
TARGET ARTICLE

The Ape That Thought It Was a Peacock: Does Evolutionary Psychology Exaggerate Human Sex Differences?

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This article looks at the evolution of sex differences in sexuality in human beings and asks whether evolutionary psychology sometimes exaggerates these differences. According to a common understanding of sexual selection theory, females in most species invest more than males in their offspring, and as a result, males compete for as many mates as possible, whereas females choose from among the competing males. The males-compete/females-choose (MCFC) model applies to many species but is misleading when applied to human beings. This is because males in our species commonly contribute to the rearing of the young, which reduces the sex difference in parental investment. Consequently, sex differences in our species are relatively modest. Rather than males competing and females choosing, humans have a system of mutual courtship: Both sexes are choosy about long-term mates, and both sexes compete for desirable mates. We call this the mutual mate choice (MMC) model. Although much of the evolutionary psychology literature is consistent with the MMC model, the traditional MCFC model exerts a strong influence on the field, distorting the emerging picture of the evolved sexual psychology of Homo sapiens. Specifically, it has led to the exaggeration of the magnitude of human sex differences, an overemphasis on men's short-term mating inclinations, and a relative neglect of male mate choice and female mate competition. We advocate a stronger focus on the MMC model.

Key words: evolutionary psychology, human mating, mutual mate choice, sex differences, sexual selection, sexual dimorphism.

With respect to human sexuality, there is a female human nature and a male human nature and these natures are extraordinarily different.—Donald Symons (1979), *The Evolution of Human Sexuality*, p. 11

Over the last few decades, evolutionary psychology (EP) has become increasingly influential within psychological science. As its profile has grown, criticisms of the field have mounted. A common criticism is that EP exaggerates the magnitude of sex differences in sexuality, including differences related to the pursuit of casual sex and to mate choice criteria (Conley, Moors, Matsick, Ziegler, & Valentine, 2011; Eagly & Wood, 1999; Miller, Putcha-Bhagavatula, & Pedersen, 2002; Zentner & Mitura, 2012). Evolutionary psychologists have resisted the criticism, charging their detractors with an ideologically motivated denial of evolved sex differences and a lack of familiarity with the claims of

modern EP (e.g., Buss, 2010; Schmitt, 2012a, 2012b; Schmitt et al., 2012). In this article, we attempt to negotiate a middle path through this thorny debate. We argue that, although some critics take an overly simplistic view of the field, there is some merit to the charge that EP exaggerates the sex differences in sexuality in our species. We trace this to a widespread schema of sexual selection that emphasizes male competition for mates and female mate choice. It is our contention that researchers in EP often have this schema lurking in the back of their minds and that it exerts a subtle—and sometimes not-so-subtle—influence on the EP image of human nature.

To be clear, we are not denying the existence of evolved psychological sex differences in our species. As our discussion will make clear, we accept both that there are differences and that they have their ultimate origin in our evolutionary history. Nonetheless, there

is still a question of exactly how large the differences are, and how best to construe them.

Two Views of Human Nature

To this end, we begin by presenting two views of sex differences in human sexuality. We call these the *males-competefemales-choose* (MCFC) model and the *mutual mate choice* (MMC) model. The MCFC model originates in Darwin's (1871) writings on sexual selection in nonhuman animals. It places a strong emphasis on sexual dimorphism, female mate choice, and male competition for mates. The MMC model, in contrast, emphasizes the idea that, as a result of high levels of male parental investment, humans evolved into a somewhat "androgynous" species—a species in which human females exhibit traits generally found only in males (e.g., competition for mates) and human males exhibit traits generally found only in females (e.g., the provision of parental care; choosiness about mates). If we imagine that all species can be located on a continuum spanning from extreme sexual dimorphism at one end to extreme sexual monomorphism at the other, the MCFC and MMC models represent attempts to locate humans on this continuum. Both sit somewhere in the middle, away from either extreme. However, the MMC model places us closer to the monomorphic end of the spectrum than does the MCFC model. The MMC model is the view we favor and will argue for in this article. Note that we are *not* arguing that the MCFC interpretation represents the singular or consensus view in EP. Elements of both models can be found in the EP literature. However, the MCFC model is important for reasons that will soon become clear.

The MCFC Model

Human beings are a sexually dimorphic species. We exhibit profound sex differences in sexuality. These trace back to sex differences in parental investment. Historically, women invested more into their offspring than men. For a start, eggs are biologically much more "expensive" than sperm. More important, mammalian reproductive physiology obliges women to bear the biological costs of a 9-month pregnancy and, until recently, several years of breastfeeding. Men's minimum contribution to the production of offspring is much smaller. Because of the sex difference in minimum parental investment, the maximum number of offspring a man can have in his lifetime is much higher than that of a woman. If a man mated with 100 women in a year, he could potentially have 100 offspring; if a woman mated with 100 men in a year, on the other hand, she would have no more offspring than if she had only mated with one. As such, males in our evolutionary past who pursued quantity of mates rather than quality had more offspring than other males, and the tendency to favor quantity became more and more

common among males over the generations (i.e., it was selected). In contrast, ancestral females who sought *quality* of mates rather than quantity had more surviving offspring than other females, and *that* tendency was selected among females. The net result is that men evolved to pursue short-term sexual relationships with as many women as possible, only opting for long-term pair bonding if they failed in this strategy, whereas women evolved to be choosier than men about their sexual partners, and to favor long-term pair bonds with men who helped provide for their offspring. Men court women and compete with one another to gain sexual access to as many women as possible. Women, in contrast, choose from among the available men. Women's choices then exert a strong selection pressure on men, shaping male courtship "ornaments" such as facial symmetry, status seeking, creative intelligence, and humor—all of which are human equivalents of the peacock's tail.

This is not, in our view, an entirely unreasonable position. That said, we suggest that every sentence is either false or, if true, potentially misleading without appropriate qualifications. To see why, consider our preferred model:

The MMC Model

Human beings are a relatively *monomorphic* species. Certainly, there are some average differences between the sexes, and certainly these trace back to the fact that women invest more in offspring than men. However, sex differences in sexuality are fairly modest in our species, precisely because sex differences in *parental investment* are fairly modest—much more modest than we would assume if we focused on gamete size, pregnancy, and lactation alone. As brain size increased in the hominin lineage,¹ our young became progressively more dependent and the childhood period became progressively longer. As a result, pair bonding and male parental care became central elements in our reproductive repertoire. This dramatically reduced the discrepancy in the maximum number of offspring that men versus women could produce. Although in principle a man could impregnate hundreds of women every year, in practice the reproductive ceiling for even the most attractive men was almost always much lower. Consequently, we exhibit reduced psychological dimorphism. Moreover, we are not the kind of species in which females alone exert mate choice or males alone compete for mates; we are a species with mutual courtship. Because men often invested in offspring, they evolved to be choosy about their mates—in other words, to pursue mate quality rather than just quantity, at least in long-term relationships. Similarly, because men differed in their capacity

¹Hominins are the group of species that evolved after the split from our common ancestor with the chimpanzees and bonobos, and which includes the australopithecines, *Homo erectus*, Neanderthals, and us.

to invest, women evolved to compete for the most desirable partners. Mutual mate choice has an important implication, namely, that sexual selection does not act wholly on human males. We are a species in which both sexes have their equivalents of the peacock's tail. Indeed, when it comes to physical beauty, the usual sex difference has arguably been reversed: Females are the "showier" sex.

To repeat, we are not suggesting that the MCFC model represents the unanimous view among evolutionary psychologists. Most would accept elements of the MMC model, including such ideas as that men exert mate choice and that both sexes pursue long-term relationships and invest in offspring. Why, then, are we emphasizing the MCFC model? The reason is that, although elements of the MMC model can be found in EP, the influence of the MCFC model is also clearly evident. This raises two issues. The first is simply that there is a contradiction in the literature. When it comes to the nature of sexuality in our species, there is some vacillating and lack of clarity. Humans are sometimes presented as an MCFC species and sometimes presented as an MMC species, but the inconsistency is rarely made explicit or resolved. The MCFC and MMC models sit together uneasily in the EP literature, and even in the work of particular researchers. The second issue is that the MCFC model distorts our understanding of our evolved nature. There is, as we will document, a tendency in EP to exaggerate the magnitude and importance of certain sex differences in our species, and much of this can be traced to the quiet influence of the MCFC model. Thus, it is our contention that the central tendency of the distribution of opinion in EP falls too close to the MCFC end of the spectrum, and a major goal of this article is to try to persuade evolutionary psychologists to migrate toward the other pole: toward the MMC model.

Overview of the Article

The article is divided into three main sections. The first discusses the historical origins of the MCFC model and makes the case that, although humans exhibit some genuine sex differences, we do not fit the standard MCFC mold. The second section discusses the evolution of pair bonding, paternal care, and mutual courtship in our species. Among other things, we discuss how the MMC model can be reconciled with individual differences and cross-cultural variability in mating patterns and childcare arrangements. Finally, the third section looks at the influence of the MCFC model within EP and argues that this model has encouraged the exaggeration of the size of the sex differences in at least three domains: short-term mating, mate choice, and competition over mates.

Origins of the MCFC Model

In this section, we look at the theoretical underpinnings of the MCFC model—sexual selection theory and parental investment theory—and ask whether these theories apply to human beings. We argue that they do indeed apply, and that they provide a better account of certain psychological sex differences than do rival sociocultural theories. However, we also argue that human beings do not fit the MCFC mold that applies so well to so many other animals. Although our species clearly exhibits some degree of dimorphism, we are closer to the monomorphic end of the monomorphism–dimorphism spectrum. This view is not inconsistent with sexual selection theory. On the contrary, it is exactly what sexual selection theory predicts for our species. This is because, although the sex difference in *minimum* parental investment is large in humans, the sex difference in *typical* parental investment is markedly smaller.

Sexual Selection and Parental Investment

The discussion of the evolution of sex differences started with Charles Darwin (1859, 1871). The great naturalist was puzzled by a widespread trend in the animal kingdom. In many species, males and females differ from one another, both morphologically and behaviorally (Andersson, 1994; Clutton-Brock, 1991; Daly & Wilson, 1983). Not only that, but the same kinds of differences occur again and again. In many vertebrate species—elephants and elephant seals, giraffes and gorillas, polar bears and pteranodons, whales and wolves—the males are larger than the females. Furthermore, in many species, males have more ornamentation or armamentation. The classic example of ornamentation is found in peacocks. Male peacocks have extravagant, colorful, and elaborate tail feathers; peahens, in contrast, are relatively drab. The classic example of armamentation is found in deer. Male deer have large and threatening antlers, which they use to intimidate and fight one another; females have none, or they have smaller ones that they rarely use. In addition to the recurring morphological differences, there are recurring behavioral differences. In species in which the males are larger than the females, the males also tend to have a stronger sex drive and greater interest in obtaining multiple mates, and tend to be more aggressive and competitive. In contrast, females in these species tend to be choosier about their sexual partners and to provide most of the parental care for their offspring. Furthermore, females generally have greater longevity. There are exceptions to all these rules, of course, but the trend is strong enough as to demand an explanation.

The explanation Darwin (1871) put forward was his theory of *sexual selection*. According to Darwin,

traits such as the peacock's tail and the deer's antlers are products of one of two processes: *intersexual selection* or *intrasexual selection*. Intersexual selection involves the sexual preferences of members of one sex (usually the females) for certain traits in the other. So, for example, peahens have a preference for males with larger-than-average tails; these males therefore have more offspring, and their offspring inherit the large tails. Over the generations, the males' tails become progressively larger. Intrasexual selection, on the other hand, involves competition between members of the same sex (usually the males) for sexual access to the other, or for access to the territories or status that are prerequisites for sexual access. The winners of these competitive interactions have more offspring than the losers, and thus any traits that gave the winners a competitive advantage are passed on at a greater frequency than competing variants. This can lead to the evolution of greater size and strength, more ferocious weaponry, and greater aggressiveness in the male of the species. These traits can be selected even if they increase their bearers' mortality risk, as long as they give a sufficiently large reproductive boost. As a result, males in these dimorphic species typically have a shorter lifespan than females.

Parental Investment and Potential Reproductive Rates

With the concepts of intersexual selection and intrasexual selection, Darwin was able to explain many of the sex differences observed in nature. However, there were various other puzzles that he did not solve. Why, for instance, is it usually the males that compete for mates and the females that exert mate choice? Why is it not just as often the other way around? In 1972, Robert Trivers set forth his answer to these questions when he linked the trend to sex differences in parental investment. According to modern *parental investment theory*, in species in which one sex invests more in offspring than the other, whether in terms of gamete size, pregnancy, or provisioning of the young, the potential reproductive rate of the higher investing sex is slower than that of the lesser investing sex, and thus the maximum number of offspring that any member of the higher investing sex can produce is lower (Clutton-Brock & Vincent, 1991). Usually, females invest more than males, and thus the maximum number of offspring any particular female can have is lower than the maximum of any particular male. The implications of this discrepancy are great.

First, because the greater-investing sex can produce fewer offspring over its lifetime, it often evolves to be choosier about its sexual partners. This is based on the principle that the more you invest, the wiser your investment needs to be. Because in many species, fe-

males invest more, females are generally choosier than males, and males are more likely to be ornamented (the ornaments being shaped by the female mate preferences). Second, because the lesser-investing sex can potentially sire many more offspring, it evolves a stronger tendency to pursue multiple matings. Because in many species, males invest less, males often have a stronger sex drive than females and a greater interest in sexual novelty. Parental investment also helps account for male-male competitiveness. In species with little male parental investment, any male can in principle impregnate not just one but many females. However, because the number of offspring a given female can have is finite, if one male has more than his "fair share" of offspring, other males must have less. Males possessing traits that increase their chances of being in the former group (the more-than-their-fair-share group) will pass those traits on to their offspring at a greater rate than those in the latter group, and thus the traits will be selected. In sum, the reason that females usually exert mate choice, and that males usually compete for females, is that females usually invest more than males in offspring.

This is not always the case, though, and some of the most persuasive evidence for parental investment theory comes from a group of species that buck the usual MCFC trend: the sex-role reversed species (Eens & Pinxten, 2000). The best examples are North American shorebirds such as jacanas, phalaropes, and spotted sandpipers (Oring, 1986). In these species, it is not the males but the females that are larger, more aggressive, and more ornamented, and the females that fight among themselves for access to the best mates. Furthermore, it is not the females but the males that are choosier about their sexual partners. These apparent counterexamples actually support Trivers's theory because, in all these species, the males are the higher-investing sex: The males single-handedly care for the eggs and feed the hatchlings. Other sex-role reversed species include the tidewater goby, various species of pipefish, and the midwife toad. Note that the most commonly cited example of a sex-role reversed animal—the seahorse—might not be role reversed after all. Although male seahorses incubate the eggs, females still tend to be somewhat choosier and males more competitive. This is because, despite the high male investment, there is little sex difference in male versus female reproductive rates (Eens & Pinxten, 2000).

The sex-role reversed species are a clear and surprising exception to the MCFC rule. However, there is another exception, and it is far more common: the sexually monomorphic species. These are often (though not always) species in which females and males form pair bonds, and both sexes invest heavily in offspring. Because both sexes invest, the discrepancy in the num-

ber of offspring each sex can produce is reduced and, consistent with parental investment theory, the normal pattern of sex differences is sharply diminished. This is most commonly found in birds; more than 90% of birds form pair bonds and tend toward monomorphism (Lack, 1968). But the same pattern is found in a handful of mammals as well. Among primates, for instance, pair bonding and monomorphism are found in some lemurs (e.g., indris), some tarsiers (e.g., pygmy tarsiers), some New World monkeys (e.g., owl monkeys, marmosets, and tamarins), and even some nonhuman apes (i.e., gibbons). But although sexually monomorphic species are fairly common, and although the pattern makes good sense in terms of parental investment theory, these species appear less frequently in discussions of sexual selection and parental investment than do unambiguously MCFC species such as peacocks and deer. The MCFC pattern is viewed as the primary outcome of sexual selection, as can be seen in the fact that the terms *male competition* and *female choice* are often treated as synonymous with intrasexual selection and intersexual selection, respectively. This emphasis on sexual dimorphism, female choice, and male competition was to have important effects when scientists started using sexual selection and parental investment to try to explain sex differences in human beings.

Injecting Some Evolutionary Biology Into Psychology

By the time evolutionary biologists brought their theories to maturity, a very different perspective on sex differences had developed elsewhere in the academy. This had its origins in the “blank slate” view of human nature, a view found to varying degrees in the work of many early luminaries of the social sciences, including the anthropologists Franz Boas and Margaret Mead, the sociologists Emile Durkheim and Karl Marx, and the psychologists John Watson and B. F. Skinner. The blank slate position implied that psychological sex differences, if they existed at all, were almost entirely the products of experience and socialization rather than biology. Social scientists could draw on a well-stocked arsenal of psychological theories to explain how this socialization might be achieved. A behaviorist approach would hold that parents and others reinforce sex-role-consistent behavior and punish sex-role-inconsistent behavior. Social learning theory would hold that people imitate relevant models, especially successful same-sex models with high status in their peer groups. Cognitive-developmental theories would hold that, during early childhood, people come to categorize themselves as either male or female and that they then strive to bring their behavior into line with their schemas of how members of their sex behave; in this way, sex-role consistent behavior becomes

self-reinforcing, rather than having to be reinforced by outside agencies. Regardless of the specifics, though, the underlying assumption was that most psychological sex differences are not part of human nature or biology. As Fausto-Sterling (1992) put it, “The key biological fact is that boys and girls have different genitalia” (pp. 152–153). Any other differences come from learning or culture.

For much of the 20th century, the blank slate view was the dominant view in the social sciences (Pinker, 2002; Tooby & Cosmides, 1992). With the popularization of sociobiology in the 1970s (Dawkins, 1976; Wilson, 1975), however, evolutionary approaches to human behavior became the locus of an academic culture war between biologically minded thinkers and advocates of the traditional social science model (Segerstråle, 2000). Scientists in both the biological and social sciences began to challenge “Nurture-Only” accounts of human sex differences and started applying sexual selection and parental investment theory to our species (Buss & Schmitt, 1993; Symons, 1979). They pointed out that, as with other placental mammals, the obligatory biological investment of human females is considerably higher than that of males. A woman must invest a minimum of 9 months into the production of any offspring and, for most of our evolutionary history, she would then have to breastfeed the infant for several years. In contrast, the minimum investment of the human male is the time and energy needed to court and impregnate the female. Given this sex difference in minimum parental investment, a number of human sex differences suddenly seemed to make good sense.

Recall that in dimorphic vertebrate species, certain morphological and behavioral traits cluster together. Males tend to be larger, to have a higher sex drive, and to be more competitive and aggressive. Females tend to be more selective about their sexual partners, to be more involved in childcare, and to have greater longevity. This all seems to apply to human beings. First, as we would expect in a species in which females invest more in offspring, there is an average sex difference in size: Across human populations, men are around 10% taller than women (Gaulin & Boster, 1985). There is also a large sex difference in lean muscle mass: Men have around 41% more fat-free muscle mass than women (Lassek & Gaulin, 2009). Second, there is good evidence that, on average, men have a greater interest in casual sex and sexual variety than women. This has been demonstrated in numerous questionnaire studies, in both Western and non-Western nations (Lippa, 2009; Peterson & Hyde, 2010; Schmitt, 2005b; Schmitt & 118 Members of the International Sexuality Description Project, 2003), and in studies looking at men and women’s receptiveness to apparently genuine sexual solicitations from strangers (Clark & Hatfield, 1989;

Guéguen, 2011; Hald & Høgh-Olesen, 2010). The difference can also be seen in real-world behavior: Men are the main consumers of pornography and prostitutes, whereas women are the main consumers of romance novels (Salmon, 2012; Symons, 1979). Third, on average, men are more competitive and physically aggressive than women. Across cultures, men engage in more direct aggression than women, especially between the ages of 20 and 30 (i.e., the time of peak mating effort), and especially when it comes to more extreme forms of violence (Archer, 2004; Daly & Wilson, 1988). Furthermore, across cultures, boys are more physically aggressive than girls (Eagly & Steffen, 1986), a pattern found also in many nonhuman anthropoid species (Symons, 1979). Fourth, women in all known societies are generally more involved in childcare than men (Wood & Eagly, 2002). This difference persists even in modern Western nations, despite the widespread ideal of gender equity and despite the availability of technologies such as baby bottles and baby formula, which enable men to care for infants just as ably as women (Buss, 2012). Fifth and finally, in virtually every nation, women have greater longevity than men (United Nations, 2009).

The fact that these sex differences are found across cultures, that the same sex differences cluster together throughout the animal kingdom, and that this cluster of differences relates not only to behavioral traits but also to “biological” traits such as body size and lifespan add up to a strong *prima facie* case that the behavioral differences have an evolutionary origin. As the evidence and arguments came to light, EP won more and more adherents. Of course, not everyone was convinced, and there were various efforts to find alternative explanations for the pattern—explanations that did not invoke innate psychological differences. We suggest, though, that none of them adequately accounts for the evidence.

Consider, for instance, Eagly and Wood’s Social Role Theory (SRT; Eagly & Wood, 1999; Wood & Eagly, 2012). SRT explains psychological sex differences in terms of the different social roles that cultures make available to their male and female members (Eagly & Wood, 1999; Wood & Eagly, 2012). Whereas most animals have relatively fixed social roles, humans have much greater behavioral flexibility. According to SRT, we evolved this flexibility to cope with the variability of our ancestral environments. Like our tools and technologies, our social roles are products of learning, innovation, and cumulative cultural evolution. In all societies to date, these processes have created a division of labor by sex, and this, according to SRT, is the main source of psychological sex differences in our species. Advocates of SRT do not rule out a role for biological sex differences in shaping men and women’s roles. However, the differences they emphasize are primarily physical rather than psychological ones. They include the fact that men are larger and

stronger than women, and the fact that women alone can get pregnant and nurse offspring. These differences mean, for instance, that men are more likely to take on roles involving heavy physical labor or aggression, whereas women are more likely to take on aparental role. Importantly, according to SRT, because the same *physical* sex differences are found in all cultures, the same *psychological* sex differences are found in all cultures as well—not because they are direct products of evolution, but because the physical differences tend to channel our social roles in certain directions.

Thus, SRT attempts to explain the cross-cultural universality of certain psychological sex differences in our species without having to posit a direct evolutionary contribution. But does the approach stand up to scrutiny? We suggest not. First, some of the central predictions of SRT are not borne out by the data. SRT implies that, in societies with higher gender equity—that is, in societies where the division of labor is less sex-linked—men and women will have more similar roles and will therefore be more similar psychologically (Wood & Eagly, 2012). Consistent with this expectation, some sex differences are indeed smaller in societies with greater gender equity. This includes differences in the importance of status and resources in a long-term mate (Eagly & Wood, 1999; Zentner & Mitura, 2012) and differences in stereotypically masculine or “agentic” behavior (see Wood & Eagly, 2012, for a review). However, many other sex differences are actually *larger* in more equitable societies. This is the case, for instance, for sex differences in attachment styles, the Big Five personality traits, certain cognitive abilities, crying patterns, depression, interpersonal violence, self-esteem, and values (summarized in Schmitt, 2012b). This mixed pattern is hard to reconcile with the idea that most sex differences stem from the division of labor by sex. It may fit better with the idea that, in modern Western societies, people are generally freer to act on their preferences and nurture their own individuality, and, as a result, sex differences often return to more natural, preagricultural levels: smaller in some cases but larger in others.

There is, however, a more serious problem with SRT. Although this approach might be able to explain the cross-cultural universality of the sex differences in question, it fails to explain the cross-species trend. As we have seen, the pattern of sex differences found in our species mirrors that found in most mammals and in many other animals. As such, considerations of parsimony suggest that the best explanation for the human differences will invoke evolutionary forces common to many species, rather than social forces unique to our own. When we find the standard pattern of differences in other, less culture-bound creatures, we inevitably explain this in evolutionary terms. It seems highly dubious, when we find exactly the same pattern in human beings, to say that, in the case of this one

primate species, we must explain it in terms of an entirely different set of causes—learning or cumulative culture—which coincidentally replicates the pattern found throughout the rest of the animal kingdom. Anyone who wishes to adopt this position has a formidable task in front of them. They must explain why, in the hominin lineage uniquely, the standard evolved psychological differences suddenly became maladaptive, and thus why natural selection “wiped the slate clean” of any biological contribution to these differences. They must explain why natural selection eliminated the psychological differences but left the correlated physical differences intact. And they must explain why natural selection would eliminate the psychological differences and leave it all to learning, when learning simply replicated the same sex differences anyway. How could natural selection favor extreme flexibility with respect to sex differences if that flexibility was never exercised and was therefore invisible to selection? No doubt social roles can help to shape sex-typical behavior, and social factors may magnify or minimize some sex differences. However, the cross-species trend provides a powerful reason to think that evolutionary forces are the primary cause of the psychological sex differences under discussion.

Even accepting this, though, questions remain about the magnitude of these evolved differences and the best way to construe them. The first question is, Does the fact that we possess these sex differences imply that we are an MCFC species?

Making Sense of the Differences

This is certainly what some sociobiologists and evolutionary psychologists have concluded. For instance, one of the founding fathers and popularizers of sociobiology, E. O. Wilson (1978), wrote,

It pays males to be aggressive, hasty, fickle, and indiscriminating. In theory it is more profitable for females to be coy, to hold back until they can identify males with the best genes. In species that rear young, it is also important for the females to select males who are more likely to stay with them after insemination. . . . Human beings obey this biological principle faithfully. (p. 29)

In other words, like peacocks, human males compete with one another for access to females and are indiscriminate in their sexual proclivities; like peahens, human females choose those males whose good genes shine through in their competitive prowess; and all of this stems ultimately from the fact that women are the primary care givers for their offspring. Of course, men often help care for their offspring as well. However, an extreme MCFC view would have to hold that this is a social invention rather than an evolved tendency,

or else that it is an evolved “second-best strategy” for men who do not have the social status or good genes necessary to obtain multiple mates instead (see, e.g., Gangestad & Simpson, 2000).

Thus, the MCFC model provides one lens through which we might interpret the sex differences in our species. On closer inspection, though, this model starts to jar with a lot of what we know about human courtship and reproductive behavior. Rather than females alone caring for offspring, human males commonly provide substantial postcoital investment (albeit less than females; Geary, 2000; Gray & Anderson, 2010; Marlowe, 2000). Rather than females exercising mate choice and males competing for females, both sexes have species-typical mate preferences (Buss, 1989), and both sexes compete for desirable members of the other sex (Buss, 1988; Campbell, 2002). These are not trivial qualifications. They make human beings an exception to the MCFC rule, and make us extremely unusual within the wider animal kingdom.

But this leaves us with a puzzle. On the one hand, we have a rich collection of sex differences that make good sense in terms of parental investment theory; on the other, we do not seem to fit the MCFC mold. How can we reconcile these apparently contradictory facts? There are two elements to our answer. First, we suggest that, although humans are somewhat dimorphic, we are closer to the monomorphic end of the spectrum than most mammals—close enough, at any rate, that we have a system of mutual mate choice rather than the more asymmetrical MCFC system. Second, sex differences in human beings are not like those found in typical MCFC species. In other animals, we often find sexually dichotomous differences in behavior. In many mammalian species, for instance, females are parental and males are simply not (Clutton-Brock, 1991). In human beings, on the other hand, sex differences usually involve modest differences in the central tendency for each group, with strongly overlapping distributions and smaller differences between groups than within them (Carothers & Reis, 2013). These are two very different types of sex differences, and it is important to avoid mistaking one for the other. Certainly, humans exhibit large sex differences in some *physical* traits, such as muscle mass and strength (Lassek & Gaulin, 2009). However, behavioral and psychological sex differences are almost always less pronounced (Hyde, 2005).² From a comparative perspective, we are a relatively monomorphic mammal, with relatively monomorphic minds.

At first glance, this assertion might appear to be inconsistent with parental investment theory. As we have seen, a common reading of the implications of Trivers’s

²The main exception to this rule concerns preferred sexual partners: The vast majority of men are primarily attracted to women, whereas the vast majority of women are primarily attracted to men.

theory for our species is that, like other mammals, the obligatory biological investment for men is much lower than that for women, and as a result, humans are highly dimorphic. The trouble with this formulation (and perhaps one of the reasons that people are inclined to exaggerate the sex differences in our species) is that it focuses on the sex difference in *minimum* parental investment, rather than in *typical* parental investment. Although the minimum investment by human males is indeed small (“a few minutes of sex and a teaspoon of semen,” as Pinker, 1997, put it, p. 468), the typical level of male investment is a lot higher. When both sexes invest heavily in offspring, the sex difference in reproductive variability is reduced, and this leads to a proportionate reduction in sexual dimorphism. Furthermore, both sexes may evolve to exert mate choice and to compete for desirable mates. This is not a radical reinterpretation of parental investment theory; Trivers (1972) himself devoted most of the second half of his seminal chapter on the theory to this point, noting that, “where male parental investment per offspring is comparable to female investment one would expect male and female reproductive success to vary in similar ways and for female choice to be no more discriminating than male choice” (p. 141). In the next section, we argue that this is exactly what is found in our species, and that it finds its ultimate origin in the evolution of human-level intelligence.

The Evolution of Mutual Mate Choice

Human beings are an exception to many general rules in biology. In many species, female mate choice alone is important; in our species, male mate choice is important as well. In many species, males alone are showy and ornamented; in our species, females are as well. In many species, males alone compete for mates; in our species, females compete as well. In many species, males invest nothing other than sperm in their offspring; in our species, men typically invest a great deal. Not only are human beings exceptional in these ways, but they all tie together into a cohesive story. The story, in brief, is as follows. Human offspring are extremely costly. Because of our large brains, our young are helpless at birth and have an extended juvenile period. Consequently, they require more care than the mother alone could provide. The high levels of investment required by human offspring led to the evolution of various forms of *allomaternal care* (care from individuals other than the mother). This includes the evolution of male parental care, often in the context of reasonably durable pair bonds. Although humans naturally engage in a wide range of mating behaviors, from monogamy to polygyny to promiscuity, the need for heavy investment in offspring meant that pair bonding and male parental care assumed a particularly important place in our reproductive repertoire. This in

turn precipitated the evolution of mutual courtship in our species: Males evolved to be choosy, and females evolved to compete for mates. In the following sections, we elaborate on each element of this story. We then consider some possible criticisms of our position.

Human Offspring Are Extremely Costly

The starting point for our argument is the fact that human offspring require an enormous amount of investment. According to one estimate, it takes 10 to 13 million calories to rear human offspring from birth to nutritional independence in a foraging or foraging/horticultural society, over and above any calories they acquire themselves during that time (Kaplan, 1994). This makes our young much costlier than the young of even our closest primate cousins (Hrdy, 2009). The high cost of rearing human offspring is largely a consequence of our high intelligence and large brains. Our brains make our offspring costly for two main reasons.

The first is that human young are altricial (i.e., they are helpless and utterly dependent at birth). This is widely believed to be the result of the confluence of two unique attributes of our species: our big brains and bipedalism. Bipedalism evolved first, and necessitated the reengineering of the pelvis. One of the side effects of this reengineering was that the pelvic canal became rather narrow. This created a major problem when selection later started favoring larger brains. How could females with narrow pelvic canals give birth to such large-brained babies? This is sometimes known as *the obstetric dilemma*. The (partial) solution that selection hit on was for hominin babies to be born earlier than is ideal, when their heads are still small enough to squeeze through the birth canal. By primate standards, human infants are born around 12 months prematurely (Martin, 1990). As Taylor (2010) put it, for the 1st year of their lives, they are “extra-uterine fetuses,” unable to move about or feed themselves. This significantly increased the amount of attention and care required during this early stage of development. (See Dunsworth, Warrener, Deacon, Ellison, & Pontzer, 2012, for an alternative explanation for the timing of human birth.)

The second reason that our offspring are so costly is that humans have an extended childhood. As Hrdy (2009) pointed out, with other Great Apes, as soon as an infant is weaned, it begins provisioning itself. For humans, the situation is very different. Although children in forager societies often gather much of their own food from early childhood, they do not start acquiring more calories than they consume until around 18 years of age (Kaplan, 1994). Once again, our brains are responsible: It takes a long time to grow a large brain and to equip it with the various skills needed for adult life in a technologically sophisticated and socially complex community. The fossil record supports the view that the

increase in brain size in the hominin lineage went hand in hand with an increase in the length of childhood. It has been estimated that australopithecines (which had brains around the size of chimpanzee brains) attained reproductive maturity at around 12 years, that *Homo erectus* (which had considerably larger brains) attained reproductive maturity at 14 to 15 years, and that *Homo sapiens* (which had larger brains again) attained reproductive maturity in their late teens (Bogin, 1999).

Not only are individual offspring costly, but human females have a comparatively short interbirth interval. Among foragers (i.e., hunter-gatherers), the typical interbirth interval is 3 to 4 years (Pennington, 2001). For other Great Apes, it is 4.5 to 8 years—a surprisingly big difference given that human infants are larger than the young of other Great Apes and take longer to reach maturity (Hrdy, 2009). The net result is that, unlike, say, female chimpanzees, women often have more than one dependent offspring at the same time: a nursing infant and a weaned but still-dependent child. None of this would be possible without significant allomaternal care.

Costly Offspring Led to the Evolution of Pair Bonding and Paternal Care

As large brains evolved in our lineage, the need for allomaternal care increased dramatically, especially during pregnancy and infancy (Marlowe, 2003a). Selection appears to have taken several paths to satisfying this need: Mothers commonly receive aid from a variety of interested parties, including grandparents (especially maternal grandmothers) and siblings (especially older sisters; Hawkes, 2005; Hrdy, 2009; Sear & Mace, 2008). For present purposes, though, the most important development was the evolution of male parental investment, often within the context of a pair bond. The idea that humans form pair bonds, and that males often invest in their young, has a long history in biological anthropology (Lovejoy, 1981; Washburn & Lancaster, 1968). Early incarnations of the idea were criticized for painting an overly simplistic picture, according to which “Man the Hunter” provisioned his dependent wife and children with meat in a stable nuclear family, suspiciously reminiscent of a 1950s-style Western family (Hawkes, 1991; Hrdy, 1981). However, with appropriate amendments and qualifications, the idea that pair bonding and biparental care are a central part of our evolutionary endowment appears to be viable (Geary, 2000; Geary & Flinn, 2001; Gray & Anderson, 2010; Kaplan, Hill, Lancaster, & Hurtado, 2000; Lancaster & Lancaster, 1985; Miller & Fishkin, 1997). In the following, we consider first the evolution of pair bonding, then the evolution of paternal care, and finally evidence for the universality of these phenomena in human beings.

Pair Bonding

Pair bonding (or monogamy) is an extremely rare mating system among mammals, found in less than 5% of species (Kleiman, 1977). Nonetheless, it appears to be a central element in humans’ reproductive repertoire. It is therefore a curious fact that our dominant mating system is more like the typical mating system of birds than that of most mammals, including our nearest relatives, the Great Apes. In making this claim, it is important to be clear about three things.

First, the claim is not that pair bonds necessarily last for life. In the absence of socially enforced lifelong monogamy, most pair bonds last for months or years but ultimately dissolve (Fisher, 1992). Note, though, that a significant minority of pair bonds do last until the end of the lifespan, even in traditional forager societies that lack rigid strictures on divorce (see, e.g., Marlowe, 2004).

Second, the claim is not that human pair bonds are always sexually exclusive. Most surveys suggest that considerably fewer than 50% of men or women in long-term committed relationships are ever unfaithful (Blow & Hartnett, 2005). Nonetheless, some are, and as a result, a certain fraction of offspring are sired by someone other than the social father (the best estimates place this at around 1–3%; Anderson, 2006; Wolf, Musch, Enczmann, & Fischer, 2012).

Third, the claim is not that pair bonding is our one “true” or natural mating system. Humans exhibit all the mating systems found in other species, including monogamy, polygyny (one man, two or more women), and even polyandry (one women, two or more men; Murdock, 1967).³ It is also not uncommon for people to engage in extrapair mating, or to engage in casual sex before marriage or between long-term relationships. Different frequencies of each of these mating behaviors are found in different cultures and different historical periods. However, with the exception of long-term polyandry, all are relatively common, and thus all are plausibly part of the evolved repertoire of the human animal. Thus, our claim is not that pair bonding is humanity’s singular mating pattern. Our claim instead is simply that the pair bond is the most common setting for sex and reproduction in our species, that it has been for a long time, and that this has left a deep imprint on our evolved nature.

Human pair bonds are held together by various factors, both social and psychological. It is the psychological factors that are most relevant here, however, as they are plausibly products of selection. They include sexual desire, romantic love, and long-term attachment (Fisher, 1992). They also include romantic jealousy (Buss, 2000). The pair bonds inspired by these

³This should not be too surprising; the mating system labels we apply to other species were originally coined by anthropologists to describe human mating patterns.

psychological states serve at least three evolutionary functions (see, e.g., Marlowe, 2000). The first is the impregnation of the female; this is, of course, closely linked to sexual desire. The second applies only to the male; it is to increase his probability of fathering the woman's offspring (this is known as the *mate guarding hypothesis*; Chapais, 2008). And the third is to facilitate male provisioning and protection of the female while she is pregnant and breastfeeding, and biparental care of the child for a time thereafter (Fisher, 1992; Marlowe, 2003a). The extent to which a pair bond serves each function depends on its duration. Some pair bonds are short-lived and thus can only serve the first two functions. But others last for many months, years, or even for life, and may therefore serve all three. It is important to remember that the proposed functions do not describe people's *motivations* for establishing pair bonds. Instead, they describe the selection pressures shaping the disposition to form these bonds—in other words, the selection pressures shaping emotions such as romantic love, long-term attachment, and jealousy. These emotions can lead people to form pair bonds without them having any awareness of the evolved function of the bond.

Paternal Care

Although pair bonds serve several functions, we maintain that the central one is paternal care. Paternal care plausibly enhanced the fitness of the men engaging in it. For one thing, given the dependency of human offspring, it may have increased the fraction of offspring reaching breeding age. In many forager societies, children without an investing father have lower survival rates than those with one (e.g., Dwyer & Minnegal, 1993; Hill & Hurtado, 1996). Admittedly, one study detected this “father effect” in only one third of small-scale societies (Sear & Mace, 2008). However, virtually all the societies in this study were agricultural societies, and thus it is unclear that the finding is representative of most of human evolution. Furthermore, survival is only one, rather exacting measure of male investment. Paternal care could boost the father's fitness even without boosting offspring survival. It could, for example, help shorten the woman's interbirth interval, through reducing the workload and calorific toll associated with raising a young child (Marlowe, 2001). This would increase the woman's fertility, which would enhance the man's fitness as well, as long as he had a reasonable probability of paternity. Finally, although the optimal situation for a pair-bonded man is to invest exclusively in his own offspring, if this option was not available, paternal investment in another man's offspring (e.g., a woman's children from a previous mate) may have increased his fitness, as long as it increased the probability that he would father the woman's next child (Daly & Wilson, 1998).

It might be observed that some men do not invest in their offspring, and that in some cultures, most men invest relatively little. This variability does not, however, undermine the claim that men have an evolved paternal psychology, *unless* that claim is taken to imply that men will invest equally in their offspring under all circumstances. A more realistic claim is that paternal investment is *facultative*—that is, that men evolved to invest more readily in some circumstances than others (Gangestad & Simpson, 2000). Consistent with this idea, there is evidence that male paternal psychology is sensitive to various evolutionarily relevant cues. For example, men invest less in offspring when their own mate value is high (Waynforth, 1999) and when females outnumber males in the local population (Marlowe, 1999a). This is presumably because men in these circumstances have more mating opportunities, and thus pursuing additional mates may boost fitness more than parenting. On the other hand, men tend to invest *more* in offspring when the offspring in question are likely to be theirs—in other words, when paternity probability is high (Apicella & Marlowe, 2004; Daly & Wilson, 1987). Variables like these may help account not only for individual differences in paternal investment within a given culture but also for average differences in paternal investment between cultures. In South American *partible paternity* societies, for instance, several men may invest in the offspring of a woman with whom they have had sexual relations (Beckerman & Valentine, 2002), but each may invest less than the average man in a society with more exclusive sexual bonds. Furthermore, in many traditional “matrilineal” societies (societies that often have low paternity probability), men typically invest more in the offspring of their sisters than the offspring of their wives (Hartung, 1985). Thus, in some situations, men may invest in children outside the context of a pair bond.

(We need not assume, incidentally, that selection has equipped men with an explicit concern about paternity. There are other possibilities. For instance, if men are more paternally inclined when involved in a close relationship, and if they are also more likely to remain in a close relationship when it appears to be sexually exclusive, then paternal investment will be correlated with paternity probability even without men necessarily fretting over the paternity of their wards—or even necessarily possessing a belief in unique paternity.)

In addition to stressing the variability of male parental investment, it is important to note that male investment is not the only source of allomaternal care in our species. Allomaternal care also often comes from grandmothers, older sisters, and other kin (especially female kin), and from unrelated female friends, perhaps in a context of reciprocal exchange (Hames, 1988; Hawkes, 2005; Hrdy, 2009). The quantity of care coming from each of these sources varies from

family to family and culture to culture (Muller, Marlowe, Bugumba, & Ellison, 2008; Sear & Mace, 2008; Waynforth, 1999). Again, this cross-cultural variability might seem to challenge the idea that humans possess an evolved, species-wide tendency to form pair bonds and engage in biparental care. We would argue, however, that despite the variability in childcare arrangements, men everywhere have the capacity to fall in love, to form pair bonds, to form bonds with their offspring, and to invest in offspring. Even when a culture is set up so that these potentialities are only sometimes actualized, the potentialities still seem to be there. This suggests that, throughout the course of our evolution, the selection pressure for investing fathers was strong enough to shape a male psychology capable of pair bonding and paternal care. In the following sections, we summarize two major lines of evidence for this assertion.

Cross-Cultural Evidence

Some of the strongest evidence comes from the cross-cultural record. Starting with pair bonding, in one influential study, Jankowiak and Fisher (1992) surveyed the ethnographies of 166 historically independent cultures drawn from the Standard Cross-Cultural Sample. Of these, explicit discussion of romantic love was present in 147 (88.6%); in the remainder, it was not clear either way. It is important that, although the researchers did not find unambiguous evidence of romantic love in every culture, romantic love was evident in at least some cultures—indeed in the majority of cultures—from every world region surveyed, including Africa, Europe, Asia, the Americas, and Polynesia. This is difficult to reconcile with the idea that love is a recent European invention. It suggests instead that, for all the variability we see in marriage patterns across cultures, romantic love is a cross-cultural universal. Other research leads to the same conclusion. Gottschall and Nordlund (2006) conducted a content analysis of traditional (precontact) literature from around the globe and concluded that romantic love was clearly detectable in 78 of 79 cultural groupings. This included a diverse and geographically disparate array of populations, including sub-Saharan Africans, Australian Aborigines, and Native Americans. Again, the fact that romantic love is so ubiquitous challenges the idea that it is a Western social construction or cultural export. It seems much more plausible that human beings are, by nature, the kind of animal that falls in love.

The cross-cultural record also suggests that humans are the kind of animal that commonly provides biparental care for its young. In 95% to 97% of mammalian species, only the females care for the young (Kleiman, 1977). We would no more expect males in these species to invest in their offspring than we would expect them to get pregnant or lactate. Humans are not

like that. Although men almost always invest less than women (Wood & Eagly, 2002), there are clear signs that they have been “set up” by selection to provide paternal care. Some of the best evidence comes from foragers, as their living conditions most closely approximate those of our ancestors throughout the majority of human evolutionary history. Based on a narrative review of the literature on forager societies, Hewlett and MacFarlan (2010) concluded that men in these societies exhibit a high level of father involvement. Fathers provide calories and shelter; transport young children; keep an eye on toddlers; transmit knowledge, skills, and status (especially to sons); and help defend the family from threats. Other, more systematic studies have reached similar conclusion. Marlowe (2000) surveyed the 186 cultures in the Standard Cross-Cultural Sample, assessing rates of paternal care among foragers, pastoralists, and agriculturalists. He looked at both direct care (e.g., holding, grooming, and babysitting) and indirect care (i.e., the provision of calories). Forager fathers again emerged as high investors. They provided the highest level of direct paternal care of all the groups, and they provided a moderate-to-high level of indirect care. Among pastoralists and agriculturalists, levels of direct paternal care were notably lower, especially for infants. However, there are two points to make about this. First, although there was *less* direct care in these societies, direct care was not absent, and this in itself makes human males very different from most male mammals. Second, men in pastoralist and agricultural societies exhibited high levels of *indirect* care—that is, they made large contributions to subsistence in these societies. So, although paternal care is absent in most mammals, it is found in humans across widely varying cultures.

Another line of cross-cultural evidence comes from a phenomenon discovered by Martin Daly and Margo Wilson, dubbed *the Cinderella effect*. In every culture that has been examined, men (and women) are more inclined to invest in their own offspring than in stepoffspring. This is the case not only in a wide range of modern industrialized nations (Daly & Wilson, 2001a) but also in small-scale foraging societies (Flinn, 1988b; Marlowe, 1999a). The pattern does not appear to be a simple product of limited coresidence of stepfathers and stepchildren: It has been found even in samples where the father has lived with the stepchild for an extended period, sometimes even from birth (Flinn, 1988b). The Cinderella effect makes good sense on the assumption that paternal investment is a product of selection: A man’s biological offspring are more likely than stepchildren to possess copies of any given gene in his genome, and thus a tendency to care selectively for one’s own offspring could increase the replication rate of any genes contributing to the development of that tendency. If, on the other hand, paternal care were an arbitrary cultural product, there would be no reason to

expect that this own-child bias would be found in every culture. Thus, cross-cultural comparisons suggest that, as with pair bonding, high male parental investment in our species plausibly has an evolutionary origin.

Hormonal Evidence

A further line of evidence comes from research on the hormonal correlates of pair bonding and paternal care. According to the Challenge Hypothesis (Wingfield, Hegner, Dufty, & Ball, 1990), polygynous species and pair bonding species differ from one another in patterns of testosterone activity in the males. In highly polygynous species (which usually exhibit little or no paternal investment), males maintain consistently high testosterone levels throughout the breeding season. In pair bonding, biparental species, on the other hand, testosterone levels are upregulated or downregulated depending on circumstances. In many birds, for instance, when males compete with other males for mates or territory, their testosterone levels run high. When, in contrast, they establish a pair bond and start investing in offspring, their testosterone levels fall (Wingfield et al., 1990). If this kind of hormonal modulation were found in human beings, it would be strong evidence that pair bonding and male parental care are products of selection in our species.

Such evidence is available. Various studies have found that men in long-term relationships or with children have lower average testosterone levels than do single men. This has been confirmed by various research groups using various methods, and studying men in both industrialized and nonindustrialized societies (Archer, 2006; Gray & Anderson, 2010; Muller et al., 2008). (The same pattern also seems to be found in women; van Anders & Goldey, 2010.) Of course, it might be argued that, rather than testosterone levels falling when men form pair bonds or start caring for children, perhaps men who have lower testosterone levels in the first place are simply more likely to form long-term relationships and take on a parental role. However, a recent longitudinal study of 624 Filipino men undermines this idea. The researchers found that men who got married and had children during the course of the 5-year study experienced a larger decline in testosterone than single, childless men (Gettler, McDade, Feranil, & Kuzawa, 2011). Furthermore, the paternal testosterone drop has been demonstrated in experimental conditions: Among men, the sound of a baby crying, when coupled with nurturant behavior, leads to a slump in testosterone levels (van Anders, Tolman, & Volling, 2012). Aside from testosterone, human pair bonding and paternal behavior have been linked to oxytocin, prolactin, and vasopressin (Gettler, McDade, Feranil, & Kuzawa, 2012; Gordon, Zagoory-Sharon, Leckman, & Feldman, 2010; Gray, Parkin, & Samms-Vaughan, 2007) in ways comparable to those observed in the males of other pair-bonding primates

(Schradin, Reeder, Mendoza, & Anzenberger, 2003) and in more distantly related pair-bonding species such as prairie voles (Young & Wang, 2004). It is hard to argue that these hormonal responses are products of socialization, as opposed to being part of the basic design of male human beings. Socialization may certainly influence levels of male parental behavior. However, the basic biological machinery of pair bonding and male parental motivation appears to be a fundamental component of the male phenotype in human beings.

Pair Bonding and Paternal Care Led to the Evolution of Mutual Courtship

It is plausible to suppose, then, that as a result of the dependency of our big-brained young, humans evolved to form pair bonds and to engage in biparental care—or more precisely, that big brains, pair bonding, and biparental care coevolved. This had important implications for our species. For one thing, it led to a reduction in the sex difference in reproductive variability (variance in the number of offspring produced by males vs. females), which in turn led to a reduction in sexual dimorphism. In addition, it kindled the evolution of mutual courtship. The fact that our young require such high levels of investment, and thus that males commonly invest in their offspring, provides a good explanation for mutual courtship in humans. Indeed, it implies that we should have been very surprised if we found anything else. Because our male ancestors were investing more and more into offspring, men evolved to be choosy about their sexual partners, at least in a long-term mating context. Men's mate preferences in turn put women under intersexual selection, which led to the evolution of “showy” females: females with secondary sexual features such as breasts, facial neoteny, and the “hourglass” figure. Finally, as a result of the availability of paternal investment of variable quality, women evolved to compete for the best mates and investors. We now consider in greater detail the evolution first of male mate choice and then of female mate competition.

Male Mate Choice

In MCFC species, males have little in the way of mate preferences, other than those that lead them to mate with females of the same species and to favor novel females over familiar ones (the *Coolidge effect*). In contrast, in species in which males invest in offspring, males typically evolve greater choosiness about their mates. The discussion of male mate choice traces back as far as Darwin (1871; see also Edward & Chapman, 2011; Johnstone, 1997). Although rare, it has now been documented in many animal groups, including various birds, lizards, fish, and insects (summarized in Hooper & Miller, 2008). Male mate choice is also found in humans. Human males have a number

of well-documented, species-typical mate preferences. These include preferences for physical traits such as a low waist-to-hip ratio, facial and bodily symmetry, neoteny, and youthfulness (Barber, 1995; Singh, 1993; Thornhill & Gangestad, 1993). They also include preferences for psychological traits such as intelligence, emotional stability, and sexual fidelity (Buss, 1989; Buss & Schmitt, 1993). Of course, no one is surprised that men have mate preferences; it is such a familiar fact of life that we take it for granted. From a comparative perspective, though, we *should* be surprised. The existence of these preferences makes our species atypical among mammals and is inconsistent with the idea that we are an MCFC species.

Some of the best evidence that humans have a long history of male mate choice is found not in males but in females. We tend to view mate preferences as products of evolution, but they are more than this; they are also *causes* of evolution. The mate preferences of one sex create a selection pressure on the other, which over many generations can shape morphological and behavioral traits in the other sex. The best-known non-human examples concern female preferences and male traits (e.g., the female widowbird's preference for long male tails; Andersson, 1994). However, the process is not always so sexually asymmetric. In species with male mate choice, male preferences exert a selection pressure on females and can shape female morphology. This can be seen in many pair bonding birds. For instance, the crown of the crested auklet (Jones & Hunter, 1993) and the feather coloration of the king penguin (Nolan et al., 2010) are found not only in males but also in females, and are thought to be products of mutual mate choice. Similarly, the ornamental coloration of female bluethroats (a passerine bird; Amundsen, Forsgren, & Hansen, 1997), and the orange spot patches of female striped plateau lizards (Weiss, 2006), appear to have been shaped by male mate choice.

In humans as well, male mate preferences have left their mark on female morphology (Barber, 1995; Ihara & Aoki, 1999). In fact, in some domains, women are more sexually selected than men; one could say in these cases that women have the larger "peacock's tail." An example can be found in the domain of physical attractiveness. Women are typically rated as better looking than men, by both men and women (Darwin, 1871; Feingold & Mazzella, 1998; Ford & Beach, 1951). The difference is plausibly a consequence of the fact that, although both sexes care about good looks in a mate, on average, men care somewhat more (Buss, 1989; Lippa, 2007). This means that, since this sex difference first evolved, there has been a somewhat stronger selection pressure on women than men for physical attractiveness—the opposite of what we find in peacocks. To take a more specific example, the fact that adult human females have permanently

enlarged breasts is plausibly a consequence of male choice. Contrary to popular opinion, enlarged mammary glands appear not to be necessary for milk delivery. The vast majority of mammals deliver milk without them, and there is little correlation between the size of a woman's breasts and her capacity to produce milk (Miller, 2000). What, then, are breasts for? A rather obvious clue can be found in the fact that most men find youthful-looking breasts sexually attractive. This has led to the suggestion that the primary evolutionary function of breasts relates to mate choice (Dixson, Grimshaw, Linklater, & Dixson, 2011). The most widely accepted suggestion is that they are honest signals of good genes, youthfulness, and nutritional status (Jasienska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004; Marlowe, 1998; Singh, 1995; for an alternative hypothesis, see Low, Alexander, & Noonan, 1987). If so, women's breasts tell us something important about ourselves, namely, that we are *not* the kind of species in which males only ever pursue sex indiscriminately and females alone exert mate choice. Breasts are evidence of male mate choice operating over many thousands of generations (Cant, 1981). The same is true of other secondary sexual features found in human females, including facial neoteny (e.g., large eyes, small noses and chins); gluteofemoral fat deposits and the hourglass figure; and lighter, smoother, less hairy skin.

The lesson that all these features teach us is this: If men in our evolutionary past did not invest in offspring, they would not have evolved strict mate preferences and thus women would be as drab as peahens. The fact that women are *not* as drab as peahens suggests a long history of male mate choice, which in turn suggests a long history of pair bonding and high male parental investment.

Female Mate Competition

A further consequence of the evolution of pair bonding and male parental motivation in our species is female competition for mates. In his classic exposition of parental investment theory, Trivers (1972) observed that "competition for mates usually characterizes males because males usually invest almost nothing in their offspring" (p. 142). However, as he then pointed out, in some species males do invest in their offspring, and where this is the case, the sexual asymmetry in mating competition is reduced. As with male mate choice, female competition is rare in the animal kingdom, but there are examples. Among Mormon crickets, for example, females compete for the male's packet of edible sperm (Gwynne, 1981). Similarly, among tamarins and marmosets (New World monkeys), males invest a great deal in offspring, and females exhibit high rates of intrasexual competition (Hrdy, 2009).

In humans as well, intrasexual competition is not limited to males. Not only do men compete with other men for the most desirable women, but women

compete with other women for the most desirable men (Buss, 1988; Simpson, Gangestad, Christensen, & Leck, 1999). As mentioned, the sex difference in muscle mass is large, suggesting that violent competition was much more common among men than women (Puts, 2010; although see Campbell, 1995). However, muscle mass dimorphism cannot be treated as the sole index of the sex difference in intrasexual competition, because violent competition is not the only type of intrasexual competition found in our species. Competition among women takes many forms. In some traditional cultures, women advertise their suitability as a spouse by displaying their cooking abilities and other domestic skills (Marshall, 1971); in others, they compete to display chastity (Dickemann, 1981). In Regency and Victorian Britain, well-to-do women competed for men in various ways, such as writing amusing letters, playing the piano, or learning foreign languages—activities that advertised their intelligence, conscientiousness, and creativity (G. F. Miller, personal communication, April 2012). In our own culture as well, female competition for mates takes varied forms. For instance, women (and men) display humor and try to convey a desirable personality (Buss, 1988), and they derogate rivals within earshot of mates or potential mates (Buss & Shackelford, 1997; Schmitt & Buss, 1996). Similarly, women compete through displays of physical attractiveness (as do men, though to a lesser extent; Buss, 1988). Despite the differences in the details across cultures, female competition is ubiquitous and makes our species an exception to the MCFC rule. As with male choosiness, female competition teaches us an important lesson about our species. If men had not evolved to form long-term bonds and invest in offspring, women would not have evolved to compete for mates. The fact that women *do* compete for mates suggests again that we have a long history of pair bonding and paternal investment.

Potential Criticisms

That, then, is our basic position on the evolution of mutual mate choice and reduced dimorphism in our species. There are various criticisms that might be leveled at this position; in this section, we deal with some of the most common.

1. You claim that humans are primarily a pair-bonding species. However, it is more accurate to say that we are primarily a polygynous species, like our cousins the gorillas.

At first glance, the ethnographic record appears to support this view. According to anthropologists, there are many more polygynous human societies than monogamous ones; Murdock's (1967) authoritative *Ethnographic Atlas* reports that the majority of societies

(83%) are polygynous. But what exactly does this mean? It means two things: (1) that monogamy is not enforced in these societies, and (2) that the number of polygynous marriages is greater than zero. In the majority of so-called polygynous societies, the majority of relationships are *not* polygynous; they are monogamous (i.e., they involve pair bonds). Again, the most pertinent evidence comes from foragers. Marlowe (2003b) looked at rates of polygyny in 36 forager groups from the Standard Cross-Cultural Survey. On average, 12.4% of married men and 20.1% of married women were married polygynously, leaving 11.1% of men single. Of course, these averages conceal a great deal of variability. One way to take account of the variability is to look at the proportion of societies that are nonpolygynous or only mildly polygynous (which Murdock defined as < 20% married polygynously) versus those that are generally polygynous (> 20% married polygynously). In Marlowe's sample, a clear majority of societies fell into the former category. In 74.2% of societies, less than 20% of married men were married polygynously; in 73.3%, less than 20% of married women were. Furthermore, in around 10% of these societies, there was no polygyny at all. Admittedly, two societies had particularly high levels of polygyny. The most extreme were the Tiwi Islanders of Northern Australia (Hart, Pilling, & Goodale, 1988), among whom 70% of married men and 90% of married women were married polygynously at the time of European contact. However, there are several reasons to interpret the Tiwi data cautiously. First, there is some question about how closely official marriage patterns among the Tiwi correspond to actual mating patterns, as a result of high rates of infidelity and illicit pair bond formation (Goodale, 1971). Second, even if we ignore this concern, levels of polygyny as high as the Tiwi's are highly atypical of human societies and thus should not exert a disproportionate influence on our picture of the evolved nature of our species.

A reasonable conclusion is that, although we are more polygynous than gibbons, we are nowhere near as polygynous as gorillas. Most male gorillas either have a harem or do not have a mate; in contrast, most men who have more than zero mates have only one. This means that, whereas only harem-holding male gorillas contribute to the gene pool of the next generation, most human males who contribute to the gene pool do so in the context of a pair bond. Consequently, our evolved sexual nature has been shaped more by pair bonding than by harem polygyny.

2. We are neither a polygynous nor a pair-bonding species. We are instead a promiscuous species, like our closest relatives, the chimpanzees and bonobos.

According to proponents of this view, promiscuous mating is humanity's solitary evolved mating system,

and long-term pair bonding is a social invention—or even a social pathology (Hrdy, 1981; Ryan & Jethá, 2010; Sherfey, 1972). There are, however, strong reasons to doubt this thesis. First, promiscuous species tend to have large testes relative to their body weight, which is an adaptation to sperm competition in the female's reproductive tract. For humans, testis weight (in grams) divided by body weight (in kilograms) is .79.⁴ It is often stated that relative human testis size is intermediate between that of polygynous/monandrous gorillas (.09–.18) and promiscuous chimpanzees (2.68–2.83), giving the impression that we are somewhere along the path to chimpanzee promiscuity (see, e.g., Buss, 2003, pp. 74–75; Shackelford, Pound, Goetz, & LaMunyon, 2005, pp. 374–375; Workman & Reader, 2008, p. 101). However, relative to body size, human testes are similar in magnitude to those of socially monogamous gibbons (.83–1) and nowhere near the size of chimp testes. This suggests a comparatively low historical level of sperm competition (Dixson, 1998; Gomendio, Harcourt, & Roldán, 1998; Short, 1979).

Other evidence points to the same conclusion. Relative to promiscuous species, humans have low sperm counts, small sperm reserves, and little optimization of sperm (summarized in Gray & Anderson, 2010). Promiscuous species also tend to evolve high white blood cell counts in order to deal with increased exposure to sexually transmitted pathogens; humans, however, have a comparatively low white blood cell count (Nunn, Gittleman, & Antonovics, 2000). Finally, promiscuous species tend to advertise fertility (or estrus) with blatant swellings, whereas in humans (as well as gibbons, gorillas, and orangutans), fertility is not advertised in this way (Dixson, 1998). Certainly, fertility is not perfectly concealed (G. F. Miller, Tybur, & Jordan, 2007; Thornhill & Gangestad, 2008). However, the absence of perfect concealment does not imply the presence of active advertisement, and if fertility were advertised in humans, we would presumably not need to employ sophisticated experimental methods to demonstrate its detectability. Thus, various lines of evidence suggest that, although promiscuous mating is part of our reproductive repertoire, we do not have the kind of obligate nonmonogamy found in chimpanzees and bonobos.

3. We are not a polygynous species, a pair-bonding species, or a promiscuous species. We have no single mating system—not because we are blank slates but because human mating behavior is designed to vary adaptively in response to circumstances.

Various evolutionary psychologists have taken this view (Buss & Schmitt, 1993; Gangestad & Simpson,

2000; Hrdy, 2009). According to Buss and Schmitt's (1993) Sexual Strategies Theory, for instance, humans have a complex menu of evolved mating strategies, rather than a single obligate strategy, with different contextual variables (including mate value, resource availability, parasite prevalence, and the adult sex ratio) drawing out different facets of our evolved mating psychology in historically adaptive ways. This pluralistic approach to mating behavior might initially seem to clash with our argument. As mentioned earlier, though, our argument does not hinge on the claim that pair bonding is the one natural human mating system. All it requires is that pair bonding has been significantly more common in the past than any other pattern, and thus that it is central to our evolved nature. The anthropological data just summarized support this view, as do various other lines of evidence (e.g., Labuda, Lefebvre, Nadeau, & Roy-Gagnon, 2010).

Certainly, there are evolutionary theories of human mating which claim that long-term pair bonding is our solitary evolved mating pattern. This includes Attachment Fertility Theory (AFT). AFT argues that natural selection has equipped us with sex-similar *long-term* attachment mechanisms but that short-term mating is merely a nonadaptive or maladaptive by-product of these mechanisms operating in evolutionarily-novel conditions (Miller & Fishkin, 1997; Miller, Pedersen, & Putcha-Bhagavatula, 2005). There are, however, good reasons to reject this view. The main one is that AFT has trouble explaining the sex difference in short-term mating predilections: the fact that, on average, men are more interested than women in casual sex (Schmitt, 2005b; Schmitt & 118 Members of the International Sexuality Description Project, 2003). As we discuss later, this difference is real and persistent (albeit much more modest than EP sometimes claims). But if short-term mating were simply a by-product of sex-similar attachment mechanisms, why would the difference exist at all? How could sex-differentiated short-term inclinations emerge as a side effect of mechanisms that are not themselves sex differentiated? AFT struggles to explain the evidence. Parental investment theory, in contrast, explains it easily and in terms of principles that apply right across the animal kingdom. Given that there is a larger sex difference in short-term than long-term mating (Buss & Schmitt, 1993; Kenrick, Sadalla, Groth, & Irost, 1990), it seems likely that natural selection has acted on our long-term versus short-term inclinations separately. If so, this implies that we have at least some adaptive flexibility in our mating behavior: We are adapted for both long-term and short-term mating. Again, though, this does not undermine our position, as our position requires only that, among our varied mating options, pair bonding has tended to predominate.

⁴This and subsequent estimates of relative testis size come from Miller et al. (2002). They were calculated from data in Dixson (1998).

4. You emphasize the importance of personal mate choice and emotions like love in solidifying pair bonds. However, for most of human history, these things were largely irrelevant because marriages were arranged by families.

It is certainly true that, in many traditional societies, parents and other interested parties exert a strong influence on marriage patterns (Apostolou, 2007, 2010; Flinn, 1988a). This is especially the case for daughters. However, we should not underestimate the importance of personal choice. To begin with, among foragers, it is typically only first marriages that are arranged. Only a minority of first marriages last for life, and subsequent unions are generally determined by the principals (Irons, 1989). Furthermore, even in arranged marriages, mate preferences and romantic love may exert some influence. They may, for instance, help determine how long the marriage lasts and how fecund it is. More than that, they may help determine whether an arranged marriage goes ahead in the first place. It is rare for parents to disregard entirely the preferences of their daughters and sons and to force them into a marriage they strongly object to (Davis & Daly, 1997; Schlegel & Barry, 1991). Finally, even when parents have total control over marriage decisions, and even when marriages are permanent unions, people can still potentially exercise mate choice through premarital sex and affairs or through eloping with a lover (Pillsworth & Barrett, 2008). Thus, although parents sometimes exert a strong influence on marital decisions, their influence is not so all-encompassing that it undermines our position.

5. Men's contribution to subsistence is not about increasing the survivability of genetic offspring. It is about gaining access to mates—in other words, it is *mating effort* rather than *parenting effort*.

This criticism is based largely on research on big-game hunting. It rests on three observations: (1) that the spoils of big-game hunting are often shared widely within the group and are not channeled selectively to the hunters' wives and children; (2) that hunting large, impressive prey animals yields fewer calories overall than hunting smaller but less impressive ones; and (3) that successful hunters often have the youngest wives, more wives, and more affairs (Hawkes, 1991; Hawkes, Rogers, & Charnov, 1995). These findings provide a good reason to think that big-game hunting is at least partly about showing off to attract mates. However, the conclusion that hunting—or male investment in general—is *solely* about attracting mates is too strong. First, hunters do sometimes channel the spoils of big-game hunting selectively to their wives and offspring (Gurven & Hill, 2009). Second, big-game hunting is not the only way that men obtain food. Among the Hadza, for instance, around one third of the calories

produced by men come from honey, and this is often preferentially shared with wives and children (Marlowe, 2003a). Third, as we mentioned earlier, food provisioning is not the only form of paternal investment, and men often provide direct care for offspring as well, especially in forager societies (Hewlett & MacFarlan, 2010; Marlowe, 2000). Finally, if male provisioning evolved solely as a way to gain access to mates, rather than to increase the survivability of one's genetic offspring, there would be no reason to expect the Cinderella effect. As such, all the evidence for the Cinderella effect argues against the claim that male provisioning is purely a matter of mating effort. More plausibly, it evolved partly as mating effort and partly as parenting effort (Bribiescas, Ellison, & Gray, 2012; Marlowe, 1999b).

An Unexpected Species

In sum, as brain size increased in the hominin lineage, our offspring became more and more biologically expensive, and pair bonding and male parental care came to occupy a larger and larger fraction of our mating behavior. This idea makes sense of various facts about human beings that we take for granted but that would otherwise be inexplicable. This includes such commonplaces as that men and women both pursue long-term relationships and fall in love, that men have species-typical mate preferences, that women compete for mates, that both sexes are prone to jealousy and engage in mate guarding, and that both sexes have secondary sexual characteristics. EP has led the field in documenting these aspects of human sexual psychology. Nonetheless, there is also a tendency within EP to exaggerate the sex differences in human beings and to push our species into the framework of the MCFC model. This is the topic of the final section of the article.

The MCFC Model in Evolutionary Psychology

At the start of the article, we suggested that there is an unresolved conflict in EP. On one hand, much of the EP literature is consistent with the idea that mutual mate choice is an important dynamic in our species. On the other, mutual choice is inconsistently present, and the MCFC model exerts an important influence as well. This can be seen in some of the field's "big picture" claims about human nature, in the research questions that are posed, and in the way the data are interpreted. In the remainder of the article, we look at the influence of the MCFC model in three main areas. First, we look at the issue of sex differences in sexual strategies, and argue that EP commonly overemphasizes men's short-term mating orientation relative to women's. Second, we look at intersexual selection, and argue that EP

commonly overemphasizes female mate choice relative to male mate choice. Finally, we look at intrasexual selection, and argue that EP sometimes overemphasizes male competition for mates relative to female competition. All these tendencies inadvertently support a view of human beings as more dimorphic than we actually are. To the extent that we accept this view, we effectively mistake ourselves for highly dimorphic animals such as peacocks or deer.

Overemphasizing Men's Short-Term Mating Orientation

One of the most famous claims in EP is that, because of sex differences in parental investment, men have evolved to be more interested than women in casual sex, sexual novelty, and the acquisition of multiple mates within a short time frame (Buss & Schmitt, 1993; Schmitt, 2005b). People had, of course, noticed this difference before EP came along. However, EP has made two major contributions. First, it has provided a cogent and compelling explanation for the sex difference. Second, it has documented its cross-cultural universality, thus strongly challenging the view that the difference is simply a product of local cultural mores. These must be counted as among the most significant contributions of EP to the understanding of our species, and we do not deny that the explanation is fundamentally correct or that the difference is genuine. Nonetheless, it is possible to exaggerate even a genuine difference, and we suggest that there is a tendency in EP to do exactly that. Modern evolutionary psychologists do *not* claim that “men are promiscuous, women are monogamous,” as some critics charge (e.g., Brym & Lie, 2007, p. 68). However, they still sometimes give an inflated impression of the difference in short-term mating inclinations.

How Large Is the Sex Difference in Sociosexuality?

To make this case, we must first establish how big the difference actually is. In doing this, we will focus on Cohen's d as our measure of effect size, as other measures (e.g., percentage of variance explained) can underestimate the real-world impact of any difference (Rosenthal & Rubin, 1979). According to a convention in psychology, a d value of .2 is considered a small effect, .5 a medium effect, and .8 a large effect (Cohen, 1988). Using this (essentially arbitrary) standard, most sex differences in psychology are rather small; as Hyde (2005) noted, 78% have an effect size less than .35.⁵ The sex difference in interest in casual sex

is conspicuously larger than the norm, with typical estimates ranging from .5 to .8 (Peterson & Hyde, 2010; Schmitt, 2005b). Evolutionary psychologists often point out that this is one of the largest sex differences that psychologists have ever uncovered, and indeed it is. But the fact that the difference is larger than most does not necessarily mean that it is large in any absolute sense. So how large is it?

To address this question, we turn to an influential cross-cultural study by Richard Lippa (2009). The study focused on *sociosexual orientation* (SO), a widely used measure of people's willingness to engage in sex outside the context of a committed relationship (Simpson & Gangestad, 1991). There are three main reasons to focus on this study. First, the sample was large and diverse: It included more than 200,000 participants from 53 nations. Second, the SO measures were limited to items asking about people's attitudes to casual sex, and thus there were no behavioral measures of SO (i.e., number of past sexual partners). This is important because behavioral measures can underestimate the sex difference in SO, as heterosexual men and women cannot always act on their inclinations but must compromise with the desires of the other sex. Finally, the study included measures of an objective sex difference—the sex difference in height—which can serve as a useful reference point to assess the magnitude of the SO difference.

Collapsing across nations, Lippa (2009) found an average effect size of $d = .74$ for the sex difference in SO (or an estimated $d = .85$ after statistically correcting for attenuation caused by using a small number of items to measure the construct). If we accept Cohen's (1988) convention, this would be deemed a large effect. However, there are several reasons to be wary of the convention. The first relates to the sex difference in height. This is a difference of which we all have an intuitive grasp: We know it exists, but we also know that there is a fair amount of overlap between the sexes, and that the difference is small compared to the differences found in animals such as gorillas and elephant seals. Crucially, though, the sex difference in height in Lippa's sample was $d = 1.63$. Thus, the modest difference in height was around *twice the magnitude* of the sex difference in SO.⁶ Even if we restrict ourselves to the handful of nations with the largest SO differences—which tend to be nations with low gender equity and low economic development—we find they fall well short of the height difference. The largest

⁵Sex differences are not unique in this respect. *Most* effects in psychology—including some of the field's most famous findings—are in the same range (Eagly, 1995). In other words, most effects are small, and thus most of the phenomena psychologists seek to explain are products of many different factors.

⁶Note that we are not arguing that, because human size dimorphism is low compared to gorillas or peacocks, humans must therefore be a monogamous species or have low dimorphism in general. For several reasons, size dimorphism is not a useful indicator of ancestral mating patterns in our species (e.g., Lassek & Gaulin, 2009). Our point is that size dimorphism—*regardless* of what it says about ancestral mating patterns or overall dimorphism—is comparatively low, but the difference in SO is half as large as that.

effect sizes were around $d = 1.2$: only around 74% the height difference. And effect sizes that large were rare; the vast majority fell below $d = 1$. This pattern is not unique to this study; Schmitt (2005b) reported very similar results. Thus, the comparison with the human height difference provides one reason to be cautious of the claim that the SO difference is an especially large difference.

A second reason relates to sexual size dimorphism in monomorphic species. In lar gibbons, for instance, the d value for the sex difference in body size is around .8 (calculated from data in Schultz, 1941, as reported by Geissmann, 1993). In other words, the sex difference in SO in humans is about the same magnitude as the sex difference in body size in gibbons. The reason this is significant is that gibbons are the archetypal example of a monomorphic primate. This means that, if we want to say that the human SO difference is large, we must also say that we were wrong to think that gibbons are monomorphic for body size; they are in fact highly dimorphic. Nor are gibbons an exceptional case. Indeed, some prototypically monomorphic species have levels of size dimorphism notably *larger* than the human SO difference. This includes prairie voles ($d = 1.54$; Dewsbury, Baumgardner, Evans, & Webster, 1980) and black swans ($d = 2.29$; Kraaijeveld, Gregurke, Hall, Komdeur, & Mulder, 2004). Of course, there are also some monomorphic species, such as beavers and common marmosets, for which the sex difference in size is close to zero (Araújo et al., 2000; McKinstry & Anderson, 1998). But this does not undermine our point. What the gibbons, prairie voles, and swans show us is that the human SO difference falls *within the range* considered monomorphic. Unless we want to say that these species are not monomorphic after all, but are actually highly dimorphic for body size, we cannot say that humans are highly dimorphic for SO.

A final point is that, in comparing the means for men versus women, it is important not to lose sight of the variation within each sex, or of the overlap between the male and female distributions. For normally distributed data, an effect size of .74 indicates around 55% overlap between the two distributions. Thus, although the average SO score is higher for men than for women, one study found that around *one third* of men—a large minority—had lower SO scores than the median woman (Simpson & Gangestad, 1991). As such, it is misleading to conclude from the difference in the means that “men are substantially more interested than women in casual sex” (Mikach & Bailey, 1999, p. 141). Such a statement focuses myopically on the central tendency for each sex, and comes perilously close to attributing the average for each group to all the group’s members. *Some* men have higher SO scores than some women, but some women have higher SO scores than many men. Certainly, natural selection has pushed the bell curve for men further to the right

than the bell curve for women, such that, if you picked one man and one woman at random, it would be a better bet that the man would be more interested than the woman in casual sex. It would not, however, be a particularly *good* bet. Based on unpublished SO data from more than 1,200 men and women, we calculated that you would win this bet only around two thirds of the time. Thus, there is clearly a sex difference, but it is nothing like the kind of dichotomous sex difference that the MCFC model (or the previous quotation) might lead us to expect.

It is certainly true that effects in the .74-to-.85 range are larger than most psychological sex differences. However, this may, paradoxically, support our case: The relatively modest sex difference in SO is one of the largest found in our species precisely because we are a relatively monomorphic animal. (For discussion of Del Giudice’s recent suggestion that psychologists underestimate sex differences by focusing on unidimensional rather than multidimensional constructs, see the appendix.)

Exaggerating the Differences?

It is reasonable to conclude, then, that the sex difference in SO, though larger than most human sex differences, involves a modest discrepancy in the central tendencies of two strongly overlapping distributions. Although this conclusion is directly based on data collected by evolutionary psychologists, it is not the impression one is likely to get from the EP literature. In various ways, EP conveys the impression that the gender gap is much larger. Arguably, the most notable way concerns some of the nonquestionnaire data used in EP to demonstrate the gap. This includes people’s responses to real-world sexual solicitations, the utilization of pornography and prostitutes, and the mating decisions of attractive or powerful men and women—people who can get what they want on the mating market without having to compromise (see, e.g., Betzig, 1986; Buss, 2012; Symons, 1979). At first glance, this evidence appears to demonstrate very large sex differences. We argue, however, that the appearance is deceptive. For various reasons, each line of evidence paints an exaggerated picture of the magnitude of the sex differences.

“Would You Go To Bed With Me?”

Consider first a famous study by Clark and Hatfield (1989). Attractive men and women approached members of the other sex on a college campus and said, “I have been noticing you around campus and I find you to be very attractive.” They then said one of three things: (1) “Would you go out with me tonight?” (2) “Would you come over to my apartment tonight?” (3) “Would you go to bed with me tonight?” Call these the date invitation, apartment invitation, and bed invitation, respectively. For the date invitation, there was

essentially no sex difference in responses: Around half the men and half the women said yes. For the apartment invitation, a large sex difference appeared: 69% of men said yes, but only 6% of women did. Finally, for the bed invitation, there was a very large sex difference: 75% of men said yes, but not a single woman did. Not only that, but of the remaining 25%, several reluctantly reported prior commitments and requested a “rain check.” The argument is *not* that this shows that men are less choosy than women; all the actors in the study were attractive. The argument is that the study shows that men—*young men*, at any rate—are more willing than women to consent to casual sex.

As mentioned, most sex differences in psychology are quite modest (Hyde, 2005). This one, however, is extremely large (Voracek, Hofhansl, & Fisher, 2005). Baumeister and Vohs (2004) suggested that the result makes perfect sense if we employ an economic metaphor, according to which men are the buyers of sex and women the sellers: If someone asked whether cars should be given away for free, most car buyers would say yes but most car dealers would say no. But does this analysis overdraw the sex difference in interest in casual sex? It probably does.

The first point to make is that the study was *not* about casual sex per se; it was about casual sex *with a total stranger*. As Clark and Hatfield (1989) themselves pointed out, a woman consenting to be alone with a male stranger is taking a greater physical risk than a man consenting to be alone with a female stranger. This may account for some of the sex difference in responses to the apartment and bed invitations. If so, the study may exaggerate the sex difference in interest in casual sex because it underestimates women’s interest. In fact, this is almost certainly the case; after all, not a single woman in the study accepted the bed invitation, but presumably no one would want to argue that not a single woman has any interest in casual sex.

Second, the explicit nature of the third invitation (“Would you go to bed with me?”) might have been more off-putting to women than men. To begin with, women may be more likely than men to attribute negative personality traits to anyone who makes such an offer (Conley, 2011). In addition, women might be more concerned than men that accepting the invitation would earn them a reputation for promiscuity. Both factors may account for some of the sex difference in responses to the bed invitation. Of course, attributional patterns and reputational concern would both constitute sex differences in their own right. However, they would not constitute sex differences *in interest in casual sex*. The Clark–Hatfield findings are usually treated as a direct, real-world measure of *that* sex difference alone. But treating them this way leads to an inflated estimate of the difference. Other factors help shape men and women’s responses as well.

Finally, we should not put too much weight on the particular set of results found in this one study. Recent replications have found smaller sex differences (Guéguen, 2011; Voracek et al., 2005). For instance, in a large replication in Denmark, Hald and Høgh-Olesen (2010) found that 2% of women agreed to have sex with a stranger, whereas only 38% of men did—in other words, a majority of men turned down the offer. The effect size for the sex difference was $d = 1.11$. This is large for a human sex difference; however, it is still only two thirds the magnitude of the human height difference. The results for the apartment invitation were perhaps even more telling: 8% of women consented, as compared to 22% of men, yielding an effect size of only $d = .41$. This is particularly striking given that most respondents presumably interpreted the apartment invitation as a veiled invitation to have sex.

In sum, there is almost certainly an average difference between the sexes in interest in casual sex, but the Clark–Hatfield study almost certainly overestimates its size. A pleasing implication of this conclusion is that it helps reconcile the results of this study with the results of the numerous surveys that find a sex difference in the same direction but of a smaller magnitude (e.g., Lippa, 2009; Schmitt, 2005b). Without such a reconciliation, we would need to reject either the Clark–Hatfield findings or all the questionnaire data, because the two lines of inquiry give very different estimates of the magnitude of the difference.

The Customer Is Always Right

Another common argument for a large sex difference in short-term orientation concerns real-world differences in men and women’s utilization of prostitution and pornography (Salmon, 2012; Symons, 1979). The question these data raise is, If the differences in SO are only modest, why do we see such immodestly large differences in these domains? Starting with prostitution, we agree that the sex difference in consumption is large, but argue that it provides an imperfect measure of the typical sex difference in SO. Only a minority of men use prostitutes regularly. Kinsey, Pomeroy, Martin, and Gebhard (1948) famously estimated that 15% to 20% of U.S. men were *regular* users; however, this is widely viewed as an inflated figure derived from an unrepresentative sample. Most estimates in sexually liberal Western nations put the figure at 2% to 4% (Brooks-Gordon, 2006; Mansson, 2005). Although many more people who pay for sex are men than women, those few who do may come disproportionately from the extreme of the distribution for SO. For normally distributed data, even a small difference in means corresponds to a large difference at the tail of the distribution. Thus, although the sex difference in SO may be large at the tail (as indicated by the utilization of prostitutes), the difference is likely to be much more modest nearer the mean, that is, for the majority

of the population. In addition, it is generally easier for women than men to obtain casual sex without paying for it, and thus the utilization of prostitutes is not a pure measure of SO, even for those at the tail of the distribution. This is not to deny that the difference is large. The point is that this large difference is a product of several causal factors and thus that, if treated as a measure of just one of those factors—in this case, the sex difference in interest in casual sex—it will overestimate the size of that difference.

Pornography is a different issue, because pornography is not consumed by only a small percentage of men. It is well known that, since becoming readily accessible on the Internet, a large segment of the male population now uses pornography on a regular basis. Less well known, however, is the fact that, during the same period, the percentage of female users has increased substantially as well (see, e.g., Hald, 2006). There is certainly still a sex difference, but how large is it? Opinions differ. According to one major meta-analysis (Peterson & Hyde, 2010), the effect size for self-reported pornography use is $d = .63$. This is larger than most sex differences in psychology, but again that may simply reflect the fact that we are a relatively monomorphic animal; it is, after all, only around 40% the size of the sex difference in height. On the other hand, it is possible that this value is an underestimate. A lot depends on the specific variable under investigation. If the variable is whether one has *ever* viewed pornography, the sex difference is considerably smaller than if the variable is how *frequently* one views pornography. Hald (2006), for instance, reported a d value of .59 for the first variable but 1.12 for the second. Now, this was a one-off study, rather than a meta-analysis, and thus we can be less assured of the finding. But even if the larger estimate does turn out to be accurate, there are two things to bear in mind. First, the effect size is still only around two thirds that of the height difference. Second, like the earlier examples, the sex difference in pornography utilization is unlikely to be solely a product of sex differences in SO. Presumably, men's greater interest in visual sexual stimuli also plays a large role (Bailey, Gaulin, Agyei, & Gladue, 1994). Many women enjoy depictions of sex outside a committed relationship, but more women than men prefer them in written rather than visual form (Ogas & Gaddam, 2011). Again, this is still a sex difference, but not a sex difference in interest in casual sex. No doubt sex differences in the consumption of pornography and prostitutes are shaped in part by evolved sex differences in SO. However, for the reasons given, the differences in consumption are likely to be larger than the differences in SO.

You Can't Always Get What You Want

A final EP argument for large SO differences starts from the premise that people's sexual behavior does not

always reveal their true desires, because most people have to compromise with the desires of the other party. One way to get around this is to look at the behavior of people who are attractive or powerful enough that they do not have to compromise but are able to get what they really want on the mating market (Buss, 2012; Symons, 1979). So, for instance, researchers have examined men's preferred mating strategies by looking at the behavior of powerful, wealthy men. The general finding is that, across cultures and throughout history, men who have more power, status, and wealth have generally had more wives, more sexual partners, and—in noncontracepting societies—more offspring than other men (Hawkes, 1991; Pérusse, 1993). This is seen in an especially vivid form among despotic leaders. The most famous example in EP is probably Ismail the Bloodthirsty, the emperor of Morocco from 1672 to 1727, who had hundreds of wives and concubines and reputedly sired 888 children (for a discussion of the accuracy of this figure, see Einon, 1998; Gould, 2000). But Ismail is not an isolated case. As Betzig (1986) documented, in all the world's traditional civilizations, kings, emperors, and other powerful men have accumulated large harems of nubile young women. Equivalently powerful women have not accumulated harems of nubile young men. The argument is that this provides an unbiased window on men's evolved desires. It shows what happens when these desires are “let off the leash” and given full expression. In short, when men have enough power to do anything they want, they choose to have hundreds or even thousands of mates.

However, there are two reasons to think that the evidence exaggerates the sex difference. First, we need to ask, Does the behavior of these despots reveal the untrammelled desires of men in general, or does it just reveal the untrammelled desires of the kinds of men who become despots? It is plausible to suppose that men who obtain and hold on to positions of great power tend to occupy the right-hand tail of the distribution of testosterone-related traits such as aggression, dominance, and polygynous inclination. As such, it is unwise to generalize from what are likely to be a highly atypical subset of men. Although there is clearly an average sex difference in desired partner number, the historical evidence may exaggerate the magnitude of this difference, because it is drawn from an unrepresentative sample.

A second point is that the “unbiased window” argument can be turned on its head. Think about some of the highest status men in modern societies: sports stars, rock stars, politicians. At first glance, it might seem that these individuals provide further proof of men's polygynous nature: They are often notorious for their sexual antics and infidelities (the famous scandal with Tiger Woods is a case in point). This initially seems to support the view that, “when they are able to do so because of high mate value, men opt for

short-term mating strategies” (Schmitt, 2005a, p. 273). However, the picture is not so simple. Many of these men are in the position where they have essentially an unlimited supply of potential sexual partners. Do all of them or even most of them eschew long-term relationships and opt instead for as many one-night stands and brief love affairs as possible? Sometimes, perhaps, but often they do not. These men—the most eligible bachelors, the highest status males in our species—often do what male chimpanzees never do: They fall in love and form long-term pair bonds. Certainly, they may fall out of love again more rapidly than lower status men, they may be choosier about their long-term partners, and they may engage in more extramarital dalliances over the course of their lifetimes (see, e.g., Lammers, Stoker, Jordan, Pollmann, & Stapel, 2011; Pérusse, 1993). However, most of them still fall in love at least once in a while, and many forgo the option of mating with multiple females for a long-term relationship and investment in offspring.

This makes good sense in light of the fact that our species spent most of its evolutionary history living in small, egalitarian groups in which high levels of allo-maternal care were necessary for offspring survival. It is only in modern cities that people potentially have access to an unquenchable supply of sexual partners, and only in modern welfare states that children have a good chance of survival even in the absence of allomaternal support. It might make evolutionary sense that high-status men living in such conditions would pursue a short-term mating strategy exclusively. However, we seem not to be that kind of animal. This is exactly what we would expect given that, for most of our evolution, we inhabited an environment in which such a strategy was not possible, and in which the dependency of our young meant that male parental investment often paid large fitness dividends. Thus, if high-status men provide a window on our evolved nature, they show us to be a species that evolved primarily in the context of small groups with high levels of pair bonding and biparental care and relatively low levels of promiscuous and extrapair mating. This is not to deny that short-term mating is part of men’s repertoire (or of women’s); clearly, it is. The point is simply that it is easy to overstate its importance and to overstate the magnitude of the sex difference.

Overemphasizing Female Choice

A natural corollary of the strong emphasis on men’s short-term, low-investment mating strategies is the relative neglect of the kind of mutual mate choice associated with long-term, high-investment mating. Although no evolutionary psychologist would deny that men have mate preferences, male choice often takes a backseat in EP to female choice. In this section, we examine how the MCFC model has biased the study

both of mate preferences and of mating displays in the human species.

Overlooking Male Mate Choice

It is commonly claimed in EP that women are choosier about their sexual partners than men. To take two examples more or less at random, Becker, Kenrick, Guerin, and Maner (2005) suggested that “women generally tend to be choosier, whereas men are more intrasexually competitive” (p. 1649), and Gaulin and McBurney (2004) argued that “women are expected to be choosier than men because of their slower reproductive rates” (p. 269). The idea that women are the choosier sex is one of the best-known claims associated with EP. Ironically, another of the best-known claims associated with EP is an exception to this rule: On average, men are choosier than women when it comes to the physical attractiveness of a prospective mate (Buss, 1989; Lippa, 2007). Even if we put this counterexample aside, though, the statement “females are choosier than males,” although true of many species, does not apply easily to our own. It is true that men may sometimes be more willing than women to lower their standards for a *casual* sexual partner (Buss & Schmitt, 1993; although see Pedersen, Putcha-Bhagavatula, & L. C. Miller, 2011). However, when it comes to the most important mating decisions of a man’s life—who he will marry, who he will have children with—the difference in choosiness is much smaller and maybe nonexistent (see, e.g., Kenrick et al., 1990). This fact of human life is even implicit in everyday folk psychology; the stereotype is that men will “sleep with anything that moves,” not that they will marry or have children with anything that moves. In long-term, committed relationships, men are about as choosy as women (Buss & Schmitt, 1993). Importantly, based on parental investment theory, we would not *expect* men to be indifferent to mate quality. Long-term relationships often involve high investment for both parties and reduce males’ opportunities for other matings. As a result, we would predict that human males would not be indiscriminate about their long-term partners. Men could not have evolved to fall in love or care for offspring if they did not also evolve some reasonably strict mate preferences

Nonetheless, the MCFC model may encourage such a strong focus on female choice that male choice is sometimes downplayed or even overlooked entirely. In various studies, researchers have tested hypotheses concerning mate preferences only in women, or have tested them in women first and men only later, as if as an afterthought. The tacit assumption seems to be that only one sex (the female) exercises mate choice—an assumption that, in effect, ignores the fact that we are a species with pair bonding and paternal care. In one study, for example, Roberts and colleagues (2005) looked at whether people with a high level of

genetic heterozygosity were more facially attractive. In the article describing the research, the authors stated that “sexual selection theory asserts that males maximize reproductive success through seeking multiple matings, while females achieve this goal through discrimination of mate quality, or choosiness” (p. 214). There was no suggestion that humans might be an exception to this MCFC pattern, and indeed the study proceeded on the tacit assumption that we are not: It examined women’s preferences for men’s faces but not men’s for women’s. This is, in effect, to ignore the fact that we are a species with mutual mate choice and to ignore the fact that our male ancestors commonly achieved reproductive success, not only through seeking multiple matings but through choosiness about mates, pair bonding, and paternal care. The fact that male mate choice could be so easily sidelined, despite its ubiquity in everyday life, is testament to the power of the MCFC model.

This is not an isolated example. Another concerns the well-known research on MHC dissimilarity and sexual attraction. MHC genes are a highly variable set of genes involved in immune system functioning. Several theoretical considerations suggest that individuals will exhibit a preference for mates whose MHC genes are as different as possible from their own. To explore this issue in humans, Wedekind, Seebeck, Bettens, and Paepke (1995) asked women to rate the scent of men varying in MHC similarity. They found that the average pleasantness rating for MHC-dissimilar men was somewhat higher than that for MHC-similar men. In a species with pair bonding and biparental care, one might expect that the researchers would look for the preference in both sexes. Initially, though, they looked only at females. Eventually, they did look at males as well and, sure enough, they found the same preference (Wedekind & Furi, 1997). This is exactly what one would expect given that males in our species typically invest in offspring and thus have well-developed mate preferences. The fact that the researchers initially looked only at the female preference—and that people discussing the MHC research often only mention the female preference—is plausibly explained in terms of the influence of the MCFC model.

The same pattern can be seen in the literature on mate-choice copying. Mate-choice copying occurs when one individual (A) finds another individual (B) more attractive simply because other members of A’s sex find B attractive too. This has been demonstrated in various nonhuman species. In one of the first studies looking at the phenomenon in humans, Waynforth (2007) predicted and demonstrated mate-choice copying in females but ignored the question of whether it also occurs in males (see also Jones, DeBruine, Little, Burriss, & Feinberg, 2007). Subsequent research confirmed that males do indeed engage in mate-choice copying (Little, Burriss, Jones, DeBruine, & Caldwell,

2008; Place, Todd, Penke, & Asendorpf, 2010). If not for the MCFC model, this might have been the default assumption from the start (for other recent examples of the female-choice bias, see, e.g., Fink, Seydel, Manning, & Kappeler, 2007; Prokosch, Coss, Scheib, & Blozis, 2009; Wilbur & Campbell, 2011; Wiszewska, Pawlowski, & Boothroyd, 2007).

Human Courtship Displays

The focus on female choice in EP can also be seen in the research on courtship displays in our species. As mentioned, mate preferences in one sex can give rise to courtship ornaments and displays in the other. It is often assumed that these are found only in polygynous species and only in one sex: the males. However, if both sexes exert mate choice, both sexes can evolve ornaments and displays, even in monogamous species. This can happen when there is assortative mating based on indicators of heritable fitness (Hooper & Miller, 2008). We saw earlier that, in many socially monogamous birds, both sexes possess courtship ornaments. Humans meet the description of a species that might too: We commonly exhibit mutual mate choice and biparental care. Various courtship displays have been suggested for our species, chief among them language, intelligence, and humor (Miller, 2000). These suggestions are still controversial. However, whether they turn out to be accurate or not, the research in this area again shows the influence of the MCFC model. Evolutionary psychologists commonly talk about these putative ornaments as if they were designed only for males to attract females and never the other way around. Implicit in this tendency is the asymmetrical mate choice of the MCFC model.

Language. Our first example concerns the evolutionary origins of the capacity for language. A number of theorists have suggested that one of the main evolutionary functions of language is courtship (e.g., Miller, 2000). One study investigating this issue (Dunbar, Marriott, & Duncan, 1997) examined the subject matter of men and women’s conversations, both in single-sex and mixed-sex groups. It was found that, when women were present, men were somewhat more likely to talk about intellectual topics, such as academic issues or politics. The researchers concluded that, compared to women, men’s “conversations are more concerned with self-promotion in what has all the characteristics of a mating lek” (p. 243). But is this an accurate interpretation? In lekking species such as peacocks, ornamented males gather together and engage in extravagant mating displays; drab females inspect them and choose the most impressive male. Does this match what we observe in human societies? It is true that, like lekking species, humans often gather in multimale/multifemale groups. However, unlike lekking species, both females and males choose, and both males and females

display. Females might be slightly less inclined to display by increasing the time they spend discussing academic matters, but they clearly display in other ways (and one might question the merits of academic discourse as a courtship display for either sex). Furthermore, in lekking species, males provide no parental care, whereas in our species they often do. The suggestion that we are a lekking species involves using average differences between the sexes (e.g., the fact that males display more vigorously than females in early courtship and that females are choosier early on) to support a dichotomous view of the sexes (i.e., that males but not females display and that females but not males exert mate choice). In other words, there is a mismatch between the claim and the evidence for that claim.

Intelligence. A second example concerns a perennial question in biological anthropology: Why did humans evolve large brains and high intelligence? A recent suggestion is that human intelligence is partly a product of sexual selection. According to the main exponent of this view, Geoffrey Miller (2000), the human brain is a sexually selected “entertainment centre,” and creative intelligence is a sexual ornament comparable to the peacock’s tail. The idea is not that any given display of creative intelligence is necessarily a deliberate effort to attract mates (although in some cases it may be). The idea is that the basic *capacity* for creative intelligence evolved in part because people with this trait were preferred as mates. This preference in turn evolved because creative intelligence is an indicator of good brain function, which in turn is an indicator of good genes.

A common criticism of Miller’s thesis focuses on the fact that sexual selection commonly produces sexual dimorphism, but humans are not dimorphic for intelligence (e.g., Betzig, 2002). This leads critics to ask, If intelligence in humans were a product of sexual selection, why does the research consistently show that there is little or no difference in average levels of intelligence? The main thing to notice about this question is that it is premised on an MCFC interpretation of Miller’s theory: Men compete through displays of intelligent behavior, and women choose those men that display the greatest intellectual prowess. Thus, to the extent that the question seems reasonable, this suggests that the MCFC model is running in the background of our thinking. If we instead had the MMC model in mind, the question would not arise and would not seem like a persuasive challenge to the theory.

Miller’s theory is *not* that women select men for intelligence; it is that each sex selects the other for intelligence (among other things) and that human intelligence evolved in a context of mutual mate choice (see, e.g., Miller, 2000, pp. 375–377). This, according to Miller, is why men and women’s average level

of intelligence is so similar. Certainly, the average reproductive payoff for above-average intelligence may have been greater for men than women, which might help explain why variance in IQ is greater among males than females (Deary, Thorpe, Wilson, Starr, & Whalley, 2003). However, this does not imply that intelligence *only* paid reproductive dividends for men, and Miller explicitly argued that it did so for both sexes. Leaving aside the issue of whether the theory is correct, it is illuminating that so many commentators assume that his argument is that intelligence (as well as art, generosity, and music) evolved to advertise *men’s* fitness to women only. No one makes the opposite mistake and assumes that intelligence evolved only for women to attract men. Nor is it only those outside the field who fall into the trap. An example from within the ranks of EP comes from Thornhill and Gangestad (2008), who, in their book, *The Evolutionary Biology of Human Female Sexuality*, devote virtually all of their discussion of Miller’s thesis to talking about the effects of intelligence on *men’s* mating success only. Indeed, the section dealing with the issue is titled “Male Intelligence and Related Attributes: Signals of Quality?” (p. 180). The authors suggest that, according to Miller, “humor and creative displays [both of which showcase intelligence] may function as mating effort, which women find attractive in sex partners” (p. 181).⁷ Similarly, Puts (2010) described Miller as “the leading proponent of a theory that men’s brains and creativity are designed to attract females” (p. 166). It is especially telling that so many people assume an MCFC interpretation of the theory when some of the best-known research in EP suggests that both sexes, not just women, put a great deal of weight on intelligence in a long-term partner (Buss, 1989). This illustrates the power of the MCFC model and shows that there remains an unresolved—and often unnoticed—tension in EP between the MCFC and MMC models.

Humor. A final example concerns the evolution of the capacity for humor. One prominent theory, already alluded to, is that humor evolved through sexual selection (Miller, 2000). As noted, if peahens select mates with larger-than-average tails, peacocks’ tails will evolve to be larger over the generations. By the same logic, if people select mates with better-than-average senses of humor, people will evolve to be more humorous over the generations. (To be precise, this will happen if variance among individuals in their ability to produce humor is attributable in part to variance among individuals in their genes, i.e., if the trait is

⁷The authors do, however, raise a number of good criticisms of the idea that intelligence is a good-genes indicator. One is that, if it were, we would expect intelligence to be particularly attractive to females seeking short-term mates. However, there is little evidence that this is the case (Thornhill & Gangestad, 2008).

partially heritable. As with virtually all traits, however, this appears to be the case; Loehlin & Nichols, 1976.) Men and women both say they want a partner who has a good sense of humor. It has been suggested, though, that each sex means something different by this: Women want a man who makes them laugh (a peacock whose tail they like), whereas men want a woman who laughs at their jokes (a peahen who likes their tail; see, e.g., Bressler, Martin, & Balshine, 2006; Kaufman, Kozbelt, Bromley, & Miller, 2008). Thus, men have a sense of humor in order to woo women, but women have a sense of humor in order to evaluate the humor-producing efforts of men. Men court and women choose. Is this accurate?

The first point to make is that, although there does appear to be a sex difference in this domain, the evidence does not support the dichotomous men-want-humor-appreciator/women-want-humor-generator view. For a start, one study found that women find it just as important that a mate finds them funny as that they find a mate funny (Bressler et al., 2006), and another found that humor production ability is associated with number of past sexual partners for men *and* women (Greengross & Miller, 2011). Moreover, there is often a discrepancy between the findings of these studies and the verbal description of those findings. Bressler et al. (2006) asked participants to say which of two prospective mates they would prefer for each of five kinds of sexual/romantic relationship (e.g., one-night stand, long-term relationship). The choice was either a humor producer or a humor appreciator. The authors summarized their findings as follows: “Women preferred those who produced humor . . . whereas men preferred those who were receptive to their own humor” (p. 121). We would challenge this description. Men in particular were evenly split between the two options: For four of the five relationship types, men were no more likely to choose humor appreciators than they were to choose humor producers. This hardly suggests that “men preferred [women] who were receptive to their own humor”; around half did and half did not. The sex difference lay in the fact that a higher *proportion* of men than women chose the humor appreciator. However, the differences in these proportions were often small. For instance, for one-night stands (which is where we might expect the biggest sex difference), around 45% of men chose the humor producer as opposed to around 55% of women—and the difference was not statistically significant. Based on these results, it would be *closer* to the truth to say that men and women were both evenly split between the options than to say that men prefer appreciators whereas women prefer producers. Overall, the study did produce evidence of a small sex difference. However, that difference is not accurately captured by saying that men want a humor appreciator whereas women

want a humor generator. Such a statement inflates the difference by squeezing nondichotomous, overlapping data into a dichotomous, MCFC mold: Males compete by producing humor, whereas females choose from among the humor-producing males. The reality is a small sex difference in the *proportion* of men and women who choose appreciators versus generators for *some* relationship types, when they are forced to choose one or the other.

In sum, language, intelligence, and humor, along with art, generosity, and musical ability, are often described as human equivalents of the peacock’s tail. However, peacocks afford a poor analogy for the role of courtship displays in humans. Other animal models offer a better fit. In a number of non-human species—species as diverse as sea dragons and grebes—males and females engage in a mutual courtship “dance,” in which the two partners mirror one another’s movements. In Clark’s grebes and Western grebes, for instance, the pair bond ritual culminates in the famous courtship rush: The male and female swim side by side along the top of the water, with their wings back and their heads and necks in a stereotyped posture (Storer & Nuechterlein, 1992). If we want a nonhuman analogue for the role of creative intelligence or humor in human courtship, we should think not of ornamented peacocks displaying while drab females evaluate them. We should think instead of grebes engaged in their mating rush or sea dragons engaged in their synchronized mirror dance. Once we have one of these alternative images fixed in our minds, we can then add the proviso that there is a slight skew such that, in the early stages of courtship, men tend to display more vigorously and women tend to be choosier. However, this should be seen as a qualification to the primary message that intelligence, humor, and other forms of sexual display are part of the mutual courtship process in our species.

Overemphasizing Male Competition

We have seen several examples of how female choice is sometimes overemphasized in EP. Our final question is whether female competition is sometimes *underemphasized*. Various commentators have suggested that it is, both in the human research and in research on other primates (e.g., Campbell, 2002; Hrdy, 1981). Such claims may be overstated; some prominent research in EP has looked at intrasexual competition in both sexes (Buss, 1988; Schmitt & Buss, 1996; Simpson et al., 1999). We still need to ask, though, whether there is a sex difference in the relative strength of intrasexual competition, and if so, how large it might be. Given that there is a sex difference in reproductive variability, the answer to the first question is probably yes. The answer to the second question, however, is less clear. On the one hand, Brown, Laland, and Borgerhoff Mulder (2009) have shown that, averaging across

groups, the sex difference in reproductive variability is relatively small, with some societies showing no difference at all (see also Betzig, 2012). This suggests a small average difference in the strength of competition over our evolutionary history. On the other hand, Puts (2010) made a strong case that various morphological traits in males—in particular, male muscularity—indicate that violent intrasexual competition was substantially more common among ancestral men than women. What evidence might resolve this issue? In other primates, body size dimorphism and canine dimorphism are useful barometers of the sex difference in intrasexual competition. In the hominin lineage, however, neither is useful (Lassek & Gaulin, 2009; Plavcan & Van Schaik, 1997), and researchers in EP have turned to other evidence instead. This includes data on sex differences in homicide rates, mortality rates, and the production of cultural displays. Unfortunately, each of these data sources may inadvertently inflate the estimates of the sex difference in intrasexual competition.

Homicide and Mortality as Assays of the Strength of Intrasexual Competition

One source of evidence bearing on the issue is archival data on violent crime. Martin Daly and Margo Wilson (1988) are the pioneers of research in this area. In an influential series of studies, they used homicide rates as a gauge of sex differences in the strength of intrasexual competition. Their key finding was that, in every culture for which there is evidence, men are more likely to kill other men than women are to kill other women (Daly & Wilson, 1988, 2001b). The vast majority of homicides involve male killers (more than 90%) and male victims (around 70%). Furthermore, these homicides are disproportionately committed by males in early adulthood (between the ages of 16 and 24), which is the time of maximum mating effort and intrasexual competition for males in many species (Wilson & Daly, 1985). Daly and Wilson's claim is not that homicide is an adaptation but rather that homicide rates are an indirect indicator of levels of intrasexual competition in a population. The impression the data give is that intrasexual competition is considerably stronger among men than women. In other words, when it comes to mate competition, we are closer to being an MCFC species than an MMC species.

Homicide records have the great advantage that the data are less prone than questionnaire studies to self-report biases and less prone than other violent crime statistics to reporting bias (virtually all homicides are reported). At the same time, though, the accuracy of the data is confounded with the extreme nature of the act in question. Focusing on an extreme and rare behavior is likely to give an exaggerated impression of the typical sex difference in intrasexual competition. This is because, as discussed earlier, even a small difference in means is associated with a large difference

at the tail of the distribution. Homicide sits at the extreme tail of the distribution for aggressive behavior. At that end of the distribution, the sex difference is extremely large. Closer to the mean, though, the difference is likely to be considerably smaller. Consistent with this suggestion, questionnaire and interview studies of aggression (which focus on less extreme, more common forms of violence than homicide) find much more modest sex differences. This is the case both in modern, Western nations (Archer, 2004) and in small-scale, non-Western societies (Hess, Helfrecht, Hagen, Sell, & Hewlett, 2010). Thus, although the homicide data suggest that intrasexual competition is more intense among males than females in our species, the difference is not as large as we might think if the homicide data were representative of the sex difference at all levels of intensity of competition.

Evolutionary psychologists have also used risky behavior as a barometer of sex differences in intrasexual selection. On average, men take more risks than women, especially in early adulthood. This can be seen, for instance, in their driving habits. Men drive faster and more recklessly, especially between the ages of 15 and 25. As a result, men are much more likely than women to die in car accidents, even taking into account differences in how much driving each sex does (Daly & Wilson, 1983). More generally, Kruger and Nesse (2004) observed that, in nations where death during childbirth has been largely eliminated, young men have 2.5 to 5 times higher mortality than young women. "Being male," they observed, "is now the single largest demographic risk factor for early mortality in developed countries" (Kruger & Nesse, 2006, p. 92). At first glance, this again suggests a large sex difference in the intensity of intrasexual competition. However, this evidence faces the same caveat as the homicide data. Although many more men than women die young, the vast majority of men do not. For instance, of U.S. men and women aged 15 to 24 in 2009, only .1% of men and .04% of women died (Kochanek, Xu, Murphy, Miniño, & Kung, 2011). Of those people who do die young, many presumably occupy the extreme right-hand tail of the distribution for risk taking. Once again, a large difference at the extremes equates to a much smaller difference at the means. Thus, although there is a large difference in the number of men vs. women who die young, the sex difference in risk proneness for the vast majority of men and women is nowhere near as large.

Culture as Intrasexual Competition

The same argument applies to another famous finding in EP. In humans, a pivotal form of intrasexual competition is competition in producing mate attraction displays (Buss, 1988). With this in mind, Miller (1998) observed that men produce an order of magnitude more cultural products than do women. In one

study, for instance, he showed that men make many more jazz records than women, and that they make most of them as young adults (Miller, 1999). Men also write more books, paint more pictures, and engage in more life-threatening stunts to earn themselves a place in the *Guinness World Records* book. Miller (1998) argued that these activities function as male mating displays: "As every teenager knows and most psychologists forget," he wrote, "cultural displays by males increase their sexual success" (p. 119). No doubt part of the reason that men have produced more cultural displays than women, at least prior to the second wave of the feminist revolution, is that women have been forced into social roles that preclude the pursuit of such activities. Nonetheless, it is reasonable to suppose that much of the remaining difference is a result of an evolved tendency for men to devote more effort than women to competitive activities and sexual displaying. There is still the question, though, of how large the average difference is. The evidence Miller presented (e.g., the number of jazz records) seems to suggest that it is very large. Again, though, without disputing Miller's findings, we suggest that, taken in isolation, they may create an inflated impression of the magnitude of the sex difference.

As with the homicide and mortality research, Miller was looking at behavior at the extreme of the distribution, that is, cultural products created by individuals who devote enough time and effort to mastering their craft and promoting themselves that their work attracts great attention via the mass media. At more normal levels of creative accomplishment, the sex difference may be nowhere near as large. Because males in our species are somewhat more sexually selected than females, more men than women may be involved in activities such as music, art, and writing in the context of sexual display. Because a small difference at the mean implies a large difference at the tail of the distribution, when we look at especially high achievement in these areas, we may see *many* more men than women. Once again, though, we may exaggerate the sex difference because of the kind of data we use to test our predictions: data from an atypical subset of human beings drawn from the tail of the distribution. To be fair, Miller's goal in assembling these data was not to estimate the precise degree of sexual dimorphism in the general population; it was simply to demonstrate the relevance of sexual selection theory to the explanation of cultural displays. Nonetheless, the focus on extreme cases may inadvertently skew our understanding of the sex difference in intrasexual competition in our species, pushing our picture of ourselves toward the MCFC model and away from the MMC.

Conclusion

Various lines of evidence suggest that the MCFC model exerts a significant influence on the evolution-

ary psychological view of human sexuality and human nature. However, the MCFC schema applies only when males' reproductive variability is much greater than females'. Humans are not this kind of species, and thus we should not be surprised that the MCFC schema does not apply well to us. In our species, men and women commonly form pair bonds, and men typically contribute to the rearing of young. Pair bonding and high male parental investment in our ancestral past reduced the sex difference in reproductive variability, which led to a reduction in sexual dimorphism and the evolution of mutual mate choice. Men's reproductive variability is still generally higher than women's, which is why men are, on average, larger and more aggressive than women, as well as being more interested in casual sex. However, this should be viewed as a qualification to the claim that we are primarily a pair bonding, biparental species rather than as the foundation stone of our emerging picture of humankind. The MMC model of human sexuality places pair bonding and biparental care at the heart of this picture. In doing so, it provides a better framework for understanding the (relatively modest) evolved sex differences found in our species.

Note

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References

- Amundsen, T., Forsgren, E., & Hansen, L. T. T. (1997). On the function of female ornaments: Male bluethroats prefer colourful females. *Proceedings of the Royal Society of London, Series B*, 264, 1579–1586.
- Anderson, K. G. (2006). How well does paternity confidence match actual paternity? Evidence from worldwide nonpaternity rates. *Current Anthropology*, 47, 513–520.
- Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.
- Apicella, C. L., & Marlowe, F. W. (2004). Perceived mate fidelity and paternal resemblance predict men's investment in children. *Evolution and Human Behavior*, 25, 371–378.
- Apostolou, M. (2007). Elements of parental choice: The evolution of parental preferences in relation to in-law selection. *Evolutionary Psychology*, 5, 70–83.
- Apostolou, M. (2010). Sexual selection under parental choice in agropastoral societies. *Evolution and Human Behavior*, 31, 39–47.
- Araújo, A., Arruda, M. F., Alencar, A. I., Albuquerque, F., Nascimento, M. C., & Yamamoto, M. E. (2000). Body weight of wild and captive common marmosets (*Callithrix jacchus*). *International Journal of Primatology*, 21, 317–324.
- Archer, J. (2004). Sex differences in aggression in real-world settings: A meta-analytic review. *Review of General Psychology*, 8, 291–322.
- Archer, J. (2006). Testosterone and human aggression: An evaluation of the challenge hypothesis. *Neuroscience and Biobehavioral Reviews*, 30, 319–345.

- Bailey, J. M., Gaulin, S., Agyei, Y., & Gladue, B. A. (1994). Effects of gender and sexual orientation on evolutionarily relevant aspects of human mating psychology. *Journal of Personality and Social Psychology*, *66*, 1081–1093.
- Barber, N. (1995). The evolutionary psychology of physical attractiveness: Sexual selection and human morphology. *Ethology and Sociobiology*, *16*, 395–424.
- Baumeister, R. F., & Vohs, K. D. (2004). Sexual economics: Sex as female resource for social exchange in heterosexual interactions. *Personality and Social Psychology Review*, *8*, 339–363.
- Becker, D. V., Kenrick, D. T., Guerin, S., & Maner, J. K. (2005). Concentrating on beauty: Sexual selection and sociospatial memory. *Personality and Social Psychology Bulletin*, *31*, 1643–1652.
- Beckerman, S., & Valentine, P. (2002). *Cultures of multiple fathers: The theory and practice of partible paternity in Lowland South America*. Gainesville: University Press of Florida.
- Betzig, L. L. (1986). *Despotism and differential reproduction: A Darwinian view of history*. Hawthorne, NY: Aldine.
- Betzig, L. L. (2002). Croaks and tails or teeth and claws? Review of Miller's Mating Mind. *Psychology*, *13*, 4.
- Betzig, L. L. (2012). Means, variances, and ranges in reproductive success: Comparative evidence. *Evolution and Human Behavior*, *33*, 309–317.
- Blow, A., & Hartnett, K. (2005). Infidelity in committed relationships II: A substantive review. *Journal of Marital and Family Therapy*, *31*, 217–233.
- Bogin, B. (1999). *Patterns of human growth*. Cambridge, MA: Cambridge University Press.
- Bressler, E. R., Martin, R. A., & Balshine, S. (2006). Production and appreciation of humor as sexually selected traits. *Evolution and Human Behavior*, *27*, 121–130.
- Bribiescas, R. G., Ellison, P. T., & Gray, P. B. (2012). Male life history, reproductive effort, and the evolution of the genus *Homo*: New directions and perspectives. *Current Anthropology*, *53*, S424–S435.
- Brooks-Gordon, B. (2006). *The price of sex: Prostitution, policy and society*. Devon, UK: Willan.
- Brown, J., Laland, K. N., & Borgerhoff Mulder, M. (2009). Bateman's principles and human sex roles. *Trends in Ecology and Evolution*, *24*, 297–304.
- Brym, R. J., & Lie, J. (2007). *Sociology: Your compass for a new world* (3rd ed.). Belmont, CA: Thomson Wadsworth.
- Buss, D. M. (1988). The evolution of human intrasexual competition: Tactics of mate attraction. *Journal of Personality and Social Psychology*, *54*, 616–628.
- Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences*, *12*, 1–49.
- Buss, D. M. (2003). *The evolution of desire: Strategies of human mating* (Rev. ed.). New York, NY: Basic Books.
- Buss, D. M. (2000). *The dangerous passion: Why jealousy is as necessary as love and sex*. New York, NY: Free Press.
- Buss, D. M. (2010). *Evolved sex differences: Not gone, not forgotten, and not explained by alternative hypotheses*. Retrieved from <https://fistfulofscience.wordpress.com/2010/10/15/david-buss-defends-evolved-sex-differences-exclusive/>
- Buss, D. M. (2012). *Evolutionary psychology: The new science of the mind* (4th ed.). Needham Heights, MA: Allyn & Bacon.
- Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review*, *100*, 204–232.
- Buss, D. M., & Shackelford, T. K. (1997). From vigilance to violence: Mate retention tactics in married couples. *Journal of Personality and Social Psychology*, *72*, 346–361.
- Campbell, A. (1995). A few good men: Evolutionary psychology and female adolescent aggression. *Ethology and Sociobiology*, *16*, 99–123.
- Campbell, A. (2002). *A mind of her own: The evolutionary psychology of women*. Oxford, UK: Oxford University Press.
- Cant, J. G. H. (1981). Hypothesis for the evolution of human breasts and buttocks. *American Naturalist*, *117*, 199–204.
- Carothers, B. J., & Reis, H. T. (2013). Men and women are from Earth: Examining the latent structure of gender. *Journal of Personality and Social Psychology*, *104*, 385–407.
- Chapais, B. (2008). *Primeval kinship: How pair-bonding gave birth to human society*. Cambridge, MA: Harvard University Press.
- Clark, R. D., & Hatfield, E. (1989). Gender differences in receptivity to sexual offers. *Journal of Psychology and Human Sexuality*, *2*, 39–55.
- Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton, NJ: Princeton University Press.
- Clutton-Brock, T. H., & Vincent, A. C. J. (1991). Sexual selection and the potential reproductive rates of males and females. *Nature*, *351*, 58–60.
- Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd ed.). Hillsdale, NJ: Erlbaum.
- Conley, T. D. (2011). Perceived proposer personality characteristics and gender differences in acceptance of casual sex offers. *Journal of Personality and Social Psychology*, *100*, 309–329.
- Conley, T. D., Moors, A. C., Matsick, J. L., Ziegler, A., & Valentine, B. A. (2011). Women, men, and the bedroom: Methodological and conceptual insights that narrow, reframe, and eliminate gender differences in sexuality. *Current Directions in Psychological Science*, *20*, 296–300.
- Costa, P. T., Terracciano, A., & McCrae, R. R. (2001). Gender differences in personality traits across cultures: Robust and surprising findings. *Journal of Personality and Social Psychology*, *81*, 322–331.
- Daly, M., & Wilson, M. (1983). *Sex, evolution, and behavior: Adaptations for reproduction* (2nd ed.). Boston, MA: Willard Grant.
- Daly, M., & Wilson, M. (1987). The Darwinian psychology of discriminative parental solicitude. *Nebraska Symposium on Motivation*, *35*, 91–144.
- Daly, M., & Wilson, M. (1988). *Homicide*. Hawthorne, NY: Aldine de Gruyter.
- Daly, M., & Wilson, M. (1998). *The truth about Cinderella: A Darwinian view of parental love*. New Haven, CT: Yale University Press.
- Daly, M., & Wilson, M. (2001a). An assessment of some proposed exceptions to the phenomenon of nepotistic discrimination against stepchildren. *Annales Zoologici Fennici*, *36*, 287–296.
- Daly, M., & Wilson, M. (2001b). Risk-taking, intrasexual competition, and homicide. *Nebraska Symposium on Motivation*, *47*, 1–36.
- Darwin, C. (1859). *On the origin of the species by means of natural selection*. London, UK: Murray.
- Darwin, C. (1871). *The descent of man and selection in relation to sex*. London, UK: Murray.
- Davis, J. N., & Daly, M. (1997). Evolutionary theory and the human family. *Quarterly Journal of Biology*, *72*, 407–435.
- Dawkins, R. (1976). *The selfish gene*. New York, NY: Oxford University Press.
- Deary, I. J., Thorpe, G., Wilson, V., Starr, J. M., & Whalley, L. J. (2003). Population sex differences in IQ at age 11: The Scottish Mental Survey 1932. *Intelligence*, *31*, 533–542.
- Del Giudice, M. (2009). On the real magnitude of sex differences. *Evolutionary Psychology*, *7*, 264–279.
- Del Giudice, M., Booth, T., & Irwing, P. (2012). The distance between Mars and Venus: Measuring global sex differences in personality. *PLoS ONE*, *7*, e29265.
- Dewsbury, D. A., Baumgardner, D. J., Evans, R. L., & Webster, D. G. (1980). Sexual dimorphism for body mass in 13 taxa of murid rodents under laboratory conditions. *Journal of Mammalogy*, *61*, 146–149.

- Dickemann, M. (1981). Paternal confidence and dowry competition: A biocultural analysis of purdah. In R. D. Alexander & D. W. Tinkle (Eds.), *Natural selection and social behavior: Recent research and new evidence* (pp. 417–438). New York, NY: Chiron Press.
- Dixon, A. F. (1998). *Primate sexuality: Comparative studies of the prosimians, monkeys, apes, and human beings*. Oxford, UK: Oxford University Press.
- Dixon, B. J., Grimshaw, G. M., Linklater, W. L., & Dixon, A. F. (2011). Eye tracking of men's preferences for female breast size and areola pigmentation. *Archives of Sexual Behavior, 40*, 51–58.
- Dunbar, R. I. M., Marriott, A., & Duncan, N. D. C. (1997). Human conversational behaviour. *Human Nature, 8*, 231–246.
- Dunsworth, H. M., Warrener, A. G., Deacon, T., Ellison, P. T., & Pontzer, H. (2012). Metabolic hypothesis for human altriciality. *Proceedings of the National Academy of Sciences, 109*, 15212–15216.
- Dwyer, P. D., & Minnegal, M. (1993). Are Kubo hunters “show-offs”? *Ethology and Sociobiology, 14*, 53–70.
- Eagly, A. (1995). The science and politics of comparing women and men. *American Psychologist, 50*, 145–158.
- Eagly, A. H., & Steffen, V. J. (1986). Gender and aggressive behavior: A meta-analytic review of the social psychological literature. *Psychological Bulletin, 100*, 309–330.
- Eagly, A. H., & Wood, W. (1999). The origins of sex differences in human behavior: Evolved dispositions versus social roles. *American Psychologist, 54*, 408–423.
- Edward, D. A., & Chapman, T. (2011). The evolution and significance of male mate choice. *Trends in Ecology and Evolution, 26*, 647–654.
- Eens, M., & Pinxten, R. (2000). Sex-role reversal in vertebrates: Behavioural and endocrinological accounts. *Behavioural Processes, 51*, 135–147.
- Einon, D. (1998). How many children can one man have? *Evolution and Human Behavior, 19*, 413–426.
- Fausto-Sterling, A. (1992). *Myths of gender: Biological theories about women and men*. New York, NY: Basic Books.
- Feingold, A., & Mazzella, R. (1998). Gender differences in body image are increasing. *Psychological Science, 9*, 190–195.
- Fink, B., Seydel, H., Manning, J. T., & Kappeler, P. M. (2007). A preliminary investigation of the association between digit ratio and women's perception of men's dance. *Personality and Individual Differences, 42*, 381–390.
- Fisher, H. E. (1992). *The anatomy of love: The natural history of monogamy, adultery, and divorce*. New York, NY: Norton.
- Flinn, M. V. (1988a). Parent-offspring interactions in a Caribbean village: Daughter guarding. In L. Betzig, M. Borgerhoff Mulder, & P. Turke (Eds.), *Human reproductive behavior* (pp. 189–200). Cambridge, UK: Cambridge University Press.
- Flinn, M. V. (1988b). Step- and genetic parent/offspring relationships in a Caribbean village. *Ethology and Sociobiology, 9*, 1–34.
- Ford, C. S., & Beach, F. A. (1951). *Patterns of sexual behavior*. New York, NY: Harper & Row.
- Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating: Trade-offs and strategic pluralism. *Behavioral and Brain Sciences, 23*, 573–587.
- Gaulin, S. J. C., & Boster, J. S. (1985). Cross-cultural differences in sexual dimorphism: Is there any variance to be explained? *Ethology and Sociobiology, 6*, 219–225.
- Gaulin, S. J. C., & McBurney, D. H. (2004). *Evolutionary psychology* (2nd ed.). Upper Saddle River, NJ: Prentice Hall.
- Geary, D. C. (2000). Evolution and proximate expression of human paternal investment. *Psychological Bulletin, 126*, 55–77.
- Geary, D. C., & Flinn, M. V. (2001). Evolution of human parental behavior and the human family. *Parenting: Science and Practice, 1*, 5–61.
- Geissmann, T. (1993). *Evolution of communication in gibbons (Hylobatidae)*. (Unpublished doctoral dissertation). Zürich, University, Zürich, Switzerland.
- 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*, 16194–16199.
- 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*, 362–370.
- Gomendio, M., Harcourt, A. H., & Roldán, E. R. S. (1998). Sperm competition in mammals. In T. R. Birkhead & A. P. Moller (Eds.), *Sperm competition and sexual selection* (pp. 667–756). New York, NY: Academic Press.
- Goodale, J. C. (1971). *Tiwi wives: A study of the women of Melville Island, North Australia*. Seattle: University of Washington Press.
- Gordon, C. (2012). *Men and women's differences extend to personality, study claims*. Retrieved from http://www.huffingtonpost.com/2012/01/09/men-and-womens-difference-personality_n_1194613.html
- Gordon, I., Zagoory-Sharon, O., Leckman, J. F., & Feldman, R. (2010). Prolactin, oxytocin, and the development of paternal behavior across the first six months of fatherhood. *Hormones and Behavior, 58*, 513–518.
- Gottschall, J., & Nordlund, M. (2006). Romantic love: A literary universal. *Philosophy and Literature, 30*, 432–452.
- Gould, R. G. (2000). How many children could Moulay Ismail have had? *Evolution and Human Behavior, 21*, 295–296.
- Gray, P. B., & Anderson, K. G. (2010). *Fatherhood: Evolution and human paternal behavior*. Cambridge, MA: Harvard University Press.
- Gray, P. B., Parkin, J. C., & Samms-Vaughan, M. E. (2007). Hormonal correlates of human paternal interactions: A hospital-based investigation in urban Jamaica. *Hormones and Behavior, 52*, 499–507.
- Greengross, G., & Miller, G. (2011). Humor ability reveals intelligence, predicts mating success, and is higher in males. *Intelligence, 39*, 188–192.
- Guéguen, N. (2011). Effects of solicitor sex and attractiveness on receptivity to sexual offers: A field study. *Archives of Sexual Behavior, 40*, 915–919.
- Gurven, M. D., & Hill, K. (2009). Why do men hunt? A reevaluation of ‘man the hunter’ and the sexual division of labor. *Current Anthropology, 50*, 51–74.
- Gwynne, D. T. (1981). Sexual difference theory: Mormon crickets show role reversal in mate choice. *Science, 213*, 779–780.
- Hald, G. M. (2006). Gender differences in pornography consumption among young heterosexual Danish adults. *Archives of Sexual Behavior, 35*, 577–585.
- Hald, G. M., & Høgh-Olesen, H. (2010). Receptivity to sexual invitations from strangers of the opposite gender. *Evolution and Human Behavior, 31*, 453–458.
- Hames, R. B. (1988). The allocation of parental care among the Yekwana. In L. Betzig, M. Borgerhoff Mulder, & P. Turke (Eds.), *Human reproductive behavior* (pp. 237–252). Cambridge, UK: Cambridge University Press.
- Hart, C. W. M., Pilling, A. R., & Goodale, J. C. (1988). *The Tiwi of North Australia* (3rd ed.). New York, NY: Holt, Rinehart, & Winston.
- Hartung, J. (1985). Matrilineal inheritance: New theory and analysis. *Behavioral and Brain Sciences, 8*, 661–670.
- Hawkes, K. (1991). Showing off: Tests of an hypothesis about men's foraging goals. *Ethology and Sociobiology, 12*, 29–54.
- Hawkes, K. (2005). The grandmother effect. *Nature, 428*, 128–129.

- Hawkes, K., Rogers, A. R., & Charnov, E. L. (1995). The male's dilemma: Increased offspring production is more paternity to steal. *Evolution and Ecology*, *9*, 1–16.
- Hess, N., Helfrecht, C., Hagen, E., Sell, A., & Hewlett, B. (2010). Interpersonal aggression among Aka hunter-gatherers of the Central African Republic: Assessing the effects of sex, strength, and anger. *Human Nature*, *21*, 330–354.
- Hewlett, B. S., & MacFarlan, S. J. (2010). Fathers' roles in hunter-gatherers and other small-scale cultures. In M. E. Lamb (Ed.), *The role of the father in child development* (pp. 413–434). Hoboken, NJ: Wiley.
- Hill, K., & Hurtado, A. M. (1996). *Demographic/life history of Ache foragers*. Hawthorne, NY: Aldine de Gruyter.
- Hooper, P. L., & Miller, G. F. (2008). Mutual mate choice can drive costly signaling even under perfect monogamy. *Adaptive Behavior*, *16*, 53–70.
- Hrdy, S. B. (1981). *The woman that never evolved*. Cambridge, MA: Harvard University Press.
- Hrdy, S. B. (2009). *Mothers and others: The evolutionary origin of mutual understanding*. Cambridge, MA: Harvard University Press.
- Hyde, J. S. (2005). The gender similarities hypothesis. *American Psychologist*, *60*, 581–592.
- Ihara, Y., & Aoki, K. (1999). Sexual selection by male choice in monogamous and polygynous human populations. *Theoretical Population Biology*, *55*, 77–93.
- Irons, W. (1989). Mating preferences surveys: Ethnographic follow-up would be a good next step. *Behavioral and Brain Sciences*, *12*, 24.
- Jankowiak, W., & Fisher, E. (1992). Cross-cultural perspective on romantic love. *Ethnology*, *31*, 149–156.
- Jasienska, G., Ziomkiewicz, A., Ellison, P. T., Lipson, S. F., & Thune, I. (2004). Large breasts and narrow waists indicate reproductive potential in women. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *271*, 1213–1217.
- Johnstone, R. A. (1997). The tactics of mutual mate choice and competitive search. *Behavioral Ecology and Sociobiology*, *40*, 51–59.
- Jones, B. C., DeBruine, L. M., Little, A. C., Burriss, R. P., & Feinberg, D. R. (2007). Social transmission of face preferences among humans. *Proceedings of the Royal Society of London, Series B*, *274*, 899–903.
- Jones, I. L., & Hunter, F. M. (1993). Mutual sexual selection in a monogamous seabird. *Nature*, *36*, 238–239.
- Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence and longevity. *Evolutionary Anthropology*, *9*, 156–185.
- Kaplan, H. (1994). Evolutionary and wealth flow theories of fertility: Empirical tests and new models. *Population and Development Review*, *20*, 753–791.
- Kaufman, S. B., Kozbelt, A., Bromley, M. L., & Miller, G. F. (2008). The role of creativity and humor in human mate selection. In G. Geher & G. F. Miller (Eds.), *Mating intelligence: Sex, relationships, and the mind's reproductive system* (pp. 227–262). Mahwah, NJ: Erlbaum.
- Kenrick, D. T., Sadalla, E. K., Groth, G., & Trost, M. R. (1990). Evolution, traits, and the stages of human courtship: Qualifying the parental investment model. *Journal of Personality*, *58*, 97–116.
- Kinsey, A. C., Pomeroy, W. B., Martin, C. E., & Gebhard, P. H. (1948). *Sexual behavior in the human male*. Philadelphia, PA: Saunders.
- Kleiman, D. G. (1977). Monogamy in mammals. *Quarterly Review of Biology*, *52*, 39–69.
- Kochanek, K. D., Xu, J., Murphy, S. L., Miniño, A. M., & Kung, H. (2011). Deaths: Final data for 2009. *National Vital Statistics Reports*, Vol. 60. New York, NY: CDC National Center for Health Statistics.
- Kraaijeveld, K., Gregurke, J., Hall, C., Komdeur, J., & Mulder, R. A. (2004). Mutual ornamentation, sexual selection and social dominance in the black swan. *Behavioral Ecology*, *15*, 380–383.
- Kruger, D. J., & Nesse, R. M. (2004). Sexual selection and the Male:Female Mortality Ratio. *Evolutionary Psychology*, *2*, 66–85.
- Kruger, D. J., & Nesse, R. M. (2006). An evolutionary life-history framework for understanding sex differences in human mortality rates. *Human Nature*, *17*, 74–97.
- Labuda, D., Lefebvre, J. F., Nadeau, P., & Roy-Gagnon, M. H. (2010). Female-to-male breeding ratio in modern humans: An analysis based on historical recombinations. *American Journal of Human Genetics*, *86*, 353–363.
- Lack, D. (1968). *Ecological adaptations for breeding in birds*. London, UK: Methuen.
- Lammers, J., Stoker, J. I., Jordan, J., Pollmann, M., & Stapel, D. A. (2011). Power increases infidelity among men and women. *Psychological Science*, *22*, 1191–1197.
- Lancaster, J. B., & Lancaster, C. (1985). Parental investment: The hominid adaptation. In D. Ortner (Ed.), *How humans adapt: A biocultural odyssey* (pp. 333–399). Washington, DC: Smithsonian Institution Press.
- Lassek, W. D., & Gaulin, S. J. C. (2009). Costs and benefits of fat-free muscle mass in men: Relationship to mating success, dietary requirements, and native immunity. *Evolution and Human Behavior*, *30*, 322–328.
- Lippa, R. A. (2007). The preferred traits of mates in a cross-national study of heterosexual and homosexual men and women: An examination of biological and cultural influences. *Archives of Sexual Behavior*, *36*, 193–208.
- 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*, 631–651.
- Lippa, R. A. (2012). Multivariate versus univariate conceptions of sex differences: Let the contest begin. Retrieved from <http://blogs.plos.org/everyone/2012/01/04/multivariate-versus-univariate-conceptions-of-sex-differences-let-the-contest-begin/>
- Little, A. C., Burriss, R. P., Jones, B. C., DeBruine, L. M., & Caldwell, C. A. (2008). Social influence in human face preference: Men and women are influenced more for long-term than short-term attractiveness decisions. *Evolution and Human Behavior*, *29*, 140–146.
- Loehlin, J. C., & Nichols, R. C. (1976). *Heredity, environment, and personality*. Austin: University of Texas Press.
- Lovejoy, O. C. (1981). The origin of man. *Science*, *259*, 118–125.
- Low, B. S., Alexander, R. D., & Noonan, K. M. (1987). Human hips, breasts and buttocks: Is fat deceptive? *Ethology and Sociobiology*, *8*, 249–258.
- Mansson, S.-A. (2005). Men's practices in prostitution and their implications for social work. In S.-A. Mansson, & C. Proveyer Cervantes (Eds.), *Social work in Cuba and Sweden: Achievements and prospects* (pp. 267–280). Göteborg, Sweden: Göteborg University.
- Marlowe, F. W. (1998). The nubility hypothesis: The human breast as an honest signal of residual reproductive value. *Human Nature*, *9*, 263–271.
- Marlowe, F. W. (1999a). Male care and mating effort among Hadza foragers. *Behavioral Ecology and Sociobiology*, *46*, 57–64.
- Marlowe, F. W. (1999b). Showoffs or providers? The parenting effort of Hadza men. *Evolution and Human Behavior*, *20*, 391–404.
- Marlowe, F. (2000). Paternal investment and the human mating system. *Behavioural Processes*, *51*, 45–61.
- Marlowe, F. W. (2001). Male contribution to diet and female reproductive success among foragers. *Current Anthropology*, *42*, 755–760.

- Marlowe, F. W. (2003a). A critical period for provisioning by Hadza men: Implications for pair bonding. *Evolution and Human Behavior*, *24*, 217–229.
- Marlowe, F. W. (2003b). The mating system of foragers in the Standard Cross-Cultural Sample. *Cross-Cultural Research*, *37*, 282–306.
- Marlowe, F. W. (2004). Mate preferences among Hadza hunter-gatherers. *Human Nature*, *15*, 365–376.
- Marshall, D. S. (1971). Sexual behavior in Mangaia. In D. S. Marshall & R. C. Suggs (Eds.), *Human sexual behavior* (pp. 103–162). New York, NY: Basic Books.
- Martin, R. D. (1990). *Primate origins and evolution: A phylogenetic reconstruction*. Princeton, NJ: Princeton University Press.
- McKinstry, M. C., & Anderson, S. H. (1998). Using snares to live-capture beaver, *Castor Canadensis*. *Canadian Field-Naturalist*, *112*, 469–473.
- Mikach, S. M., & Bailey, J. M. (1999). What distinguishes women with unusually high numbers of sex partners? *Evolution and Human Behavior*, *20*, 141–150.
- Miller, G. F. (1998). How mate choice shaped human nature: A review of sexual selection and human evolution. In C. B. Crawford & D. L. Krebs (Eds.), *Handbook of evolutionary psychology: Ideas, issues, and applications* (pp. 87–129). Mahwah, NJ: Erlbaum.
- Miller, G. F. (1999). Sexual selection for cultural displays. In R. Dunbar, C. Knight, & C. Power (Eds.), *The evolution of culture* (pp. 71–91). Edinburgh, Scotland: Edinburgh University Press.
- Miller, G. F. (2000). *The mating mind: How sexual choice shaped the evolution of human nature*. London, UK: Vintage.
- Miller, G. F., Tybur, J. M., & Jordan, B. D. (2007). Ovulatory cycle effects on tip earnings by lap dancers: Economic evidence for human estrus? *Evolution and Human Behavior*, *28*, 375–381.
- Miller, L. C., & Fishkin, S. A. (1997). On the dynamics of human bonding and reproductive success: Seeking windows on the adapted-for human environment interface. In J. A. Simpson & D. T. Kenrick (Eds.), *Evolutionary social psychology* (pp. 197–235). Mahwah, NJ: Erlbaum.
- Miller, L. C., Pedersen, W. C., & Putcha-Bhagavatula, A. D. (2005). Promiscuity in an evolved pair-bonding system: Mating within and outside the Pleistocene box. *Behavioral and Brain Sciences*, *28*, 290–291.
- Miller, L. C., Putcha-Bhagavatula, A. D., & Pedersen, W. C. (2002). Men's and women's mating preferences: Distinct evolutionary mechanisms? *Current Directions in Psychological Science*, *11*, 88–93.
- Muller, M. N., Marlowe, F. W., Bugumba, R., & Ellison, P. T. (2008). Testosterone and paternal care in East African foragers and pastoralists. *Proceedings of the Royal Society of London, Series B*, *276*, 347–354.
- Murdock, G. P. (1967). *Ethnographic atlas*. Pittsburgh, PA: University of Pittsburgh Press.
- Nolan, P. M., Dobson, F. S., Nicolaus, M., Karels, T. J., McGraw, K. J., & Jouventin, P. (2010). Mutual mate choice for colorful traits in king penguins. *Ethology*, *116*, 635–644.
- Nunn, C. L., Gittleman, J. L., & Antonovics, J. (2000). Promiscuity and the primate immune system. *Science*, *290*, 1168–1170.
- Ogas, O., & Gaddam, S. (2011). *A billion wicked thoughts: What the world's largest experiment reveals about human desire*. New York, NY: Dutton.
- Oring, L. W. (1986). Avian polyandry. In R. J. Johnston (Ed.), *Current Ornithology*, Vol. 3 (pp. 309–351). New York, NY: Plenum.
- Pedersen, W. C., Putcha-Bhagavatula, A. D., & Miller, L. C. (2011). Are men and women really that different? Examining some of Sexual Strategies Theory (SST)'s key assumptions about sex-distinct mating mechanisms. *Sex Roles*, *64*, 629–643.
- Pennington, R. (2001). Hunter-gatherer demography. In C. Panter-Brick, R. H. Layton, & P. Rowley-Conwy (Eds.), *Hunter-gatherers: An interdisciplinary perspective* (pp. 170–204). Cambridge, UK: Cambridge University Press.
- Pérusse, D. (1993). Cultural and reproductive success in industrial societies: Testing the relationship at the proximate and ultimate levels. *Behavioral and Brain Sciences*, *16*, 267–322.
- Peterson, J. L., & Hyde, J. S. (2010). A meta-analytic review of research on gender differences in sexuality, 1993–2007. *Psychological Bulletin*, *136*, 21–38.
- Pillsworth, E. G., & Barrett, H. C. (2008). *Women's subordination and resistance in Shuar marriage: A case for female choice in the evolution of human mating*. Manuscript in preparation.
- Pinker, S. (1997). *How the mind works*. London, UK: Penguin.
- Pinker, S. (2002). *The blank slate: The modern denial of human nature*. New York, NY: Viking.
- Place, S. S., Todd, P. M., Penke, L., & Asendorpf, J. B. (2010). Humans show mate copying after observing real mate choices. *Evolution and Human Behavior*, *31*, 320–325.
- Plavcan, M., & Van Schaik, C. (1997). Interpreting hominid behavior on the basis of sexual dimorphism. *Journal of Human Evolution*, *32*, 345–374.
- Prokosch, M. D., Coss, R. G., Scheib, J. E., & Blozis, S. A. (2009). Intelligence and mate choice: Intelligent men are always appealing. *Evolution and Human Behavior*, *30*, 11–20.
- Puts, D. A. (2010). Beauty and the beast: Mechanisms of sexual selection in humans. *Evolution and Human Behavior*, *31*, 157–175.
- Roberts, S. C., Little, A. C., Goslinga, L. M., Perrett, D. I., Carter, V., Jones, B. C., . . . Petric, M. (2005). MHC-heterozygosity and human facial attractiveness. *Evolution and Human Behavior*, *26*, 213–226.
- Rosenthal, R., & Rubin, D. B. (1979). A note on percent variance explained as a measure of the importance of effects. *Journal of Applied Social Psychology*, *9*, 395–396.
- Ryan, C., & Jethá, C. (2010). *Sex at dawn: The prehistoric origins of modern sexuality*. New York, NY: HarperCollins.
- Salmon, C. A. (2012). The pop culture of sex: An evolutionary window on the worlds of pornography and romance. *Review of General Psychology*, *16*, 152–160.
- Schlegel, A., & Barry, H. (1991). *Adolescence: An anthropological inquiry*. New York, NY: Free Press.
- Schmitt, D. P. (2005a). Fundamentals of human mating strategies. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 258–291). Hoboken, NJ: Wiley.
- Schmitt, D. P. (2005b). Sociosexuality from Argentina to Zimbabwe: A 48-nation study of sex, culture, and strategies of human mating. *Behavioral and Brain Sciences*, *28*, 247–275.
- Schmitt, D. P. (2012a). *Men, women, and interplanetary promiscuity: Men and women are both promiscuous by design (monogamous, too)*. Retrieved from <http://www.psychologytoday.com/blog/sexual-personalities/201202/men-women-and-inter-planetary-promiscuity>
- Schmitt, D. P. (2012b). When the difference is in the details: A critique of Zentner and Mitura (2012). Stepping out of the Cave-man's Shadow: Nations' Gender Gap Predicts Degree of Sex Differentiation in Mate Preferences. *Evolutionary Psychology*, *10*, 720–726.
- Schmitt, D. P., & Buss, D. M. (1996). Strategic self-promotion and competition derogation: Sex and conflict effects on perceived effectiveness of mate attraction tactics. *Journal of Personality and Social Psychology*, *70*, 1185–1204.
- Schmitt, D. P., Jonason, P. K., Byerley, G. J., Flores, S. D., Illbeck, B. E., O'Leary, K. N., . . . Qudat, A. (2012). A reexamination of sex differences in sexuality: New studies reveal old truths? *Current Directions in Psychological Science*, *21*, 135–139.
- Schmitt, D. P., & 118 Members of the International Sexuality Description Project. (2003). Universal sex differences in the desire for sexual variety: Tests from 52 nations, 6 continents, and 13 islands. *Journal of Personality and Social Psychology*, *85*, 85–104.

- Schradin, C., Reeder, D. M., Mendoza, S. P., & Anzenberger, G. (2003). Prolactin and paternal care: Comparison of three species of monogamous new world monkeys (*Callicebus cupreus*, *Callithrix jacchus*, and *Callimico goeldii*). *Journal of Comparative Psychology*, *117*, 166–175.
- Sear, R., & Mace, R. (2008). Who keeps children alive? A review of the effects of kin on child survival. *Evolution and Human Behavior*, *29*, 1–18.
- Segerstråle, U. (2000). *Defenders of the truth: The sociobiology debate*. Oxford, UK: Oxford University Press.
- Shackelford, T. K., Pound, N., Goetz, A. T., & LaMunyon, C. W. (2005). Female infidelity and sperm competition. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 372–393). Hoboken, NJ: Wiley.
- Sherfey, M. J. (1972). *The nature and evolution of female sexuality*. New York, NY: Random House.
- Short, R. V. (1979). Sexual selection and its component parts, somatic and genital selection, as illustrated by man and the Great Apes. *Advances in the Study of Behavior*, *9*, 131–158.
- Simpson, J. A., & Gangestad, S. W. (1991). Individual differences in sociosexuality: Evidence for convergent and discriminant validity. *Journal of Personality and Social Psychology*, *60*, 870–883.
- Simpson, J. A., Gangestad, S. W., Christensen, P. N., & Leck, K. (1999). Fluctuating asymmetry, sociosexuality, and intrasexual competitive tactics. *Journal of Personality and Social Psychology*, *76*, 159–172.
- Singh, D. (1993). Adaptive significance of female physical attractiveness: Role of waist-to-hip ratio. *Journal of Personality and Social Psychology*, *65*, 293–307.
- Singh, D. (1995). Female health, attractiveness, and desirability for relationships: Role of breast asymmetry and waist-to-hip ratio. *Ethology and Sociobiology*, *16*, 465–481.
- Storer, R. W., & Nuechterlein, G. L. (1992). Western Grebe (*Aechmophorus occidentalis*) and Clark's Grebe (*Aechmophorus clarkii*). In A. Poole (Eds.), *The birds of North America*, No. 26 (pp. 1–24). Ithaca, NY: Cornell Lab of Ornithology.
- Symons, D. (1979). *The evolution of human sexuality*. New York, NY: Oxford University Press.
- Taylor, T. (2010). *The artificial ape: How technology changed the course of human evolution*. New York, NY: Palgrave Macmillan.
- Thornhill, R., & Gangestad, S. W. (1993). Human facial beauty: Averageness, symmetry, and parasite resistance. *Human Nature*, *4*, 237–269.
- Thornhill, R., & Gangestad, S. W. (2008). *The evolutionary biology of human female sexuality*. Oxford, UK: Oxford University Press.
- Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19–136). New York, NY: Oxford University Press.
- 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, IL: Aldine Press.
- United Nations. (2009). *World population prospects*. New York, NY: United Nations.
- van Anders, S. M., & Goldey, K. L. (2010). Testosterone and partnering are linked via relationship status for women and 'relationship orientation' for men. *Hormones and Behavior*, *58*, 820–826.
- van Anders, S. M., Tolman, R. M., & Volling, B. L. (2012). Baby cries and nurturance affect testosterone in men. *Hormones and Behavior*, *61*, 31–36.
- Voracek, M., Hofhansl, A., & Fisher, M. L. (2005). Clark and Hatfield's evidence of women's low receptivity to male strangers' sexual offers revisited. *Psychological Reports*, *97*, 11–20.
- Washburn, S., & Lancaster, C. (1968). The evolution of hunting. In R. B. Lee & I. DeVore (Eds.), *Man the hunter* (pp. 193–303). Chicago, IL: Aldine Press.
- Waynforth, D. (1999). Differences in time use for mating and nepotistic effort as a function of male attractiveness in rural Belize. *Evolution and Human Behavior*, *20*, 19–28.
- Waynforth, D. (2007). Mate choice copying in humans. *Human Nature*, *18*, 264–271.
- Wedekind, C., & Furi, S. (1997). Body odor preferences in men and women: Do they aim for specific MHC combinations or simply heterozygosity? *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *264*, 1471–1479.
- Wedekind, C., Seebeck, T., Bettens, F., & Paepke, A. J. (1995). MHC-dependent mate preferences in humans. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *260*, 245–249.
- Weiss, S. L. (2006). Female-specific color is a signal of quality in the striped plateau lizard (*Sceloporus virgatus*). *Behavioral Ecology*, *17*, 726–732.
- Wilbur, C. J., & Campbell, L. (2011). Humor in romantic contexts: Do men participate and women evaluate? *Personality and Social Psychology Bulletin*, *37*, 918–929.
- Wilson, E. O. (1975). *Sociobiology: The new synthesis*. Cambridge, MA: Belknap Press.
- Wilson, E. O. (1978). *On human nature*. Cambridge, MA: Harvard University Press.
- Wilson, M., & Daly, M. (1985). Competitiveness, risk taking, and violence: The young male syndrome. *Ethology and Sociobiology*, *6*, 59–73.
- Wingfield, J. C., Hegner, R. E., Dufty, A. M., Jr., & Ball, G. F. (1990). The "challenge hypothesis": Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *American Naturalist*, *136*, 829–846.
- Wiszevska, A., Pawlowski, B., & Boothroyd, L. G. (2007). Father-daughter relationship as a moderator of sexual imprinting: A facialmetric study. *Evolution and Human Behavior*, *28*, 248–252.
- Wolf, M., Musch, J., Enczmann, J., & Fischer, J. (2012). Estimating the prevalence of nonpaternity in Germany. *Human Nature*, *23*, 208–217.
- Wood, W., & Eagly, A. H. (2002). A cross-cultural analysis of the behavior of women and men: Implications for the origins of sex differences. *Psychological Bulletin*, *128*, 699–727.
- Wood, W., & Eagly, A. H. (2012). Biosocial construction of sex differences and similarities in behavior. In J. M. Olson & M. P. Zanna (Eds.), *Advances in experimental social psychology*, Vol. 46 (pp. 55–123). London, UK: Elsevier.
- Workman, L., & Reader, W. (2008). *Evolutionary psychology: An introduction* (2nd ed.). Cambridge, UK: Cambridge University Press.
- Young, L. J., & Wang, Z. (2004). The neurobiology of pair bonding. *Nature Neuroscience*, *10*, 1048–1054.
- Zentner, M., & Mitura, K. (2012). Stepping out of the cave-man's shadow: Nations' gender gap predicts degree of sex differentiation in mate preferences. *Psychological Science*, *23*, 1176–1185.

Appendix

Del Giudice and Unidimensional versus Multidimensional Variables in Psychology

In the target article, we argue that the sex difference in sociosexuality (SO: roughly, willingness to engage in casual sex) is larger than most sex differences in psychology but is nonetheless relatively modest. One potential criticism of this suggestion comes from Marco Del Giudice (2009; Del Giudice, Booth,

& Irwing, 2012). Del Giudice argued that psychologists often underestimate the true magnitude of sex differences by focusing on single traits rather than multidimensional variables. The potential problem with the standard single-trait approach can be seen if we consider differences in men and women's body shapes (Lippa, 2012). Using the standard approach, we would look at a series of traits separately—waist-to-hip ratio, torso-to-leg ratio, and so on—and find a relatively small difference for each. We would then take the average of these small differences and conclude that the overall difference in body shape is small. However, noted Del Giudice, this would be a misleading conclusion. The body shapes of men and women are very different—different enough that people can almost always correctly classify silhouettes as male or female. The correct approach would be to treat the individual traits as a single multidimensional variable, and estimate the effect size of that variable. There are effect size estimates that do exactly this; Del Giudice favors the Mahalanobis distance D (the multivariate generalization of Cohen's d).

When applied in the psychological realm, the technique yields surprising results. For instance, assessing the Big Five personality traits one by one, the sex differences are relatively modest (generally less than $d = .3$; Costa, Terracciano, & McCrae, 2001). When bundled together, however, the difference turns out to be much larger. In one study, Del Giudice and colleagues (2012) found an effect size of 2.71 for the sex difference in “global personality.” This led one of the coauthors on the article, Paul Irwing, to make the rather extreme claim that, psychologically, men and women are “virtually different species” (as cited in C. Gordon, 2012).

What are we to make of this argument? First, even if we accept the validity of the method, we need to be cautious about what the results imply. It is important to note that claims about effect sizes for multidimensional constructs do not undermine claims made about effect sizes for unidimensional variables. So, for example, the fact that sex differences in global personality are large does not undermine the claim that sex differences in lower-level personality traits (such as openness or extraversion) are small. This is directly relevant to SO. Our claim is that the sex difference in SO is comparatively small. No doubt, if we were to consider SO in tandem with other variables, the effect size for the resulting multidimensional variable would be larger. But this does not undermine our claim that *the sex difference in SO* is comparatively small. Of course, one could then ask whether it is more appropriate to use single variables or multidimensional variables. The answer to that question is that it depends on one's research question. As Del Giudice (2009) himself noted, however, “Most evolutionary hypotheses are highly domain-specific, and may be best answered

by comparisons on single variables” (p. 274). This, we suggest, is the case for SO. The evolutionary hypotheses under consideration relate specifically to men and women's willingness to engage in casual sex, not to more general variables such as, say, global sexual personality (whatever that might be).

Thus, even if we accept the validity of the method, our conclusions about SO remain intact. However, there are several reasons to question the validity of the method. First, it is a basic fact about the Mahalanobis D that the more unidimensional variables you include in your analysis, the larger the effect size will be. This has an awkward implication. No two groups will be identical on every measure. Even for very similar populations—New Zealanders and Australians, for example—there will inevitably be many variables for which there are small average differences. If you were to take enough of these variables and treat them as a single multidimensional variable, you could use Del Giudice's method to “prove” that, psychologically, New Zealanders and Australians are virtually different species. And you could prove the same thing for any two groups: right-handers and left-handers, blue-eyed girls and brown-eyed girls, and so forth. As long as you included enough unidimensional variables in the final multidimensional variable, the different-species conclusion would be inevitable. The inevitability suggests that it is the method that is driving the conclusion, rather than the true nature of the populations under discussion.

But the most damning criticism of the method, in our view, is that adding new unidimensional variables increases the overall effect size regardless of the direction of the effect for each variable. Aggression provides a good example. If we look at physical aggression and verbal aggression in isolation, the average score for each is higher for men than for women (Archer, 2004). If we combine these variables and treat them as a single multidimensional variable, the effect size of the sex difference is noticeably larger than for either alone. If we then add *indirect* aggression, the effect size is larger again (Del Giudice, 2009). The natural interpretation is that men are much more aggressive than women, and that the difference is much larger than we would think if we looked at each unidimensional variable on its own, or if we only considered physical and verbal aggression. The problem is, however, that for indirect aggression, the sex difference actually goes in the other direction: The average score for women is slightly *higher* than that for men (Archer, 2004). Nonetheless, when you include it in the multidimensional variable, the overall effect size simply grows. This raises serious questions about how to interpret any results gleaned from this method.

For all these reasons, Del Giudice's method does not undermine our claim that the sex difference in SO is modest.