is hidden because it favors the same traits that are associated with male dominance. They dismiss this possibility, however, because some of the traits that were rated high in dominance were not rated high in attractiveness. For example, whereas greater body girth was associated with a higher likelihood of defeating other men in a physical fight (as judged by a man's male peers), only men of intermediate girth were judged more attractive by female raters. A follow-up study, which included more male participants, more raters, an additional assessment time point for a participant's mating success, and an expanded suite of objectively and subjectively rated participant traits, however, found significant correlations between a male participant's sexual attractiveness (as rated by women) and his physical dominance (as rated by men) ($r_s = .55$; Kordsmeyer, Hunt, Puts, Ostner, & Penke, 2018). Alongside these correlations, objectively measured traits, such as voice pitch and physical strength, contributed significantly to both a man's overall attractiveness and overall dominance. Likewise, subjectively measured traits, such

as facial attractiveness and facial dominance, were associated with both a man's overall attractiveness and overall dominance. In other words, many of the same traits associated with a man's success in male-male competition were associated with female choice. Nevertheless, only perceived success in male-male competition was ultimately associated with a man's mating success (gauged as a composite score of number of sexual partners, one-night stands, and non-relationship sexual partners).

That a man's facial attractiveness contributed significantly to his overall dominance rating is of some interest. This finding suggests that success in male-male competition may rely on more than fighting ability or aggression. Like Hill and colleagues' (2013) initial study of American university students, Kordsmeyer and colleagues (2018) sampled a Western population of male participants and raters from Germany. It may be that, at least in Western contexts, a man's attractiveness to women may be one of the domains of competition among men. The finding that only dominance predicted men's mating success should therefore be interpreted within the context of female choice. In traditional and non-industrial societies, however, where more physical and intimidation-dependent forms of male-male competition predominate, attractiveness may not predict men's competitive success. But even in traditional and, perhaps, ancestral societies, female choice may have served an important role in the evolution of men's traits. Ancestral women's preference for competitive men may have favored the winners of male contests and, in so doing, amplified the importance of male competitiveness. Thus, even if female choice is less intense in a particular generation, ancestral female choice may have influenced male traits and forms of competition.

Evolutionarily, women may have saved valuable cognitive resources if they outsourced some of their mate preferences to the selective power of male-male competition. Doing so may

have allowed them to pay attention to a handful of men's traits that are predictive of competitive success (e.g., facial and vocal masculinity, physical strength) while leaving other traits associated with competitive success to the selective power of male contests. Contrary to Hill and colleagues' (2013) conclusion that female choice probably does not mirror the effects of male-male competition, it may be that the effects of female choice are drowned out by the correlated effects of male-male competition on men's traits.

That female choice may actively promote the outcomes of male-male competition is suggested by Seffrin and Ingulli's (2021) analyses of the effects of physical aggression, intelligence, education, and other variables on the mating success of over 12,000 American men and women. As in the previously discussed studies, Seffrin and Ingulli primarily measured respondents' short-term mating success. Unlike the prior studies, however, Seffrin and Ingulli tracked these indicators longitudinally. Predictably, physical aggression and indirect markers of competitiveness such as intelligence and educational attainment were associated with mating success among men. But one finding is particularly relevant to the present discussion: among men, steady increase in physical aggression over time predicted an increased rate of sex partner accumulation over the same period. According to the authors, this finding indicates that women are drawn to aggressive men. That is, if the effect of aggression on mating success depended only on defeating rivals, then there would be a one-to-one relationship between aggression and mating success. But because increases in aggression were associated with even greater increases in mating success suggests that access to mates following the defeat of rivals is followed by the ability to attract even more mates. In their discussion, Kordsmeyer and colleagues (2018) suggest female choice outside the realm of male attractiveness as a promising avenue for future research.

Indeed, if women sometimes prefer dominance over attractiveness, using attractiveness ratings as a proxy for female choice may underestimate its power in ancestral and modern societies.

Just because male competitiveness plays a central role in female choice does mean that there is no room for female preferences for other male traits and behaviors, including attractiveness, charm, intelligence, creativity, or paternal care. But even male traits that are subsumed by their contribution to competitiveness (as Kordsmeyer and colleagues' [2018] study appears to suggest for attractiveness), may have been, or are currently, under direct female choice. This may be the case even though the effect of these traits on men's mating success is hidden to empirical observation. Theoretical and empirical considerations in sexual selection suggest that mate preferences are unlikely to evolve if they do not contribute to reproductive success (Symons, 1979/1981, pp. 206-252). In economically developed cultures, for example, women consider more feminine male faces to be more attractive (Kočnar, Saribay, & Kleisner, 2019), which may be indicative of ecologically or culturally facultative female preferences for traits that are not associated with dominance. It is therefore likely that ancestral women's individual mating decisions influenced men's evolution in ways that were not entirely constrained by male-male competition or parental dictates. Given these considerations, scholars should not abandon the search for traits and behaviors under female choice that may be unrelated to competitiveness.

Nevertheless, it is likely that a preference for male competitiveness ensures that women select optimal reproductive partners. Such a preference may be of particular importance in our species considering that competitive domains vary greatly across cultures and time periods. What worked for knights and troubadours in the Middle Ages might not work for today's businessmen and contractors. It would therefore make sense for women to pay more attention to a man's

status among his rivals and colleagues than to his skills within one or another potentially ephemeral competitive domain. If markers of status and competitive formidability are relatively stable over evolutionary time, then it is likely that selection would have more easily favored women's perceptions and cognitions to attend to these markers rather than to more arbitrary skills and predispositions. In this way, much of the heavy lifting in female choice would be outsourced to the perceptions and cognitions of other men. Crowned victors and leaders are easy to spot. A knight's grip on a sword or a programmer's line of code are not. One exception to an overall preference for competitiveness, however, may be women's preference for strength and muscularity. The evolution of such a specific preference is likely considering the ubiquity of physical combat in the animal world and the obvious benefits of physical strength in this context.

Evolutionary psychologists sometimes discuss women's mate preferences as if they evolved in isolation from one another. In an otherwise excellent overview of what women want in a mate, Buss (2003) refers to "at least a dozen distinctive preferences, each corresponding to a resource that helps women to solve critical adaptive problems" and to the "multiple facets" of women's preferences that "correspond perfectly with the multiple facets of adaptive problems that were faced by our women ancestors thousands of years ago" (pp. 47-48). Women likely have multiple, trait-specific mate preferences that are each indicative of a unique evolutionary history. But it is more parsimonious to view some of the more specific preferences as instantiations of a more general preference for competitiveness. This applies to markers of social status, which, according to Buss, includes markers of current hierarchical status as well as future status (e.g., education and likelihood of professional success). It also applies to many of the other traits for which, Buss believes, women evolved a distinct preference (e.g., resourcefulness, age, ambition and industriousness, intelligence, and size and strength). Buss's contention that

selection has “focused women’s preferences laser-like on the most adaptively valuable characteristics” and that each preference “tracks one component” of a man’s mate value (p. 21) may not accurately describe women’s mate preferences at the cognitive level. Cognitive attunement to competitive formidability, on the other hand, allows women to identify men who possess many of the qualities associated with, e.g., status, intelligence, ambition, etc., even if it does not track all the benefits associated with each trait.

In summary, evolutionary psychological and behavioral research has expanded our understanding of the biological roots of what women and men prefer in sexual and romantic partners. But mate preferences are only one side of the coin. Mate choice does not evolve in an evolutionary vacuum. It is opportunistic and practical, using whatever cues are available in the selection of optimal reproductive partners. For much of human evolutionary history, those cues were furnished by the outcomes of intrasexual competition, outcomes that were of particular importance in the evolution of men’s traits.

Human Fatherhood

Female choice sometimes selects for male traits that can be dissociated from male competitiveness. That women’s evolved mate preferences include non-competitive male traits is suggested by the imperfect correspondence between male traits favored in competitive encounters and the traits women prefer in prospective mates (Hill et al., 2013; Saxton, Mackey, McCarty, & Neave, 2016). That such distinct female preferences exist at all suggests that, even if their contribution to human reproductive success over the course of evolution was slight, their compounded effects are responsible, at least in part, for men’s physical and behavioral design features today.

One influence on the forms of reproductive behavior observed in a species is the spatial environment. According to the dimensionality hypothesis (see Puts, 2010), more intense forms of intrasexual competition are favored in environments where members of one sex can effectively exclude reproductive competitors from monopolizing access to members of the other sex. As discussed by Puts, burrow-dwelling animals, such as dung beetles, for example, can more easily control access to prospective mates than animals that inhabit three-dimensional environments, such as free-swimming dolphins or air-dwelling insects. Similarly, land-dwelling primates—especially species inhabiting easily monopolizable feeding patches, such as gorillas—exhibit greater levels of male-male competition than arboreal primates, whose habitat is less easily controlled by any one male. Although chimpanzees and bonobos, our closest surviving relatives, are mostly land-dwelling, the omnivorous nature of their diets (and, hence, greater spatial range) probably reduces the extent to which dominant males can exclude subordinate males from reproductive opportunities.

Ancestral humans inhabited two-dimensional environments that allowed for some degree of male monopolization of females but also gave females some degree of reproductive autonomy. As hominins began to populate caves (by at least 200,000 years ago; Wadley et al., 2020), there were perhaps further increases in male monopolization of females and attendant male-male competition. Nevertheless, owing to our ancestors' foraging lifestyle, which allowed for globe-spanning migrations, ancestral human habitats were highly variable. Habitat variability, in turn, gave ancestral females more reproductive autonomy. The evolution of concealed ovulation, which, to some extent, encouraged ancestral males to form lengthier pair bonds with mates (Strassmann, 1981), likewise gave females an additional physiological advantage in sexual and reproductive decision-making (though see Krems et al., 2021, for a

proposed role of female-female competition in the evolution of concealed ovulation). These environmental and physiological developments granted more opportunity to females to exercise their mate preferences—preferences that did not often align with the outcomes of male-male contests. One such preference resulted in the evolution of human fatherhood.

The Biological Function of Paternal Investment

As expanded habitats and concealed ovulation increased the costs of polygynous mating strategies for ancestral men, an additional social phenomenon allowed for the evolution of human fatherhood: paternity certainty (Geary, 2000). Men increasingly found themselves in the vicinity of mates whose ovulatory status was relatively concealed (though see Jones et al., 2018, and Jünger, Kordsmeyer, Gerlach, & Penke, 2018, for evidence of cycle-dependent increases in women's sex drive and attraction to male bodies) and whose behavior had to be monitored lest they mate with a competitor. Evidence for the adaptive role of such mate guarding behavior comes from studies on the functional role of men's sexual jealousy (Buss, 2018; Edlund et al., 2018) and its institutionalization in cross-cultural norms and religious practices governing female sexuality (Blake, Fourati, & Brooks, 2018). Although mate guarding probably imposed some limitations on women's reproductive autonomy, concealed ovulation allowed women to extract more resources from mates in exchange for continuous sexual access. Obtaining additional resources was important in ancestral environments marked by unpredictable ecological threats to food and shelter. The evolution of human cognitive sophistication and the attendant increase in brain size made securing resources even more important for ancestral women for at least two reasons: (1) fetal development made women increasingly immobile and vulnerable to malnutrition, and (2) offspring cognitive development required more resources, both prenatally and postnatally, than could be provided by mothers alone (Geary, 2000; Jasienska, 2020).

Women's increasing reliance on others for additional resources incentivized female sexual fidelity because men whose paternity could be assured were more likely to invest resources in a woman and her offspring (Geary, 2000).

Human infants and toddlers require high levels of material investment and emotional intimacy. Without such care, children risk developmental delay or, worse, early mortality. For much of our evolutionary history, maternal care, albeit necessary, was often not enough to ensure that a child survived and thrived. This was particularly the case in unpredictable environments such as those of our hunter-gatherer ancestors and remains so to this day (Alio et al., 2011; Geary, 2000). Research suggests that children who receive only maternal care are more vulnerable to physical and social stressors (see Geary, 2000, for review). Although infant mortality has been vastly reduced with the advent of better medicine and state-level support for mothers and children, infant and child mortality soared in preindustrial societies and almost certainly was substantial in ancestral hunter-gatherer environments. This does not mean that fathers were the invariable and only source of supplemental support for children; anthropological accounts point to the ubiquity of family members—e.g., grandparents, aunts, uncles, and older siblings—and friends as additional sources of childcare (Hrdy, 2009; Page, et al., 2019). Childrearing often did take a village. But virtually every society that has been studied—from relatively egalitarian Western societies marked by high levels of paternal investment to societies that earlier anthropologists believed had a “fatherless culture,” such as the Mosuo of Southwest China—acknowledges fatherhood as an institution and practices paternal investment, even if some or the majority of men invest little or no resources in their offspring (Mattison, Scelza, & Blumenfeld, 2014).

Men experience physiological changes when they become fathers—changes that are associated with functional shifts away from a competitive mindset and toward a parenting mindset (Grebe, Sarafin, Strenth, & Zilioli, 2019). Testosterone, for example, subsides with increasing levels of romantic commitment (i.e., single men have higher testosterone than men who are in a long-term relationship) (Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002). Buttressing the case for the adaptive role of human fatherhood, fathers experience an additional decrease in testosterone relative to men who are in a relationship but who are childless (Gray, Jeffrey Yang, & Pope Jr, 2006). Although debate over the causal factors underlying these shifts is ongoing, there are probably bidirectional influences between dispositional hormone differences and context-dependent effects of fatherhood (Gettler, McDade, Feranil, & Kuzawa, 2011).

The universal nature of human fatherhood and its attendant physiology are therefore strongly indicative of its evolved function. But is there evidence for its selective advantage under female choice? In other words, if men could increase their reproductive success by investing in offspring that they were confident of having sired, what, if any, evidence exists that women's mate preferences also shaped this behavior?

Fatherhood Under Female Choice

Paternal care under female choice can select for either direct care or for traditionally male reproductive strategizing, such as resource acquisition and provisioning within the context of a long-term sexual relationship. With respect to resource provisioning, it is helpful to further distinguish the effects of female choice on traits that are associated with the acquisition of resources needed to secure mating access from its effects on traits that are associated with the acquisition of resources needed to provision a woman and her offspring. The challenge is that the

effect of female choice for investing fathers on men's reproductive success (however it is measured) may be lost to empirical observation if it selects for the same traits associated with success in mating access. Measuring men's mating success as a function of their *willingness* (rather than ability) to invest resources may therefore be of use in assessing whether there is a unique role for female choice on men's resource provisioning behavior in the domestic realm. But female choice for men's direct paternal care may be a more immediately fruitful area of investigation than one focused on resource provisioning.

According to Gettler (2010), direct paternal care, which includes carrying and grooming of infants and children (as distinguished from indirect care, which includes provisioning and resource defense), contributed to human evolutionary success and likewise explains men's unique physiological response to interaction with children (see previous discussion of testosterone decreases associated with fatherhood). Infant carrying is an intimate—and intimacy-building—activity. Unlike the carrying of heavy spears or hunted prey, it requires a certain degree of physical and emotional responsiveness, which would have been especially necessary in ancestral hunter-gatherer environments marked by as much as 20 kilometers of daily movement (Leonard & Robertson, 1992, as cited in Gettler, 2010). It is therefore conceivable that women's mate preferences would have been shaped by selection to prefer potential fathers who were affectionate, tender, and responsive to them and their offspring. Gettler argues that direct paternal care—specifically, male carrying of infant offspring—allowed for shorter inter-birth intervals by reducing mothers' fertility-reducing energy costs directly and by hastening infant weaning. If the reproductive benefits of carrying offspring outweighed the potential benefits of seeking alternative mates or even of providing only indirect care to their current offspring, then men's physiology and psychology should reflect this evolutionary trajectory.

Although it is plausible that men evolved specifically to carry their infant offspring, my view is that men's proclivity for direct paternal care is more general. First, there is increasing evidence that ancestral human foragers sometimes resided in sedentary, hierarchically stratified communities that were made possible by reliable supplies of wild flora or fauna (see, e.g., Cannon & Yang, 2006; Hutchinson et al., 2016; Singh & Glowacki, 2021). If so, the need for frequent movement and, in turn, the need for fathers to carry offspring would have been less pressing. Second, women in sedentary, urban environments prefer men who are good fathers more than they prefer men who offer other desirable qualities (Lu, Zhu, & Chang, 2015), suggesting that the utility of direct paternal care relies on more than just infant-carrying ability or some other delimited trait. Indeed, as Gettler's own research on paternity-mediated hormonal shifts and evidence of men's emotional and behavioral attachment to offspring indicate (Grossmann et al., 2002), human fathers exhibit multiple psychophysiological signatures of adaptation to direct paternal care.

The most direct line of evidence for the selective power of female choice on fatherhood comes from women surveyed on what traits they find most attractive in prospective mates. Buss and Shackelford (2008), for example, asked 107 married women of differing physical attractiveness to rate their desire for men's traits separated into good genes, good investment ability, good parenting, and good partner categories. Traits associated with good parenting included desire for children, fondness for children, liking children, wanting to raise children well, having emotional stability and maturity, and being kind and understanding. Buss and Shackelford found that physically attractive women reported greater desire for traits across all mate choice categories, whereas less attractive women prioritized some traits over others. This finding suggests that higher mate value allows women to be more selective across all mate-

choice categories, one of which is fatherhood. Similarly, Lu and colleagues (2015) conducted a three-study investigation, involving over 12,000 Chinese female participants, into whether women of high socioeconomic status prefer men who are good fathers over men with good genes or men who are good providers. The researchers reasoned that women who are well off can provide for themselves and their offspring and should therefore prioritize mates who offer paternal care over other reproductive benefits. They found that, overall, regardless of socioeconomic status or rural versus urban background, women valued good fathers more than they valued good providers or good genes. Even women who were experimentally manipulated to identify as either poor or in a good economic situation valued fatherhood regardless of experimental condition. Moreover, in line with the researchers' hypothesis, women of higher socioeconomic status, urban women, and women who were made to feel economically well-off valued fatherhood more so than women in actual or perceived economic deprivation.

As is the case with all survey research, there are limitations to how much of it can be generalized to real world decision-making. Another difficulty specifically pertaining to the research on women's self-reported mate preferences is the relatively arbitrary distinctions between traits indicative of good fathering and those indicative of resource provisioning, good genes, etc. Although the researchers based these distinctions on common correlated factors derived from participant responses, the labeling of these factors as "good genes," or "good parenting" is somewhat limited by a researcher's subjective judgment. There is often no clear distinction between a man's evolved resource provisioning behavior outside and within the fatherhood role. Similarly, there is no clear distinction between a man's paternal investment as a manifestation of fatherhood and paternal investment as a form of courtship. Regarding Lu and colleagues' (2015) hypothesis that women in economically well-off circumstances should be

especially desirous of men who are good fathers, there is no clear rationale as to why they should not likewise be as desirous of men who have good genes. If anything, women's greater ability to provide for themselves can reasonably lead them to value healthy, attractive men and supplement the lack of paternal investment with nannies or daycare. In this light, the researchers' claim that well-off women should value fatherhood over good genes because good genes were valued only in so far as they compensated women for men's higher mortality in perilous environments sounds like a *post hoc* argument. Notwithstanding these limitations, women's self-reported desire for men who are willing to engage in direct paternal care favors the fatherhood-under-female-choice hypothesis. Indeed, a follow-up study by Lu and colleagues suggested that Chinese men who are of lower mate value than their wives may compensate for their lack of good genes and resources by increasing their level of paternal care (Chang, Lu, & Zhu, 2017). If so, paternal care may be a conditional reproductive strategy that appeals to female choice when other strategies are unavailable.¹

Another line of evidence in favor of female choice for direct paternal care comes from the association between the hormone prolactin (PRL) and fatherhood. In some ways, PRL is the opposite of testosterone in that fatherhood is associated with its increase among males in species marked by high levels of both maternal and paternal care. In a sample of Filipino men ($n = 289$), Gettler and colleagues (2012) found that fatherhood was associated with greater levels of PRL—particularly among the fathers of infants. Because initial differences in PRL among childless men did not predict fatherhood at a follow-up period, PRL likely functions to motivate paternal care in response to the birth of a child. What was not expected, however, was the finding that childless men with higher levels of PRL also reported a greater number of lifetime sexual

¹Admittedly, men may practice paternal care to increase the probability of offspring survival rather than as a form of courtship.

partners and a higher likelihood of having engaged in sexual activity in the preceding month.

Although these findings contradict prior research on the association between PRL and decreased mating effort, the authors propose that it is possible for PRL to contribute to the signaling of fatherhood potential to prospective mates. However, the authors suggest that PRL may likewise signal immune function in addition to being a necessary precursor for healthy sexual physiology (e.g., men with low levels of PRL are more likely to experience erectile dysfunction, premature ejaculation, and a lower sperm count—see Corona et al., 2014), which would explain the association between PRL and high sexual activity among the study participants.

Kindness is sought in prospective mates the world over, often superseding sex-specific preferences such as women's preference for high earning capacity and men's preference for physical attractiveness (Buss, 1989). Kind romantic partners predictably add to the quality and durability of a relationship, and it is plausible that a cooperative relationship with fewer points of friction adds to a couple's eventual reproductive success (e.g., by allowing for smoother negotiation of household and resource acquisition tasks). Kindness may therefore be under the selective power of mate choice regardless of its effects, if any, on offspring. Nevertheless, the selective role of female choice on men's direct paternal care, which is manifest in traits such as kindness and physically or verbally affectionate behavior, deserves more theoretical and empirical attention in the human evolutionary sciences. Researchers might, for example, track differences in the expression of kindness across romantic and childcare contexts.

There is some suggestive research that traits associated with direct paternal care, such as kindness and fondness for children, may be subject to female choice. A study of women's divergent mating strategies (Roney, Hanson, Durante, & Maestripieri, 2006), for example, revealed that some of women's mate preferences differ depending on whether they are

evaluating men as short-term or long-term relationship prospects. For a brief affair, women emphasized good looks and masculinity. For a committed relationship, women emphasized traits such as “likes children,” kindness, and, as in the brief affair scenario, good looks. What is most suggestive of female choice is that the female raters ($n = 29$) had no direct knowledge of whether the men whose photographs they were evaluating actually liked children. Nevertheless, female raters’ subjective evaluations of men’s fondness for children corresponded to the men’s own responses on an “interest in infants” measure. This suggests that women are attending to morphological cues in men’s faces that are indicative of a psychological predisposition. Of note, women’s subjective ratings of men’s masculinity, a trait that women found attractive when evaluating men as potential short-term mates, likewise corresponded to objective measures of men’s testosterone. Such correspondence between direct measures of men’s traits and women’s secondhand perceptions of these traits, in addition to these traits’ utility in predicting women’s romantic interest, speaks to the evolution of sophisticated mate evaluation mechanisms on the part of women and multiple physical and psychological targets of female choice on the part of men.

Other research examined whether one particular trait may be indicative of a man’s potential to be a good father: beardedness. An initial study by Dixson and colleagues (2018) into whether women’s preference for bearded men differs across the menstrual cycle (i.e., whether this mate preference is sensitive to conception probability) showed that women ($n = 52$) preferred a bearded man’s face over a clean-shaven man’s face regardless of menstrual cycle status. Traditionally considered to be a marker of dominance and masculinity, beardedness, as Dixson and colleagues (2019) discovered in a follow-up study, may serve as an indicator of good fathering skills as well. Despite being somewhat complicated by the multiple hypotheses tested

and the inclusion of a wide range of predictor and moderator variables, the results suggest that women ($n = 2419$) attend to beardedness as a signal of both a man's masculinity and suitability as a father. One thread of evidence in favor of female choice for good fathers can be extracted from bearded men's higher attractiveness ratings among childless women and higher fathering suitability ratings among mothers and women pregnant with their first child. This narrative should be treated with caution, however, given the wide array of—sometimes contradictory—findings.

The previously discussed studies are part of ongoing research into women's evolved reproductive strategies. There are some indications that women's mate preferences, particularly in the short-term mating domain, ebb and flow with the menstrual cycle (Gildersleeve, Haselton, & Fales, 2014; though see Jones et al, 2018, and Wood, Kressel, Joshi, & Louie, 2014). Although many questions in this area of investigation are not yet settled, and despite its share of methodological hurdles, the picture that is emerging is that women employ a dual mating strategy marked by a preference for (1) dominant and physically attractive men on the one hand and (2) committed providers and carers who are invested in them and their offspring on the other (though, as suggested by Dixson and colleagues' [2018, 2019] research into beardedness, these targets of female choice may not be mutually exclusive—indeed, as Buss and Shackelford's [2008] findings suggest, women who are high in mate value are more likely to attract men who are high in traits associated with both short-term and long-term attractiveness). Men may likewise employ a dual mating strategy, perhaps regulated by changes in testosterone, by shifting between competition for access to mating opportunities and direct paternal care within the context of a pair-bond. Whether some men are more physically or behaviorally predisposed toward one or the other strategy or whether all men have the capacity to shift from one to the

other in response to ecological and social factors (see Geary, 2000, for discussion of human paternal investment as a “facultative” adaptation) is still under dispute. Regardless, it is becoming increasingly clear that fatherhood should be included as one of many contenders for female choice in investigations of human mate preferences.

The importance of competitiveness for men’s reproductive success does not negate the importance of fatherhood for at least two reasons. First, studies that rely on the Sociosexual Orientation Inventory (SOI), or similar measures, are limited to tracking primarily short-term mating success due to their emphasis on number of sexual partners, one-night stands, etc. These measures, while important, are biased toward measuring only one facet of men’s reproductive life. Measures such as those employed by Međedović (2021) (e.g., relationship length, number of children and grandchildren, etc.), or even Kordsmeyer’s and colleagues’ (2018) measure of conception probability, can help to supplement this research by measuring the success of other reproductive strategies that may be more aligned with fatherhood. Indeed, across widely divergent taxa, there are often multiple strategies—some compatible with one another, others not—that animals of the same species use to achieve reproductive success (West-Eberhard, 2003, pp. 394-416). Second, no measure is problem-free. We should be mindful of the fact that reproductive success today, especially in post-industrial environments with available contraception, is different from that of our evolutionary past. Whether fatherhood is or is not shown to be associated with reproductive success today is of limited use in determining its evolutionary importance as a worthwhile reproductive strategy adopted by some ancestral men. Nevertheless, although no measure of reproductive success is perfect, some may echo past reproductive dynamics better than others. When assessed with measures such as number of children and grandchildren (e.g., Međedović, 2021) or probability of childhood survival and

social integration, the contribution of fatherhood to men's reproductive success seems likely—especially so in light of Lu and colleagues' (2015) finding that Chinese women, regardless of socioeconomic or ecological context, value fatherhood potential over all other qualities in prospective mates. Cross-cultural and cross-historical evidence for fatherhood as a contributor to reproductive success (reviewed in Geary, 2000) also speaks to the evolutionary importance of men's long-term reproductive strategies. Of course, as discussed previously, there are multiple lines of evidence for the adaptive role of men's competitiveness, and traits that contribute to men's competitiveness may likewise contribute to men's ability to invest in offspring. It is only appropriate that fatherhood be investigated as a distinct target of female choice.

Although there is enough suggestive evidence for the important role of fatherhood in women's mate choice, the perceptual and cognitive levels at which this preference has been selected and maintained are uncertain. Brase (2006), for example, advances evidence in favor of a more general level at which the preference for fatherhood may be activated in a woman's nervous system. In the first of two experiments, Brase showed internet respondents ($n = 1793$) a series of images depicting either opposite- or same-sex models engaged in various behaviors indicative of parenting quality, general helpfulness, and general compassion, among other traits. Results showed that women rated male models in good parenting scenarios as most attractive (whether as a dating, sexual, or marital partner), followed by models in neutral and bad parenting scenarios, respectively. Men's attractiveness ratings of female models did not differ by parenting condition. Although these results are in line with theoretical considerations for the evolution of fatherhood via female choice, women rated male models showing compassion toward an elderly person as even more attractive than good parenting models. (Brase's second experiment found

that male and female college students [$n = 120$] are equally attracted to good parenting qualities, but only in the context of a long-term relationship.)

That women were more attracted to men exhibiting compassion to an older person than to men exhibiting specifically good parenting behavior indicates that women's mate preferences may be even more general than my conceptualization of them in the current article would suggest. It is plausible that a more general preference for kindness, compassion, or empathy can be as effective in selecting for good fathers as a more specific preference for, say, kindness toward children. Although I suspect that recurrent selection pressures across generations of female choice will have left traces of perceptual and cognitive evaluation mechanisms that are sensitive to cues of fatherhood, we cannot rule out more general preferences until evidence of these traces is uncovered. Following Brase (2006), and in accordance with Williams's (1966) theoretical examination of levels of selection, a parsimonious account of mate choice requires that we rule out simpler, more general preferences before positing the existence of preferences that are specifically tailored to one or another sexually selected trait.²

Discussion

The current article is admittedly incomplete in its discussion of female choice in human evolution. I did not discuss research on female preferences for specific anatomical properties of male genitalia (both pre- and post-copulation) (e.g., Costa, Miller, & Brody, 2012; Mautz, Wong, Peters, & Jennions, 2013; Prause, Park, Leung, & Miller, 2015), the sperm-retention or mate-evaluation functions of the female orgasm (Puts, Welling, Burriss, & Dawood, 2012), or post-copulatory female physiology as an additional domain of female reproductive choice (Jokiniemi

² See also Renoult, Bovet, and Raymond (2016) for evidence of a more general, cross-species hedonic preference for easily processed stimuli underlying human evaluations of facial attractiveness and Ryan (2021) for a review of generalist sensory biases as precursors to the evolution of mate preferences.

et al., 2020). Other mate preferences may be subsumed within other domains or may even fall outside of any overarching domain (e.g., assortative mating for physical, cognitive, behavioral, or ideological similarity or similarity in age). No doubt, there are other promising avenues for research. Nevertheless, competitiveness and fatherhood circumscribe two overarching domains of female choice for male behavioral characteristics in our species. As such, a focus on competitiveness and fatherhood would include more specific traits and behaviors that may be under selection through female choice. As discussed, women's mate preferences for intelligence and educational attainment, for example, may function as specific implementations of female mate preferences for male competitive formidability. Similarly, preferences for intelligence, creativity, and playfulness (Chick, Yarnal, & Purrington, 2012; Miller, 2000; Puts, 2010) may function as specific instantiations of a general preference for fatherhood if these traits predict optimal caregiving.

Cognitive Implications

Research into whether mate preferences conform to such a hierarchical structure can also inform our understanding of cognitive architecture, more generally. There is ongoing debate over whether the mind consists of innumerable functionally specific modules (or evolved psychological mechanisms) or relies on a few general-purpose mechanisms that can solve a multitude of reproductively relevant tasks. This debate, much like the nature vs. nurture debate, is past its expiration date. As Pietraszewski and Wertz (2021) suggest, arguments over whether the mind is modular, or how modular the mind is, arise because opposing sides do not realize that they are arguing from different levels of analysis. If we limit ourselves to only the functional level, arguments over modularity turn moot. The mind is entirely mechanistic, albeit attended with myriad non-adaptive byproducts and noise. Some mechanisms are activated by more

abstract stimuli (e.g., edges and shapes) whereas other mechanisms are activated by more holistic stimuli (e.g., human faces and artifacts). Due to the mind's hierarchical nature, the mechanisms that are activated by abstract stimuli are of a "lower level" and feed into the mechanisms that are activated by more holistic stimuli. Mechanisms that handle judgments of facial attractiveness, for example, cannot make their judgements without input from lower-level mechanisms that track the edges and shapes that make up a human face. Similarly, mechanisms that track a potential mate's competitiveness or paternal behavior are fed multiple stimuli from lower-level sensory modalities (e.g., Is the potential mate muscular? Is he the center of attention within his coalition? Is he responsive to a child?), but they may not be attuned to less-relevant, peripheral stimuli (e.g., How sharp are the potential mate's spears? How great is his repertoire of children's songs?). Specific mate preferences may or may not be under partner choice. And even if a specific mate preference has evolved (e.g., women's preference for masculine faces), it may not predict reproductive success if considered in isolation. However, when considered as part of a hierarchical structure of one or a few overarching domains of partner choice (a part whose relevance may depend on ecological, social, or historical context), the preference in question can be assigned its rightful place in the psychological taxonomy of mating behavior. Kordsmeyer (in press) takes a similar approach in advocating for a more inclusive view of human capital, broadly defined, as a general measure of reproductive fitness.

One outstanding question is how many evolved psychological mechanisms there are. Given that there was an ancestral limit to the number of reproductive problems that the mind evolved to solve, there must be a limit to the number of adaptive mechanisms of which the mind is composed. Of relevance to the current discussion, ancestral female attunement to a select number of low-level cues indicative of either male competitiveness or proneness to paternal

behavior would have reduced the need to evolve other, more specific female mate preferences. Note, however, that the mechanisms underlying this attunement are specialized and functionally fit and cannot be described as “general-purpose” or capable of solving every task, ancestrally relevant or otherwise. The mind is specialized at both low-level sensorimotor scales and high-level perception-cognition scales. As multiple scholars in the evolutionary and cognitive sciences have suggested, pervasive specialization enhances rather than dampens physiological and behavioral flexibility (Barrett & Kurzban, 2006; Cosmides & Tooby, 1997; West-Eberhard, 2003, pp. 56-88). Nevertheless, the present discussion of hierarchical mate preferences favors an account of the mind that incorporates several psychologically pervasive species-typical motivations that are elaborated by ecological and social inputs over the course of maturation. Specialization of function does not mean that an organism evolves a dedicated mechanism to deal with every granular aspect of reality. Indeed, this cannot be the case because, even though reality can be subdivided indefinitely, organisms cannot evolve an infinite supply of mechanisms to deal with each respective subdivision. What organisms can do is apply the mechanisms that they already have toward new adaptive problems. Female mate preferences, by virtue of canalized developmental processes, are responsive to displays of male dominance and paternal care. But the displays that females respond to, and the contexts of their occurrence, are largely determined by environmental contingencies that may not even last a generation.

Humanity supplies us with culturally specific examples of male dominance contests. From horse racing to drag racing, dueling to skateboarding, there is no shortage of ways in which men have competed to distinguish themselves in the eyes of prospective mates. This does not mean that women rely on a general-purpose cognitive mechanism to evaluate men in one or another culturally transient competitive milieu. Our brains often duplicate and repurpose

psychological mechanisms and suites of psychological mechanisms toward newly learned tasks or even toward domains that are different from those of their evolutionary origin. Psychological mechanisms are algorithmic in that they were shaped by natural selection to carry out one or a limited set of processes regardless of how wide or narrow the spectrum of inputs to them may be. Psychological mechanisms should therefore be conceptualized based on their function rather than content. In this way, an overarching mate preference for competitiveness can be developmentally refined to attend to cues of male status in a wide variety of contexts, be it on a battlefield or on the floor of the stock exchange.

Such considerations lead us to the following questions: When humans are seeking mates, are they implementing one or a combination of mating strategies? If they are implementing a combination of strategies, what is their level of awareness of each strategy? Can each strategy be traced to a dedicated neurocognitive mechanism or does it arise from a combination of mechanisms that are not specifically dedicated to one or another mating strategy but that are selectively activated by predictable ecological and social inputs? If some mating strategies are of a higher order than others, might we see correlations between specific behavioral strategies if they represent specific instantiations of a single overarching strategy (i.e., do they reflect the same latent factor)? (Note that empirically testing this hypothesis can go a long way toward falsifying or supporting the currently proposed framework and for discovering additional overarching domains of mate choice not currently discussed.) How plastic or context-dependent are the strategies under study and what are their developmental antecedents? Are specific instantiations of general strategies more developmentally malleable than the overarching strategies of which they are a part? What is the genetic architecture underlying each level of a mating strategy and do different mating strategies rely on different or shared genetic elements?

Answering these questions in the coming years necessitates interdisciplinary collaboration and a focus on both distal and proximate levels of behavioral analysis.

Testing the validity of the current framework will likely get easier with advances in neuroimaging, neurogenetics, and with the increasing use of large, cross-cultural samples in behavioral research. One prediction is that overarching mate-choice domains should conform to a hierarchical activation pattern in an evaluator's brain, with local areas feeding into larger cortical networks in a way that is isomorphic with specific mate preferences activating the overarching domains of which they are a part. Genetic activation patterns in an evaluator's brain might likewise be similar for different preferences if the preferences are indicative of a target's mate value within an overarching domain. At the level of the evaluated target, a trait's fitness score should correlate with another trait's fitness score if the traits are indicative of a shared fitness domain. The currently proposed framework should not be expected to exclude specific traits for consideration in studies of mate choice. Although some proposed preferences might not withstand empirical scrutiny, it is likely that others did evolve as mate choice criteria but are only activated in specific contexts. Overarching domains, I predict, are universal. But the specific preferences within them probably vary across time and place. Recent endeavors to expand social science research to include participants from non-WEIRD societies, alongside advances in paleogenetics, can help to resolve these and other longstanding questions about human evolution.

References

- Alio, A. P., Mbah, A. K., Kornosky, J. L., Wathington, D., Marty, P. J., & Salihu, H. M. (2011). Assessing the impact of paternal involvement on racial/ethnic disparities in infant mortality rates. *Journal of Community Health, 36*(1), 63-68. doi:10.1007/s10900-010-9280-3
- Apostolou, M. (2007). Sexual selection under parental choice: The role of parents in the evolution of human mating. *Evolution and Human Behavior, 28*(6), 403-409. doi:10.1016/j.evolhumbehav.2007.05.007
- Apostolou, M. (2008). Bridewealth and brideservice as instruments of parental choice. *Journal of Social, Evolutionary, and Cultural Psychology, 2*(3), 89-102. doi:10.1037/h0099352
- Apostolou, M. (2010). Sexual selection under parental choice in agropastoral societies. *Evolution and Human Behavior, 31*(1), 39-47. doi:10.1016/j.evolhumbehav.2009.06.010
- Apostolou, M. (2015). Parent-offspring conflict over mating: Domains of agreement and disagreement. *Evolutionary Psychology, 13*(3), 1-12. doi:10.1177/1474704915604561
- Apostolou, M. (2017). Individual mate choice in an arranged marriage context: Evidence from the standard cross-cultural sample. *Evolutionary Psychological Science, 3*(3), 193-200. doi:10.1007/s40806-017-0085-9
- Balish, S. M., Deaner, R. O., Rainham, D., & Blanchard, C. (2016). Sex differences in sport remain when accounting for countries' gender inequality. *Cross-Cultural Research, 50*(5), 395-414. doi:https://doi.org/10.1177/1069397116665815
- Barrett, H. C., & Kurzban, R. (2006). Modularity in cognition: Framing the debate. *Psychological Review, 113*(3), 628-647. doi:10.1037/0033-295X.113.3.628

- Berglund, A., Bisazza, A., & Pilastro, A. (1996). Armaments and ornaments: An evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society*, 58, 385-399. doi:<https://doi.org/10.1006/bijl.1996.0043>
- Bernhardt, P. C., Dabbs, J. M., Fielden, J. A., & Lutter, C. D. (1998). Testosterone changes during vicarious experiences of winning and losing among fans at sporting events. *Physiology & Behavior*, 65(1), 59-62. doi:10.1016/S0031-9384(98)00147-4
- Bjorklund, D. F., & Shackelford, T. K. (1999). Differences in parental investment contribute to important differences between men and women. *Current Directions in Psychological Science*, 8(3), 86-89. doi:10.1111/1467-8721.00020
- Blake, K. R., Fourati, M., & Brooks, R. C. (2018). Who suppresses female sexuality? An examination of support for Islamic veiling in a secular Muslim democracy as a function of sex and offspring sex. *Evolution and Human Behavior*, 39(6), 632-638. doi:10.1016/j.evolhumbehav.2018.06.006
- Booth, A., Shelley, G., Mazur, A., Tharp, G., & Kittok, R. (1989). Testosterone, and winning and losing in human competition. *Hormones and Behavior*, 23(4), 556-571. doi:10.1016/0018-506X(89)90042-1
- Brase, G. L. (2006). Cues of parental investment as a factor in attractiveness. *Evolution and Human Behavior*, 27(2), 145-157. doi:10.1016/j.evolhumbehav.2005.06.003
- Burk, C. L., Mayer, A., & Wiese, B. S. (2019). Nail-biters and thrashing wins: Testosterone responses of football fans during World Cup matches. *Physiology & Behavior*, 209, 112596. doi:10.1016/j.physbeh.2019.112596

Buser, T., Niederle, M., & Oosterbeek, H. (2014). Gender, competitiveness, and career choices.

The Quarterly Journal of Economics, 129(3), 1409-1447.

doi:<https://doi.org/10.1093/qje/qju009>

Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences*, 12(1), 1-14.

doi:doi.org/10.1017/S0140525X00023992

Buss, D. M. (2003). *The evolution of desire: Strategies of human mating (revised edition)*. Basic Books.

Buss, D. M. (2018). Sexual and emotional infidelity: Evolved gender differences in jealousy prove robust and replicable. *Perspectives on Psychological Science*, 13(2), 155-160.

doi:[10.1177/1745691617698225](https://doi.org/10.1177/1745691617698225)

Buss, D. M., & Shackelford, T. K. (2008). Attractive women want it all: Good genes, economic investment, parenting proclivities, and emotional commitment. *Evolutionary Psychology*, 6(1), 134-146. doi:[10.1177/147470490800600116](https://doi.org/10.1177/147470490800600116)

Buss, D. M., Abbott, M., Angleitner, A., Asherian, A., Biaggio, A., Blanco-Villasenor, A., . . . Yang, K. S. (1990). International preferences in selecting mates: A study of 37 cultures. *Journal of Cross-Cultural Psychology*, 21(1), 5-47. doi:[10.1177/0022022190211001](https://doi.org/10.1177/0022022190211001)

Caillaud, D., Levréro, F., Gatti, S., Menard, 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: The Official Publication of the American Association of Physical Anthropologists*, 135(4), 379-388.

doi:[10.1002/ajpa.20754](https://doi.org/10.1002/ajpa.20754)

- Candolin, U. (2000). Increased signalling effort when survival prospects decrease: Male-male competition ensures honesty. *Animal Behaviour*, 60(4), 417-422.
doi:10.1006/anbe.2000.1481
- Cannon, A., & Yang, D. Y. (2006). Early storage and sedentism on the Pacific Northwest Coast: ancient DNA analysis of salmon remains from Namu, British Columbia. *American Antiquity*, 71(1), 123-140. doi:10.2307/40035324
- Carré, J. M., Campbell, J. A., Lozoya, E., Goetz, S. M., & Welker, K. M. (2013). Changes in testosterone mediate the effect of winning on subsequent aggressive behaviour. *Psychoneuroendocrinology*, 38(10), 2034-2041. doi:10.1016/j.psyneuen.2013.03.008
- Chagnon, N. A. (2013). *Noble savages: My life among two dangerous tribes - the Yanomamö and the anthropologists*. New York: Simon & Schuster.
- Chang, L., Lu, H. J., & Zhu, X. Q. (2017). Good genes, good providers, and good fathers and mothers: The withholding of parental investment by married couples. *Evolutionary Behavioral Sciences*, 11(2), 199-211. doi:10.1037/ebs0000086
- Chawla, D. S. (2017, May 12). No, wearing red doesn't make you hotter. *Slate*. Retrieved from <https://slate.com/technology/2017/05/dont-wear-red-in-your-online-dating-profile.html>
- Chick, G., Yarnal, C., & Purrington, A. (2012). Play and mate preference: Testing the signal theory of adult playfulness. *American Journal of Play*, 4(4), 407-440. Retrieved from <https://eric.ed.gov/?id=EJ985599>
- Corona, G., Wu, F. C., Rastrelli, G., Lee, D. M., Forti, G., O'Connor, D. B., . . . Group, E. S. (2014). Low prolactin is associated with sexual dysfunction and psychological or metabolic disturbances in middle-aged and elderly men: the European Male Aging Study (EMAS). *The Journal of Sexual Medicine*, 11(1), 240-253. doi:10.1111/jsm.12327

- Cosmides, L., & Tooby, J. (1997). Evolutionary psychology: A primer. Retrieved from <http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.615.8167&rep=rep1&type=pdf>
- Costa, R. M., Miller, G. F., & Brody, S. (2012). Women who prefer longer penises are more likely to have vaginal orgasms (but not clitoral orgasms): Implications for an evolutionary theory of vaginal orgasm. *The Journal of Sexual Medicine*, 9(12), 3079-3088. doi:10.1111/j.1743-6109.2012.02917.x
- 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. Retrieved from <https://www.journals.uchicago.edu/doi/abs/10.1086/283163>
- Darwin, C. (2006/1871). The descent of man, and selection in relation to sex. In E. O. Wilson (Ed.), *From so simple a beginning: The four great books of Charles Darwin* (pp. 767-1248). New York: Norton.
- De Waal, F. B., & Hoekstra, J. A. (1980). Contexts and predictability of aggression in chimpanzees. *Animal Behaviour*, 28(3), 929-937. doi:[https://doi.org/10.1016/S0003-3472\(80\)80155-2](https://doi.org/10.1016/S0003-3472(80)80155-2)
- Derenko, M. V., Malyarchuk, B. A., Wozniak, M., Denisova, G. A., Dambueva, I. K., Dorzhu, C. M., . . . Zakharov, I. A. (2007). Distribution of the male lineages of Genghis Khan's descendants in northern Eurasian populations. *Russian Journal of Genetics*, 43(3), 334-337. Retrieved from <https://link.springer.com/article/10.1134/S1022795407030179>
- Dijkstra, P. D., Schaafsma, S. M., Hofmann, H. A., & Groothuis, T. G. (2012). 'Winner effect' without winning: unresolved social conflicts increase the probability of winning a subsequent contest in a cichlid fish. *Physiology & Behavior*, 105(2), 489-492.

- Dixon, B. J., Kennedy-Costantini, S., Lee, A. J., & Nelson, N. L. (2019). Mothers are sensitive to men's beards as a potential cue of paternal investment. *Hormones and Behavior*, 113, 55-66. doi:10.1016/j.yhbeh.2019.04.005
- Dixon, B. J., Lee, A. J., Blake, K. R., Jasienska, G., & Marcinkowska, U. M. (2018). Women's preferences for men's beards show no relation to their ovarian cycle phase and sex hormone levels. *Hormones and Behavior*, 97, 137-144. doi:10.1016/j.yhbeh.2017.11.006
- Edlund, J. E., Heider, J. D., Nichols, A. L., McCarthy, R. J., Wood, S. E., Scherer, C. R., . . . Walker, R. (2018). Sex differences in jealousy: The (lack of) influence of researcher theoretical perspective. *The Journal of Social Psychology*, 158(5), 515-520. doi:10.1080/00224545.2017.1365686
- Fortune, R. F. (1939). Arapesh warfare. *American Anthropologist*, 41(1), 22-41.
- Fox, E. A. (2002). Female tactics to reduce sexual harassment in the Sumatran orangutan (*Pongo pygmaeus abelii*). *Behavioral Ecology and Sociobiology*, 52(2), 93-101. Retrieved from <https://link.springer.com/article/10.1007/s00265-002-0495-x>
- Fuxjager, M. J., Oyegbile, T. O., & Marler, C. A. (2011). Independent and additive contributions of postvictory testosterone and social experience to the development of the winner effect. *Endocrinology*, 152(9), 3422-3429. doi:10.1210/en.2011-1099
- Gallup, A. C., & Fink, B. (2018). Handgrip strength as a Darwinian fitness indicator in men. *Frontiers in Psychology*, 9(439). doi:10.3389/fpsyg.2018.00439
- Gardner, E. J., Neville, M. D., Samocha, K. E., Barclay, K., Kolk, M., Niemi, M. E., . . . Hurles, M. E. (2020). Sex-biased reduction in reproductive success drives selective constraint on human genes. *BioRxiv*. doi: <https://doi.org/10.1101/2020.05.26.116111>

- Garza, R., Pazhoohi, F., & Byrd-Craven, J. (2021). Women's preferences for strong men under perceived harsh versus safe ecological conditions. *Evolutionary Psychology*, 1-11. doi:10.1177/14747049211032351
- Geary, D. C. (2000). Evolution and proximate expression of human paternal investment. *Psychological Bulletin*, 126(1), 55-77. doi:10.1037/0033-2909.126.1.55
- Geniole, S. N., Bird, B. M., Ruddick, E. L., & Carré, J. M. (2017). Effects of competition outcome on testosterone concentrations in humans: An updated meta-analysis. *Hormones and Behavior*, 92, 37-50. doi:10.1016/j.yhbeh.2016.10.002
- Gerloff, U., Harung, 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. doi:10.1098/rspb.1999.0762
- Gettler, L. T. (2010). Direct male care and hominin evolution: why male-child interaction is more than a nice social idea. *American Anthropologist*, 112(1), 7-21. doi:10.1111/j.1548-1433.2009.01193.x
- Gettler, L. T., McDade, T. W., Feranil, A. B., & Kuzawa, C. W. (2011). Longitudinal evidence that fatherhood decreases testosterone in human males. *Proceedings of the National Academy of Sciences*, 108(3), 16194-16199. doi:10.1073/pnas.1105403108
- Gettler, L. T., McDade, T. W., Feranil, A. B., & Kuzawa, C. W. (2012). Prolactin, fatherhood, and reproductive behavior in human males. *American Journal of Physical Anthropology*, 148(3), 362-370. doi:10.1002/ajpa.22058

- Gildersleeve, K., Haselton, M. G., & Fales, M. R. (2014). Do women's mate preferences change across the ovulatory cycle? A meta-analytic review. *Psychological Bulletin*, 140(5), 1205-1259. doi:10.1037/a0035438
- Gladue, B. A., Boechler, M., & McCaul, K. D. (1989). Hormonal response to competition in human males. *Aggressive Behavior*, 15(6), 409-422. doi:10.1002/1098-2337(1989)15:6<409::AID-AB2480150602>3.0.CO;2-P
- Gonzalez-Bono, E., Salvador, A., Serrano, M. A., & Ricarte, J. (1999). Testosterone, cortisol, and mood in a sports team competition. *Hormones and Behavior*, 35(1), 55-62. doi:10.1006/hbeh.1998.1496
- Gorelik, G., & Bjorklund, D. F. (2015). The effect of competition on men's self-reported sexual interest. *Evolutionary Psychological Science*, 1(3), 141-149. doi:10.1007/s40806-015-0016-6
- Gray, P. B., Jeffrey Yang, C. F., & Pope Jr, H. G. (2006). Fathers have lower salivary testosterone levels than unmarried men and married non-fathers in Beijing, China. *Proceedings of the Royal Society B: Biological Sciences*, 273(1584), 333-339. doi:10.1098/rspb.2005.3311
- Gray, P. B., Kahlenberg, S. M., Barrett, E. S., Lipson, S. F., & Ellison, P. T. (2002). Marriage and fatherhood are associated with lower testosterone in males. *Evolution and Human Behavior*, 193-201. doi:10.1016/S1090-5138(01)00101-5
- Grebe, N. M., Sarafin, R. E., Strenth, C. R., & Zilioli, S. (2019). Pair-bonding, fatherhood, and the role of testosterone: A meta-analytic review. *Neuroscience & Biobehavioral Reviews*, 98, 221-233. doi:10.1016/j.neubiorev.2019.01.010

- Grossmann, K., Grossmann, K. E., Fremmer-Bombik, E., Kindler, H., Scheuerer-Englisch, H., & Zimmermann, A. P. (2002). The uniqueness of the child–father attachment relationship: Fathers’ sensitive and challenging play as a pivotal variable in a 16-year longitudinal study. *Social Development*, 11(3), 301-337. doi:10.1111/1467-9507.00202
- Gusmão, L., Brión, M., & Gomes, I. (2008). The human Y chromosome male-specific polymorphisms and forensic genetics. In M. J. Bogusz (Ed.), *Handbook of Analytical Separations* (Vol. 6, pp. 969-1000). Elsevier Science BV.
- Hattori, T., & Wilczynski, W. (2014). Differences in forebrain androgen receptor expression in winners and losers of male anole aggressive interactions. *Brain Research*, 1582, 45-54. doi:10.1016/j.brainres.2014.07.028
- Henrich, J. (2020). *The WEIRDest people in the world*. New York: Farrar, Straus and Giroux.
- Hill, A. K., Hunt, J., Welling, L. L., Cárdenas, R. A., Rotella, M. A., Wheatley, J. R., . . . Puts, D. A. (2013). Quantifying the strength and form of sexual selection on men's traits. *Evolution and Human Behavior*, 34(5), 334-341. doi:10.1016/j.evolhumbehav.2013.05.004
- Hill, K., & Hurtado, A. M. (2017). *Ache life history: The ecology and demography of a foraging people*. New York: Routledge.
- Hodges-Simeon, C. R., Gurven, M., & Gaulin, S. J. (2015). The low male voice is a costly signal of phenotypic quality among Bolivian adolescents. *Evolution and Human Behavior*, 36(4), 294-302. doi:10.1016/j.evolhumbehav.2015.01.002
- Hrdy, S. (2009). *Mothers and others: The evolutionary origins of mutual understanding*. Cambridge: Belknap, Harvard.

- Hutchinson, D. L., Norr, L., Schober, T., Marquardt, W. H., Walker, K. J., Newsom, L. A., & Scarry, C. M. (2016). The Calusa and prehistoric subsistence in central and south Gulf Coast Florida. *Journal of Anthropological Archaeology*, 41, 55-73.
doi:10.1016/j.jaa.2015.10.004
- Jasienska, G. (2020). Costs of reproduction and ageing in the human female. *Philosophical Transactions of the Royal Society B*, 375(1811), 20190615. doi:10.1098/rstb.2019.0615
- Jeffery, K. J., Abernethy, K. A., Tutin, C. E., Anthony, N. A., & Bruford, M. W. (2007). Who killed Porthos? Genetic tracking of a gorilla death. *Integrative zoology*, 2(2), 111-119.
doi:10.1111/j.1749-4877.2007.00050.x
- Jokiniemi, A., Magris, M., Ritari, J., Kuusipalo, L., Lundgren, T., Partanen, J., & Kekäläinen, J. (2020). Post-copulatory genetic matchmaking: HLA-dependent effects of cervical mucus on human sperm function. *Proceedings of the Royal Society B*, 287(1933), 20201682.
doi:10.1098/rspb.2020.1682
- Jonason, P. K., Li, N. P., & Madson, L. (2012). It is not all about the Benjamins: Understanding preferences for mates with resources. *Personality and Individual Differences*, 52(3), 306-310. doi:10.1016/j.paid.2011.10.032
- Jones, B. C., Hahn, A. C., Fisher, C. I., Wang, H., Kandrik, M., & DeBruine, L. M. (2018). General sexual desire, but not desire for uncommitted sexual relationships, tracks changes in women's hormonal status. *Psychoneuroendocrinology*, 88, 153-157.
doi:10.1016/j.psyneuen.2017.12.015
- Jones, B. C., Hahn, A. C., Fisher, C. I., Wang, H., Kandrik, M., Han, C., . . . DeBruine, L. M. (2018). No compelling evidence that preferences for facial masculinity track changes in

- women's hormonal status. *Psychological Science*, 29(6), 996-1005.
doi:10.1177/0956797618760197
- Jünger, J., Kordsmeyer, T. L., Gerlach, T. M., & Penke, L. (2018). Fertile women evaluate male bodies as more attractive, regardless of masculinity. *Evolution and Human Behavior*, 39(4), 412-423. doi:10.1016/j.evolhumbehav.2018.03.007
- Kaplan, H. S. (1997). The evolution of the human life course. In K. W. Finch (Ed.), *Between Zeus and Salmon: The biodemography of aging* (pp. 175-211). Washington, D.C.: National Academy of Sciences.
- Kayser, M., Brauer, S., Weiss, G., Schiefenhövel, W., Underhill, P., Shen, P., . . . Stoneking, M. (2003). Reduced Y-chromosome, but not mitochondrial DNA, diversity in human populations from West New Guinea. *American Journal of Human Genetics*, 72(2), 281-302. doi:10.1086/346065
- Kočnar, T., Saribay, S. A., & Kleisner, K. (2019). Perceived attractiveness of Czech faces across 10 cultures: Associations with sexual shape dimorphism, averageness, fluctuating asymmetry, and eye color. *PLOS ONE*, 14(11), e0225549.
doi:10.1371/journal.pone.0225549
- Kordsmeyer, T. L. (in press). Capital as an integrative conceptualisation of human characteristics, behaviour, and outcomes predicting reproductive success and evolutionary fitness. *Evolutionary Psychological Science*.
- Kordsmeyer, T. L., Hunt, J., Puts, D. A., Ostner, J., & Penke, L. (2018). The relative importance of intra- and intersexual selection on human male sexually dimorphic traits. *Evolution and Human Behavior*, 39(4), 424-436. doi:10.1016/j.evolhumbehav.2018.03.008

- Kraft, C., & Mayeux, L. (2018). Associations among friendship jealousy, peer status, and relational aggression in early adolescence. *The Journal of Early Adolescence*, 38(3), 385-407. doi:10.1177/0272431616670992
- Krems, J. A., Claessens, S., Fales, M. R., Campenni, M., Haselton, M. G., & Aktipis, A. (2021). An agent-based model of female rivalry hypothesis for concealed ovulation in humans. *Nature Human Behaviour*, 1-10. Retrieved from <https://www.nature.com/articles/s41562-020-01038-9>
- LaFreniere, P. (2011). Evolutionary functions of social play: Life histories, sex differences, and emotion regulation. *American Journal of Play*, 3(4), 464-488. Retrieved from <https://eric.ed.gov/?id=EJ985542>
- Lehmann, G. K., & Calin-Jageman, R. J. (2017). Is red really romantic? Two pre-registered replications of the red-romance hypothesis. *Social Psychology*, 48(3), 1-10. doi:10.1027/1864-9335/a000296
- Lippa, R. A. (2009). Sex differences in sex drive, sociosexuality, and height across 53 nations: Testing evolutionary and social structural theories. *Archives of Sexual Behavior*, 38(5), 631-651. doi:10.1007/s10508-007-9242-8
- Lu, H. J., Zhu, X. Q., & Chang, L. (2015). Good genes, good providers, and good fathers: Economic development involved in how women select a mate. *Evolutionary Behavioural Sciences*, 9(4), 215-228. doi:10.1037/ebbs0000048
- Marcinkowska, U. M., Rantala, M. J., Lee, A. J., Kozlov, M. V., Aavik, T., Cai, H., . . . Dixon, B. J. (2019). Women's preferences for men's facial masculinity are strongest under favorable ecological conditions. *Scientific Reports*, 9(1), 1-10. doi:10.1038/s41598-019-39350-8

- Markey, P. M., & Markey, C. N. (2010). Changes in pornography-seeking behaviors following political elections: An examination of the challenge hypothesis. *Evolution and Human Behavior*, 31(6), 442-446. doi:10.1016/j.evolhumbehav.2010.06.004
- Markey, P., & Markey, C. (2011). Pornography-seeking behaviors following midterm political elections in the United States: A replication of the challenge hypothesis. *Computers in Human Behavior*, 27(3), 1262-1264. doi:10.1016/j.chb.2011.01.007
- Mattison, S. M., Scelza, B., & Blumenfield, T. (2014). paternal investment and the positive effects of fathers among the matrilineal Mosuo of Southwest China. *American Anthropologist*, 116(3), 591-610. doi:10.1111/aman.12125
- Mautz, B. S., Wong, B. B., Peters, R. A., & Jennions, M. D. (2013). Penis size interacts with body shape and height to influence male attractiveness. *Proceedings of the National Academy of Sciences*, 110(17), 6925-6930. doi:10.1073/pnas.1219361110
- Mazur, A., Booth, A., & Dabbs Jr, J. M. (1992). Testosterone and chess competition. *Social Psychology Quarterly*, 55(1), 70-77. doi:10.2307/2786687
- Međedović, J. (2021). Reproductive ecology of short and long-term mating: implications for sexual selection and life history theory. *PsyArXiv*. Retrieved from <https://psyarxiv.com/6zcnm/download?format=pdf>
- Mesterson-Gibbons, M. (1999). On the evolution of pure winner and loser effects: A game-theoretic model. *Bulletin of Mathematical Biology*, 61(6), 1151-1186. Retrieved from <https://link.springer.com/article/10.1006/bulm.1999.0137>
- Miller, G. (2000). Sexual selection for indicators of intelligence. In G. Bock, J. Goode, & K. Webb (Eds.), *The Nature of Intelligence (Novartis Foundation Symposium 233)* (pp. 260-275). New York: Wiley.

- Mitani, J. C., Gros-Louis, J., & Richards, A. F. (1996). Sexual dimorphism, the operational sex ratio, and the intensity of male competition in polygynous primates. *The American Naturalism*, 147(6), 966-980. Retrieved from <https://www.journals.uchicago.edu/doi/abs/10.1086/285888>
- Moore, L. T., McEvoy, B., Cape, E., Simms, K., & Bradley, D. G. (2006). A Y-chromosome signature of hegemony in Gaelic Ireland. *The American Journal of Human Genetics*, 78(2), 334-338. doi:<https://doi.org/10.1086/500055>
- Muller, M. N. (2002). Agonistic relations among Kanyawara chimpanzee. In C. Boesch, G. Hohmann, & L. Merchant (Eds.), *Behavioural Diversity in Chimpanzees and Bonobos* (pp. 112-124). Cambridge: Cambridge University Press.
- Nindl, B. C., Scoville, C. R., Sheehan, K. M., Leone, C. D., & Mello, R. P. (2002). Gender differences in regional body composition and somatotrophic influences of IGF-I and leptin. *Journal of Applied Physiology*, 92(4), 1611-1618. doi:10.1152/japplphysiol.00892.2001
- Page, A. E., Thomas, M. G., Smith, D., Dyble, M., Viguiier, S., Chaudhary, N., . . . Migliano, A. B. (2019). Why care for someone else's child? Testing adaptive hypotheses in Agta foragers. *Nature Human Behaviour*, 3(11), 1154-1163. doi:10.1038/s41562-019-0679-2
- Parikh, V. N., Clement, T. S., & Fernald, R. D. (2006). Androgen level and male social status in the African cichlid, *Astatotilapia burtoni*. *Behavioural Brain Research*, 166(2), 291-295. doi:10.1016/j.bbr.2005.07.011
- Penton-Voak, I. S., Jacobson, A., & Trivers, R. (2004). Populational differences in attractiveness judgments of male and female faces: Comparing British and jamaican samples. *Evolution and Human Behavior*, 25(6), 355-370. doi:10.1016/j.evolhumbehav.2004.06.002

- Pietraszewski, D., & Wertz, A. E. (2021). Why evolutionary psychology should abandon modularity. *Perspectives on Psychological Science*. doi:10.1177/1745691621997113
- Prause, N., Park, J., Leung, S., & Miller, G. (2015). Women's preferences for penis size: a new research method using selection among 3D models. *PLOS ONE*, 10(9), e0133079. doi:10.1371/journal.pone.0133079
- Prokop, Z. M., Michalczyk, Ł., Drobnik, S. M., Herdegen, M., & Radwan, J. (2012). Meta-analysis suggests choosy females get sexy sons more than “good genes”. *Evolution: International Journal of Organic Evolution*, 66(9), 2665-2673. doi:10.1111/j.1558-5646.2012.01654.x
- Puts, D. A. (2010). Beauty and the beast: Mechanisms of sexual selection in humans. *Evolution and Human Behavior*, 31(3), 157-175. doi:10.1016/j.evolhumbehav.2010.02.005
- Puts, D. A., Welling, L. L., Burriss, R. P., & Dawood, K. (2012). Men's masculinity and attractiveness predict their female partners' reported orgasm frequency and timing. *Evolution and Human Behavior*, 33(1), 1-9. doi:10.1016/j.evolhumbehav.2011.03.003
- Renoult, J. P., Bovet, J., & Raymond, M. (2016). Beauty is in the efficient coding of the beholder. *Royal Society Open Science*, 3(3), 160027. doi:10.1098/rsos.160027
- Roney, J. R., Hanson, K. N., Durante, K. M., & Maestripieri, D. (2006). Reading men's faces: Women's mate attractiveness judgments track men's testosterone and interest in infants. *Proceedings of the Royal Society B*, 273, 2169-2175. doi:10.1098/rspb.2006.3569
- Roser, M., Appel, C., & Ritchie, H. (2013). *Human Height*. Retrieved from OurWorldInData.org: <https://ourworldindata.org/human-height>
- Ryan, M. J. (2021). Darwin, sexual selection, and the brain. *Proceedings of the National Academy of Sciences*, 118(8), e2008194118. doi:10.1073/pnas.2008194118

- Saxton, T. K., Mackey, L. L., McCarty, K., & Neave, N. (2016). A lover or a fighter? Opposing sexual selection pressures on men's vocal pitch and facial hair. *Behavioral Ecology*, 27(2), 512-519.
- Saxton, T. K., Mackey, L. L., McCarty, K., & Neave, N. (2016). A lover or a fighter? Opposing sexual selection pressures on men's voca pitch and facial hair. *Behavioral Ecology*, 27(2), 512-519. doi:10.1093/beheco/arv178
- Sayres, M. A., Lohmueller, K. E., & Nielsen, R. (2014). Natural selection reduced diversity on human Y chromosomes. *PLoS Genetics*, 10(1), e1004064.
doi:<https://doi.org/10.1371/journal.pgen.1004064>
- Scalise Sugiyama, M. (2011). The forager oral tradition and the evolution of prolonged juvenility. *Frontiers in Psychology*, 2(133). doi:10.3389/fpsyg.2011.00133
- Scelza, B. A. (2011). Female choice and extra-pair paternity in a traditional human population. *Biology Letters*, 7(6), 889-891. doi:10.1098/rsbl.2011.0478
- Schaefer, K., Mitteroecker, P., Gunz, P., Bernhard, M., & Bookstein, F. L. (2004). Craniofacial sexual dimorphism patterns and allometry among extant hominids. *Annals of Anatomy- Anatomischer Anzeiger*, 186(5-6), 471-478. doi:10.1016/S0940-9602(04)80086-4
- Schmitt, D. P. (2005). Sociosexuality from Argentina to Zimbabwe. *Behavioral and Brain Sciences*, 28(2), 247-311. doi:10.1017/s0140525x05000051
- Seffrin, P., & Ingulli, P. (2021). Brains, brawn, and beauty: The complementary roles of intelligence and physical aggression in attracting sexual partners. *Aggressive Behavior*, 47(1), 38-49. doi:10.1002/ab.21934

- Sell, A., Lukazsweski, A. W., & Townsley, M. (2017). Cues of upper body strength account for most of the variance in men's bodily attractiveness. *Proceedings of the Royal Society B: Biological Sciences*, 284(1869), 20171819. doi:doi.org/10.1098/rspb.2017.1819
- Shackelford, T. K., Schmitt, D. P., & Buss, D. M. (2005). Universal dimensions of human mate preferences. *Personality and Individual Differences*, 39(2), 447-458.
doi:10.1016/j.paid.2005.01.023
- Singh, M., & Glowacki, L. (2021). Human social organization during the Late Pleistocene: Beyond the nomadic-egalitarian model.
doi:https://doi.org/10.32942/osf.io/vusye
- Stanton, S. J., Beehner, J. C., Saini, E. K., Kuhn, C. M., & LaBar, K. S. (2009). Dominance, politics, and physiology: Voters' testosterone changes on the night of the 2008 United States presidential election. *PLOS ONE*, 4(10), e7543. doi:10.1371/journal.pone.0007543
- Stoffel, M. A., Acevedo-Whitehouse, K., Morales-Durán, N., Grosser, S., Chakarov, N., Krüger, O., . . . Hoffman, J. I. (2020). Early sexual dimorphism in the developing gut microbiome of northern elephant seals. *Molecular Ecology*, 29(11), 2109-2122.
doi:https://doi.org/10.1111/mec.15385
- Strassmann, B. I. (1981). Sexual selection, paternal care, and concealed ovulation in humans. *Ethology and Sociobiology*, 2(1), 31-40. doi:10.1016/0162-3095(81)90020-0
- 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. doi:10.1016/j.cub.2017.05.039
- Symons, D. (1979/1981). *The evolution of human sexuality*. New York: Oxford University Press.

- Taylor, A. B. (1997). Relative growth, ontogeny, and sexual dimorphism in Gorilla (Gorilla gorilla gorilla and G. g. beringei): Evolutionary and ecological considerations. *American Journal of Primatology*, 43(1), 1-31. doi:[https://doi.org/10.1002/\(SICI\)1098-2345\(1997\)43:1<1::AID-AJP1>3.0.CO;2-0](https://doi.org/10.1002/(SICI)1098-2345(1997)43:1<1::AID-AJP1>3.0.CO;2-0)
- Thompson, M. E., Machanda, Z. P., Fox, S. A., Sabbi, K. H., Oтали, E., González, N. T., . . . Wrangham, R. W. (2020). Evaluating the impact of physical frailty during ageing in wild chimpanzees (Pan troglodytes schweinfurthii). *Philosophical Transactions B*, 375(1811), 20190607. doi:<https://doi.org/10.1098/rstb.2019.0607>
- Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man, 1871-1971* (pp. 136-179). Chicago: Aldine-Atherton.
- Trivers, R. L. (1974). Parent-offspring conflict. *Integrative and Comparative Biology*, 14(1), 249-264. doi:10.1093/icb/14.1.249
- UNODC. (2019). *Global study on homicide*. Vienna.
- von Rueden, C., Alami, S., Kaplan, H., & Gurven, M. (2018). Sex differences in political leadership in an egalitarian society. *Evolution and Human Behavior*, 39(4), 402-411. doi:<https://doi.org/10.1016/j.evolhumbehav.2018.03.005>
- Wadley, L., Esteban, I., de la Peña, P., Wojcieszak, M., Stratford, D., Lennox, S., . . . Sievers, C. (2020). Fire and grass-bedding construction 200 thousand years ago at Border Cave. *Science*, 369(6505), 863-866. doi:10.1126/science.abc7239
- Walter, K. V., Conroy-Beam, D., Buss, D. M., Asao, K., Sorokowska, A., Sorokowski, P., . . . Zupančič, M. (2020). Sex differences in mate preferences across 45 countries: A large-scale replication. *Psychological Science*, 408-423. doi:10.1177/0956797620904154

- Watts, D. P., Muller, M., Amsler, S. J., Mbabazi, G., & Mitani, J. C. (2006). Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. *American Journal of Primatology*, 68(2), 161-180. doi:<https://doi.org/10.1002/ajp.20214>
- West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. New York: Oxford University Press.
- White, S. A., Nguyen, T., & Fernald, R. D. (2002). Social regulation of gonadotropin-releasing hormone. *Journal of Experimental Biology*, 205(17), 2567-2581. Retrieved from <https://jeb.biologists.org/content/205/17/2567.short>
- Williams, G. C. (1966). *Adaptation and natural selection: A critique of some current evolutionary thought*. Princeton: Princeton University Press.
- Wingfield, J. C., Hegner, R. E., Dufty Jr, A. M., & Ball, G. F. (1990). The "challenge hypothesis": theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *The American Naturalist*, 136(6), 829-846. Retrieved from <https://www.journals.uchicago.edu/doi/abs/10.1086/285134>
- Wood, W., Kressel, L., Joshi, P. D., & Louie, B. (2014). Meta-analysis of menstrual cycle effects on women's mate preferences. *Emotion Review*, 6(3), 229-249. doi:10.1177/1754073914523073
- Wrangham, R. W., & Peterson, D. (1996). *Demonic males: Apes and the origins of human violence*. Boston: Houghton Mifflin.
- Zihlman, A. L., Stahl, D., & Boesch, C. (2008). Morphological variation in adult chimpanzees (Pan troglodytes verus) of the Taï National Park, Côte d'Ivoire. *American Journal of Physical Anthropology*, 135(1), 34-41. doi:<https://doi.org/10.1002/ajpa.20702>