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David Frederick
Chapman University, dfrederi@chapman.edu

Tania A. Reynolds
Florida State University

Maryanne L. Fisher
St. Mary's University, Canada

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The Importance of Female Choice

Evolutionary Perspectives on Constraints, Expressions, and Variations in Female Mating Strategies

DAVID A. FREDERICK, TANIA A. REYNOLDS, AND MARYANNE L. FISHER

Introduction

All animals face two major challenges. The first challenge is simply to survive to an age at which they can produce offspring. If animals are killed by predators or succumb to failing internal organs before developing the ability to reproduce, their genes are lost forever. Animals that spend all of their energy on maintaining their bodies and avoiding predators, however, face a similar fate: the end of their genetic lines. Thus, the second challenge for individuals is to find ways to successfully pass on their genes. Reproduction is the engine that drives evolution. Genes that produce traits, tactics, and behaviors that promote reproduction, even at the expense of long-term survival, can carry forward to future generations.

The solutions to the challenge of reproduction vary dramatically across species, and these solutions often differ between females and males. Honey bees and bowerbirds serve as useful examples of two extremely different mating systems. Among honey bees, the queen bee launches into a mating flight and is chased by drone males. When the male catches up to her and they copulate, his genitals explode, snapping off inside the queen. The snapped off penis acts as a genital plug to prevent other males from fertilizing the queen (for a review of insect sexual behaviors, see Zuk, 2011). Male bowerbirds, on the other hand, attempt to impress females with their skills at building nests. These nests, called bowers, are complex structures shaped like small huts. The males decorate the bowers with flowers, feathers, stones, and even small bits of plastic and glass if found. They may steal decorations from other male bowers to put the finishing touches on their structures. The females then inspect the bowers carefully and are more likely to mate with males with more impressive bowers (Borgia, 1985).

There can also be considerable variation in mating behaviors *within each sex*. Not all females of a species display the same mating preferences or behaviors. There can also be considerable variation in preferences and choices of a given female over time and across different situations. Rather than being coy and passive, females may display a wide array of preferences and behaviors, from nearly iron-clad monogamy to seeking matings with many males. Although the importance of female choice in shaping sex differences in behavior and morphology was historically underappreciated, female preferences and behaviors can substantially shape male behaviors, male traits, and entire mating systems.

In writing this chapter, we have three overarching goals. The first is to briefly introduce the reader to some of the influential perspectives on sexual selection and female mate choice in evolutionary biology over the past few decades, with a focus on parental investment theory (Trivers, 1972). The second goal is to then present two influential theories in evolutionary psychology that have been applied to understand variations in women's mating preferences and choices: sexual strategies theory (Buss & Schmitt, 1993) and strategic pluralism theory (Gangestad & Simpson, 2000).

Although the importance of female choice has gained widespread acceptance in the biological sciences (see Milam, 2010, for a review), the influence that female choice has on mating systems can be limited by many factors (Andersson, 1994). For example, it has been proposed that active choices by women played a relatively unimportant role in shaping the human mating system across evolutionary history because women's parents often maintained firm control over reproductive decision-making (Apostolou, 2007). Moreover, some scholars argue that male-male competition, rather than female choice, shaped many male traits (e.g., Puts, 2010). Readers might infer that this latter view harkens back to earlier days of evolutionary biology, where "very few scientists framed their research in terms of Darwinian sexual selection, and when they talked about courtship behavior, their attention was focused on male-male competition" (Milam, 2010, p. 167). However, we agree with Puts (2010) that in the recent human literature there has been an overemphasis on contexts where individuals are relatively free to express their mate preferences. As Puts suggests, the shift towards studying mate choice has sometimes come at the expense of studying the influence of intrasexual competition in humans. Theories relating to the development of male traits have sometimes underestimated the role of male-male competition in their explanations for these traits. The advent of patriarchal systems and male control over sexuality likely constrained women's ability to exercise free choice of mates across human evolutionary history (Smuts, 1995). The third goal of this chapter is to examine and critique these claims regarding the factors that limit female choice, and to show how women exercise choice even in societies where parents and men attempt to severely restrict women's mate choice.

Parental Investment Theory and the Power of Female Choice in the Animal Kingdom

Eager Males and Coy, Discriminating Females?

According to the theory of *natural selection*, individuals with certain traits are more likely to survive than individuals without these traits. When heritable genetic predispositions are partly or completely responsible for the development of these traits, they can be passed on from parent to offspring. In his text *On the Origin of Species by Means of Natural Selection*, Charles Darwin (1859) puzzled over the existence of sex differences in behavior and morphology. If all individuals are under the same selective pressures to survive and reproduce, why would differences emerge?

He reasoned that in addition to the process of natural selection, the process of *sexual selection* shaped the evolution of traits that function to maximize reproductive success rather than survival. In his view, however, males competed with each other to display these traits whereas females did not. He wrote, "This depends, not on a struggle for existence, but on a struggle between males for possession of females: the result is not death to the unsuccessful competitor, but few or no offspring" (Darwin, 1859; p. 136). Through the process of *intrasexual selection*, males competed with other males for access to mates, developing traits that made them more effective in deterring, defeating, or intimidating other males. *Intrasexual competition* can involve situations in which males fight in order to gain a higher rank in the dominance hierarchy. Dominant males may effectively exclude subordinate males from the mating pool through intimidation and fights. In extreme cases, females can only mate with the most dominant males, because these males are the only ones available to mate with. Female choice becomes nonexistent.

Through the process of *intersexual selection*, males of some species developed traits that are attractive to members of the other sex, even when these traits hamper survival. Whereas males were described as active competitors, females were described as "less eager" to engage in sex than the male; and Darwin notes that, "as the illustrious Hunter long ago observed, she 'requires to be courted'; she is coy, and may often be seen as endeavoring for a long time to escape from the male" (Darwin, 1859; p. 273). In this view, females had to develop a discerning sense to appreciate visual, auditory, and olfactory beauty, and males had to develop the capacity to compete in these arenas. In *The Descent of Man*, Darwin (1871) proposed that these different selection pressures lead men to develop superior physical and mental capacities in order to effectively compete for mates, whereas the rather passive selection of mates by females did not necessitate the evolution of strong female bodies or minds (for a review, see Milam, 2010).

Darwin's observations of sex differences in mating strategies were later supported by Bateman (1948). Bateman proposed that the coyness of females produces greater variance among males than females in terms of reproductive

success: Some males have many mates and other males have none, whereas females tend to differ little from each other. For example, in a study of fruit flies, he reported that males had more variance in their number of offspring than did females. Borrowing language from Charles Darwin, he attributed this observed difference to the "undiscriminating eagerness in males and discriminating passivity in females." Although later research showed that his results failed to establish this claim convincingly (Gowaty, Kim, & Anderson, in press; Gowaty, Steinichen, & Anderson, 2003; Tang-Martinez & Ryder, 2005) and more generally it is now recognized that intrasexual competition for mates can be intense among females (Rosvall, 2011), his framework laid the groundwork for scientists to endorse the myth of the passive and coy female.

Noted evolutionary theorist George Williams (1966) later summarized these proposed differences between females and males, which lead to sex differences in mate preferences and mating behaviors. Williams (1966, pp. 183–185) stated:

It is commonly observed that males have a greater readiness for reproduction than females. This is understandable as a consequence of the greater physiological sacrifice that is made by females for the production of each surviving offspring. A male mammal's essential role may end with copulation, which involves a negligible expenditure of energy and materials on his part, and only a momentary lapse of attention from matters of direct concern to his safety and well-being. The situation is markedly different for the female, for which copulation may mean a commitment to a prolonged burden, in both the mechanical and physiological sense, and its many attendant stresses and dangers. Consequently, the male having little to lose in his primary reproductive role, shows an aggressive and immediate willingness to mate with as many females as may be available. If he undertakes this reproductive role and fails, he has lost very little. If he succeeds, he can be just as successful for a minor effort as a female could be only after a major somatic sacrifice. Failure for a female mammal may mean weeks or months of wasted time. The mechanical and nutritional burden of pregnancy may mean increased vulnerability to predators, decreased disease resistance, and other dangers for a long time. Even if she successfully endures these stresses and hazards she can still fail completely if her litter is lost before weaning. Once she starts on her reproductive role she commits herself to a certain high minimum of reproductive effort. Natural selection should regulate her reproductive behavior in such a way that she will assume the burdens of reproduction only when the probability of success is at some peak value that is not likely to be exceeded.

The traditional coyness of the female is thus easily attributed to adaptive mechanisms by which she can discriminate the ideal moment and circumstances for assuming the burdens of motherhood . . .

The greater promiscuity of the male and greater caution of the female is found in animals generally.

The emergence of these perspectives was seized upon by Trivers (1972), who coalesced them into the highly influential parental investment theory.

Parental Investment Theory

Parental investment is the time, energy, and resources that parents allocate to offspring, which then reduces their ability to invest in any other offspring. Trivers (1972) proposed that the existence of sex differences in parental investment leads to sex differences in mating behavior. In general, when one sex invests more in an individual offspring, that sex is thought to be more selective when choosing a mate.

One key difference between females and males of many species is the physiologically *obligatory costs of reproduction*. For males, costs of reproduction are highly variable. The minimum cost for a male mammal is potentially as low as a few seconds or minutes of sexual intercourse. In mammals, the possibility of an extremely low cost reproductive act always exists for males and never exists for females. Mammalian reproduction requires pregnancy and lactation for females, setting a high obligatory minimum investment in offspring. For example, a woman's investment begins with 40 weeks of pregnancy in which caloric needs are elevated by 8–10% (Dufour & Sauther, 2002). Pregnancy is followed by a period of lactation, lasting about 2.5 years in hunter-gatherers (Kaplan, Hill, Lancaster, & Hurtado, 2000), in which caloric needs are elevated by 26% (Dufour & Sauther, 2002). According to parental investment theory, males can afford to be less choosy than females because their act may pose minimal cost. The costs are usually more than minimal, however, and can include care by males of offspring. The proposed overall higher costs of reproduction for females than for males may lead females to be more selective in whom they choose as mates.

A second noteworthy difference between females and males is their *reproductive potential*, particularly among mammals. For females, the number of offspring that can be produced is limited by life history factors such as gestational length and length of time between births. For males, the number of offspring that can be produced and live to the age of reproduction is limited by access to females and the extent to which offspring require male care to survive. Thus, according to this logic, there is greater incentive for males to seek out multiple partners in order to maximize the number of offspring produced, particularly for species where male caretaking of offspring is unnecessary or results in fewer surviving offspring than a promiscuous strategy.

A third important distinction between female and male mammals is the *internal gestation of offspring*. Females always have *maternal certainty*, meaning that

they can be sure that the offspring they give birth to is genetically related to them. Males, on the other hand, always face *paternal uncertainty*. They can never be entirely confident that the offspring they are raising is genetically related to them because they can never be sure that they were the only male to have intercourse with their female partner.

This theory then allows one to hypothesize that behavioral patterns, psychological predispositions, and physical structures evolved in response to the specific challenges each sex faced. The choosiness of females forces males to engage in intense intrasexual competition. Males compete with each other to develop traits that are attractive to females or that enable them to successfully bully other males. For example, males in some species have evolved physiological traits such as horns or large body sizes that enable them to acquire desirable territories and resources, as well as potentially enabling the use of force to prevent competitor males from mating with a preferred female. Males can often produce offspring at a higher rate than females (number of offspring in a given unit of time), perhaps favoring the evolution of preferences for seeking multiple mates (Clutton-Brock & Parker, 1992). Overall, from Darwin until the 1970s, this vision of males as eager and aggressive and females as passive and coy dominated the early work on sexual selection and female choice.

Eager Females and Coy, Discriminating Males?

Females across many species, however, are anything but coy. In her cheeky take on animal sexual behavior, Olivia Judson (2003) dons the persona of Dr. Tatiana, a sex advice columnist for the forlorn, curious, and insecure members of the animal kingdom. Many of her readers express concern regarding the seemingly "promiscuous" behavior of females:

Dear Dr. Tatiana,

I'd prefer to keep my identity secret, since I am writing to you not about me or my species but about my noisy neighbors—a group of chimpanzees. When those girls come into heat, it's enough to make a harlot blush. Yesterday I saw a girl screw eight different fellows in fifteen minutes. Another time I saw one swing between seven fellows, going at it 84 times in eight days. Why are they such sluts?

Observations of highly *proceptive* behavior by female primates—initiating sexual behavior with multiple males—directly challenged traditional views of female sexual motivations in the field of primatology, and even in popular culture. Hrdy (1977, 1981) provided some of the first challenges to the conclusions drawn from parental investment theory. Her accounts of sexual behavior among Hanuman langur monkeys revealed sexually ardent behavior by females, who would mate with multiple males. Hrdy proposed that this female promiscuity had adaptive

benefits for females because it created *paternity confusion*, so that males would not know which infants were genetically related to them. This paternity confusion would be important among langurs because the males in this species routinely engage in infanticide, killing off the infants of rival males when joining a troop of new females. Behaviors that deter infanticide would be highly advantageous, because infanticide represents a loss of considerable energy, time, and resources that was invested by females in their offspring. Thus, if males perceived a possibility of genetic relatedness, they might be less likely to engage in infanticide, and the females would not lose their investment.

The strongly held view that females were passive and coy began to fall to the wayside. Primatologists discovered that the social partner of a female was not necessarily the father of her offspring, which called into question prior work on mate selection and extrapair copulations. The males involved in these extrapair sexual relationships were actively sought out by females (Fedigan, 1992). Thus, the role of female choice, as opposed to male competition or coercion, has been a subject of debate in both the empirical and theoretical literature on extrapair mating (Arnqvist & Kirkpatrick, 2005; Griffith, 2007; Griffith, Owens, & Thuman, 2002; Westneat & Stewart, 2003), but it is clear that females of many species seek out opportunities to mate with some males over others.

It is not the case that females are choosy and males are indiscriminate in their mating, although it is true that the minimum obligatory costs to reproduction are higher for females than males. Less often discussed, however, is the fact that males may face very high costs if they are required to allocate energy, time, and resources prior to conception. These costs can include energy expended while seeking mates, securing the necessary territories to attract mates, competing with other males for limited resources, guarding resources, and producing sperm. Males simply cannot mate indiscriminately because doing so may result in a waste of their energy. Greater choosiness by females induces males to engage in costly displays, which in turn may limit the reproductive potential of males by decreasing the energy they would otherwise dedicate toward finding alternative mates. In this view, females exert substantial influence over the mating system by systematically choosing some males over others.

The implication of parental investment theory is that there are key differences (e.g., obligatory costs, reproductive potential, and internal gestation) between female and male mammals that may influence females to be choosier than males on average. There can be, however, incentives for both sexes to be choosy, just as there are varying reasons why one might engage in short-term mating versus long-term pair bonds, which we review later in the chapter. The exact balance of these incentives depends on a wide variety of factors, such as the costs of bearing offspring, fragility of offspring, the potential reproductive benefits, and the relative reproductive potential of females and males given the local ecological circumstances. Parental investment theory falls short of capturing all of these nuances; the differences in obligatory costs and reproductive potential between the sexes

are just two of the many factors that potentially influence the relative sex differences and similarities that lead to distinct sexual preferences and choices.

What Are Females Choosy About?

Females can seek direct and indirect benefits from their mates. When researchers speak of selection for *direct benefits*, they generally are referring to the idea that females choose a mate because he possesses a trait that directly increases her health, survival, or lifetime reproductive output. This can include selection of males who are more fertile, provide superior resources, offer more parental care, or otherwise reduce females reproductive costs (Kokko, Brooks, Jennions, & Morley, 2003). Kirkpatrick and Ryan (1991) specify some of the forms of direct selection, including choosing a male because he provides resources, because the male has high sperm fertility, and because choosing the male reduces the costs of searching for other potential mates. Further, parental ability may also be one such trait in species where males provide care to offspring (Goodenough, McGuire, & Wallace, 2001). This form of selection simply suggests that a male will be chosen because of the tangible benefits he can immediately provide the female, regardless of what kind of genes the male will pass on to offspring. This form of selection has been rather uncontroversial, because it is easy to see how females directly benefit by mating with males who provide resources such as food and protection to their mates.

In contrast, *indirect benefits* are conferred to the offspring of the females through genetic inheritance. Males with genes that promote robust or attractive bodies will produce offspring who are more likely to inherit these genes and therefore be more likely to develop robust or attractive bodies. Several types of indirect selection have been identified. Historically, two of these forms have been pitted against each other: Runaway selection and good-genes selection. Recent evidence, however, suggests that these two forms of selection are not as different as was once thought.

Runaway Selection

Runaway selection occurs when a female preference and a male trait evolve together (Fisher, 1930). It has typically been claimed that this trait may be “arbitrary”—that these traits don’t necessarily signal anything about the general quality or condition of the individuals. For example, a gene might predispose males to develop orange spots and predispose females to prefer orange spots. Males who display brighter and brighter orange markings then become even more prevalent in future generations, producing stronger and stronger attractions by females. These traits, however, can directly reduce the likelihood that a male will survive (e.g., predators will find him easier to spot). This runaway selection process is also

referred to as the *sexy sons hypothesis*: females who mate with males with sexy traits (e.g., orange markings) will produce sons with sexy traits. In this way, females who mate with these males are receiving a strong indirect benefit because their sons will go on to attract many females, improving the female's genetic representation in future generations (Fisher, 1930; Goodenough, McGuire, & Wallace, 2001; Hall, Kirkpatrick, & West, 2000; Kirkpatrick, 1989; Kirkpatrick & Barton, 1997; Kokko, Brooks, McNamara, & Houston, 2002).

Markers of Heritable Fitness

In contrast to runaway selection, females may choose males with certain traits and behaviors that indicate a male is in robust condition. For example, males with larger weapons, more attractive features, or higher energy levels may possess genes that contribute to the creation of these traits. The physical traits and behavioral patterns that are associated with these genetic predispositions are sometimes called "indicators of good genes." We instead recommend calling these traits "*markers or indicators of heritable fitness*." The term "good genes" (and the implied converse, "bad genes") carries with it evaluative connotations that may be misinterpreted. Males who are better able to display these markers of heritable fitness may be preferred as mates, especially if the female is seeking indirect benefit with limited outlook toward any future paternal investment.

Women might improve their reproductive success by mating with men whose offspring may inherit genes predisposing the development of robust bodies. This is not a surefire strategy of course: due to recombination of genetic material during meiosis and the unique combination of genes created when two individuals reproduce, offspring may not develop these traits to the same extent as their parents. Although this form of female choice was historically contrasted with runaway selection, Kokko et al. (2002) point out that both forms of selection can be placed along the same continuum. Kokko et al. reason that as runaway selection for a trait occurs in a population, only males with certain advantageous qualities will be able to produce the most extravagant examples of these traits. Runaway selection will ultimately lead to preferences for males who are signaling good genes through the production of these extravagant traits. Preferences for good genes traits likely start in the same manner that preferences for runaway traits start. In order for females to preferentially select males with traits associated with a good genes trait, females must have some form of sensory bias favoring these traits—otherwise, there is no way for females to selectively choose men with this trait. Thus, to a large degree, similar processes are operating for both forms of selection.

It is reasonable to expect that both sexes seek mates who show indicators of heritable fitness. It is interesting, then, that in the literature on nonhuman animals, there has been much research devoted to male attractiveness and far less on female attractiveness (e.g., Alcock, 2005; Andersson, 1994). Females appear to

value male attractiveness because it is a cue of genes that confer fitness benefits to offspring through increased viability or reproductive success (e.g., Kokko et al., 2003; Møller & Thornhill, 1997). A variety of traits have been proposed as markers of heritable fitness, including the degree of fluctuating asymmetry. It has been proposed that more symmetrical individuals possess fewer genetic mutations and have encountered fewer parasites and diseases during development. Thus, females may attend to symmetry, or to traits correlated with symmetry, when selecting a mate (Møller & Thornhill, 1997).

Some traits are markers of heritable fitness because they demonstrate that a male is in *good condition*. The exact definition of "condition" varies, but it can refer to aspects of the organism such as nutritional state or energy reserves, and higher condition confers greater reproductive fitness.

Life history theory provides one means for understanding this concept of good condition. Life history theorists think of organisms as entities that capture energy from the environment and then convert it to survival and reproduction enhancing activities. These actions include the development of metabolically expensive physical features that are attractive to the opposite sex (for a review, see Kaplan & Gangestad, 2005). Due to differences in genetic composition, combined with the challenges faced during development, individuals differ in their ability to allocate energy to generating energetically costly traits that are attractive to the other sex. According to the *handicap principle* proposed by Zahavi (1975), males who display traits that are costly to maintain (e.g., the peacock's train) are attractive to females precisely because the traits are difficult to produce. Hence, the traits serve as an *honest signal* that the male is in good enough condition to produce them.

The logic of the markers of heritable fitness argument, however, does not entail that these males are healthier. For example, male peacocks with large trains can have high parasite loads because they are using more of their energy budgets on developing the sexy traits than on immune system maintenance. Depending on ecological circumstances, a male in good condition might be better served by burning through his metabolic resources to vigorously display, even if this erodes his long-term health and leads to death before the male with a smaller energy budget. There can be a negative, positive, or neutral correlation between costly signals and various indicators of health (Kokko et al., 2002).

The idea that females would be attracted to a trait that requires males to waste their energies on developing useless traits like the peacock's train is initially counterintuitive. Why would females prefer a trait that is harmful to the well-being of the male? It is useful to consider an analogy provided by Dawkins (2006), who asked readers to imagine two men running a race. One of the men is carrying a large boulder and the other man is not. The man carrying the boulder reaches the finish line around the same time as the man with no such encumbrances. Which man would be more impressive? Obviously, the man carrying the boulder grabs

our attention because he has displayed his strength despite bearing a burdensome handicap. Females who mate with males displaying these metabolically burdensome traits increase the likelihood that their offspring will possess these traits. Their male offspring who display these traits will then have an advantage over other males when seeking mates, increasing their mothers' ultimate reproductive success.

As an extension of Zahavi's hypothesis, Folstad and Karter (1992) introduced the *immunocompetence signaling hypothesis*. This hypothesis suggests that secondary sexual characteristics are reliable indicators of mate quality because the reproductive hormones required for their development, including testosterone, suppress the immune system (e.g., Peters, 2000; Rantala, Vainikka, & Kortet, 2003). The expression of testosterone-linked traits reveals that men are in good enough condition to withstand the deleterious effects of immunosuppression, and women who selected these men as mates would have transmitted features associated with good condition to their offspring. The link between testosterone level and immunosuppression has been challenged as weak to nonexistent (Roberts, Buchanan, & Evans, 2004), however, with some researchers suggesting that testosterone redistributes the number of circulating leukocytes into target tissues rather than suppressing the immune system (Braude, Tang-Martinez, & Taylor, 1999).

An alternative perspective suggests that testosterone-linked traits are costly signals for reasons other than immunocompetence (see Kaplan & Gangestad, 2005; Kokko et al., 2003). In this view, males in good condition benefit more than other males from devoting a greater share of their energy budget toward mating effort (e.g., competing for mates, displaying attributes desired by mates) than parenting or somatic effort. Higher testosterone is associated with more effort allocated to mating (McIntyre et al., 2006) as well as greater size and muscle mass (Bhasin, 2003), which may be used to attract potential mates. It is critical to note that one has limited efforts to devote to tasks. Effort allocated to developing and maintaining these mating-related attributes reduces the budget that is available for maintaining other attributes (e.g., immunocompetence, somatic upkeep) and can increase other energy demands (e.g., increased metabolism; Buchanan et al., 2001). This view suggests that there is a wider array of costs beyond simply immunosuppression that cause these traits to be indicators of heritable fitness.

Regardless of whether the evidence favors the immunocompetence or the more general cost model, the prediction is the same: the traits produced by high levels of testosterone are cues of heritable fitness and/or good condition because they reliably indicate that the male can afford to generate these costly traits. Consequently, there would be advantages for evolved female preference of these traits because, all else equal, males displaying them sire more viable offspring.

In practice, however, it can be difficult to distinguish between female preferences for direct versus indirect benefits. As Wong and Candolin (2005) observe,

Mate choice can present choosy individuals with both direct material gains that increase their fecundity and/or survival, as well as indirect benefits that improve offspring viability and/or attractiveness. Competitive ability may correlate with some of these benefits if, for example, males that are adept in competition also monopolise the best resources or territories... Moreover, dominance could correlate with genetic benefits if sons inherit their father's competitive prowess, resulting in dominant males siring successful sons. (p. 2)

For example, Frederick and Haselton (2007) suggest that displays of behavioral dominance and greater levels of muscularity could be preferred by females because of direct benefits (i.e., greater protection to her and offspring) and indirect benefits (i.e., these males may produce offspring with genetic predispositions to rapidly develop muscularity). These two types of benefits—direct and indirect—can be obtained by females through short-term sexual liaisons or longer-term partnerships with an investing male.

Evolutionary Psychology and Female Choice of Short-Term and Long-Term Partners: Sexual Strategies Theory and Strategic Pluralism Theory

The processes and preferences identified by these biological perspectives helped to inspire two highly influential theories of mate choice in evolutionary psychology: Sexual strategies theory (Buss & Schmitt, 1993) and strategic pluralism theory (Gangestad & Simpson, 2000). Both of these theories are consistent with the logic of Trivers (1972), who proposed that females and males do not follow one fixed mating strategy. Rather, they deploy multiple or mixed strategies depending on species-specific characteristics. For example, Trivers proposed that in "species where there has been strong selection for male parental care, it is more likely that a mixed strategy will be the optimal male course—to help a single female raise young, while not passing up opportunities to mate with other females whom he will not aid" (p. 145) and that "Psychology might well benefit from attempting to view human sexual plasticity as an adaptation to permit the individual to choose the mixed strategy best suited to local conditions and his own attributes" (p. 146). Sexual strategies theory and strategic pluralism theory emphasize the variety of mating strategies that women and men follow, and how these strategies may differ for each sex, on average. Both of these perspectives provide logic for understanding the importance of female choice, and the motivations that women may have for seeking short-term affairs. According to these theories, humans have evolved the capacity to follow a mix of short-term and long-term strategies depending on fitness-related circumstances.

Sexual Strategies Theory: The Mating Strategy Menu

Buss and Schmitt (1993) proposed an evolutionary theory of human mating strategies, which they called *sexual strategies theory*. This theory focuses on variations in mating preferences and strategies within each sex and between women and men. They proposed that men and women pursued short-term and long-term reproductive strategies in the ancestral past. Regarding sex differences, they reason that women and men differed on average in the challenges that they faced over the course of human ancestral history. The fact that these challenges may have differed in their intensity or frequency for women and men may have led to the evolution of different physical traits and psychological predispositions to help each sex overcome these challenges. The theory leads to the prediction that men will devote a larger proportion of their total mating effort toward short-term mating than do women because of the higher obligatory costs of sex for women (for a review, see Schmitt, 2010).

They specify, however, that women will also seek short-term mates, and that women and men face different challenges evaluating or attracting a potential short-term mate. They propose that men are more likely to face the problem of finding numerous, willing short-term partners who do not require substantial commitment or investment, as well as the problem of identifying women who are likely to be currently fertile. Men may solve the problem of identifying fertile women by attending to cues of age such as wrinkles in the skin and the presence or absence of secondary sexual characteristics (e.g., breast development). They propose a different set of challenges for women. For example, they propose that access to sexual partners has been less of a challenge for women than for men. In contrast, women are faced with the need to identify partners who are willing and able to invest time and resources in the relationship, and who can provide protection from potentially violent males.

Central to the sexual strategies theory is the idea that women can benefit from pursuing both short-term and long-term strategies. For women, short-term affairs can lead to the securing of a new mate, or finding a potential back up mate. It can also enable women to mate with men who have markers of heritable fitness, such as symmetry and masculinized faces: traits that are hypothesized to be associated with genetic predispositions for healthier, sexier, or more robust body types.

Strategic Pluralism Theory: The Importance of Individual Differences and Mating Context

Strategic pluralism theory builds on the logic of parental investment theory and sexual strategies theory (Gangestad & Simpson, 2000). Gangestad and Simpson proposed that one's genetic sex and one's physical traits can influence whether a person pursues a short-term or long-term mating strategy and the traits they prefer in these partners. According to this view, men have evolved predispositions

to pursue reproductive strategies that are contingent on their value on the mating market. More attractive men accrue reproductive benefits from spending more time seeking multiple mating partners and relatively less time investing in offspring. In contrast, the reproductive effort of less attractive men, who do not have the same mating opportunities, is better allocated to investing heavily in their mates and offspring, and spending relatively less time seeking additional mates.

From a woman's perspective, the ideal is to attract a partner who confers both direct long-term benefits and indirect genetic benefits. Not all women, however, will be able to attract long-term mates with markers of heritable fitness who are willing and able to make substantial investments in terms of resources, protection, and care of offspring. Males with these attractive traits may be desirable to more women and therefore may have more opportunities to pursue a short-term mating strategy and to provide fewer direct benefits to their partners. Consequently, women face *mating trade-offs* when choosing a partner, between men who display markers of heritable fitness but lack inclination to provide direct benefits and men who are willing to provide benefits but lack these markers.

One solution to these trade-offs is to simply seek short-term mates who will not provide long-term investment, but who will pass on beneficial heritable traits to their offspring. A second partial solution to the problem of trade-offs is that women may pursue a dual-mating strategy by securing investment from a long-term mate and obtaining genetic benefits from extrapair mates (Fisher, 1992, 2011; Haselton & Gangestad, 2006). Consistent with this logic, women are most attracted to men other than their primary mate when fertility is highest within the ovulatory cycle (and thus the benefits of extrapair mating for genetic benefits are highest; Gangestad, Thornhill, & Garver-Apgar, 2005). This is especially true for women whose primary mates lack sexual attractiveness—the women who, in theory, have the most to gain from extrapair mating for good genes (Gangestad, Thornhill, & Garver-Apgar, 2005; Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006). More generally, women find men with traits linked to higher testosterone levels more attractive during the highest fertility phase of their cycle relative to luteal and menstrual phases (DeBruine et al., 2010; Gangestad & Thornhill, 2008)

One prediction that follows from the dual-mating logic is that men who display cues to fitness will be chosen most often as affair partners. One such proposed cue is low fluctuating asymmetry: the extent to which the left half of the body develops differently than the right half. It has been proposed that higher fluctuating asymmetry is associated with genetic mutations and history of disease and parasite infection (see Møller & Thornhill, 1997). Therefore, more symmetrical individuals may be in better condition. Women may attend to symmetry per se or to traits that are correlated with symmetry when evaluating a man as a potential partner. Thornhill and Gangestad (1994) examined the self-reported number of sexual partners of men varying in symmetry. As predicted, more symmetrical men reported having a greater overall number of sex partners, more sexual affairs,

and a greater number of sex partners who were themselves mated to other men at the time of the affair. Hughes and Gallup (2003) found a similar pattern in men with higher shoulder-to-hip ratios, as did Frederick and Haselton (2007) with muscularity, both traits that are linked with testosterone. In sum, both theory and existing evidence suggest that women attend to cues of fitness when selecting sex partners, particularly short-term mates and affair partners (for a brief review of research on mate preferences, see Gallup & Frederick, 2010).

These two theories have provided useful guides for generating testable predictions regarding the variation in mating preferences, the distinct choices faced by the sexes, and the choices faced by members within each sex. A key point of contention, however, has been the extent to which female choice is exercised in humans.

Constraints on Female Choice: Particularly Stark in Humans?

The literature on women's mating preferences in evolutionary psychology has been dominated by the idea that preferences have a strong influence on choice, that these preferences emerged across the course of our evolutionary history, and that women have the ability to exercise choice (Buss, 1996; Miller, 1998). Female choice can be limited by males, however, through tactics such as mate-guarding, where males attempt to monitor and curtail the movements of their partner (Buss, 1988; Kokko & Morrell, 2005). This importance of female mate choice has been recently challenged through two influential articles focusing on the constraints placed on female mate choice by males (Puts, 2010) and by parents (Apostolou, 2007). More generally, Darwinian feminists have argued that several unique factors have contributed to the emergence of particularly patriarchal cultures with extensive control over female behaviors (Smuts, 1995). After reviewing these claims, we discuss evidence that women have found ways to exercise choice, even in the context of severe constraints.

Constraints on Female Choice by Males

Puts (2010) suggests that research on sexual selection in humans has been overly skewed toward investigations of mate choice and that research on *contest competition*—where force or threats of force have been used to control mating opportunities—have been relatively neglected. More specifically, the claim is that contest competition was the main form of mating competition among men. Frequent contest competitions create strong selection pressures on males to become larger and more powerful, which provides advantages over smaller males and increases the average size difference between males and females across evolutionary time. The increased size of males enables males to more effectively monopolize females.

Traditionally, it has been argued that sexual dimorphism in humans is rather modest, suggesting a lack of contest competitions. For example, sexual dimorphism in height is a modest 8% (Gaulin & Boster, 1985) and sexual dimorphism in overall body mass is also a modest 15–20% (Mayhew & Salm, 1990). Puts (2010) proposes, however, that these measures are misleading. In Western societies, men are 40% heavier than women when examining fat-free mass index (Lassek & Gaulin, 2009; Mayhew & Salm, 1990) and men have 60% more total lean muscle mass than women. Men also have 80% greater arm muscle mass and 50% more lower body muscle mass (Abe, Kearns, & Fukunaga, 2003). Lassek and Gaulin (2009) note that the sex difference in upper-body muscle mass in humans is similar to the sex difference in fat free mass in gorillas (Zihlman & MacFarland, 2000), the most sexually dimorphic species of all living primates. This sexual dimorphism in muscle mass leads men to have approximately 90% greater upper body strength and the average man is stronger than over 99% of women (Abe et al., 2003; Lassek & Gaulin, 2009). The extent to which this is true across a wide variety of cultures would be informative as to the extent to which these sex differences are exacerbated or limited by ecological or cultural factors.

One source of this greater upper body strength may be unrelated to contest competitions. Greater upper body strength, combined with faster running speeds, may have been adaptations that facilitated big-game hunting. They may have also arisen in part from violent confrontations between men. Traits associated with testosterone, such as deep voices, jaw size, brow size, and muscularity enhance perceptions that a male is physically intimidating. Although much research has examined the extent to which women prefer these traits, Puts (2010) notes that women often prefer only moderate or average levels of some these features. Thus, it may be the case that males are not displaying these traits in order to attract women.

Although men lack “weapons” commonly seen in species with frequent contest competitions (e.g., horns, large canines, antlers), men have had the ability to construct weapons such as sharpened stones for millions of years. This ability can allow strong upper body strength to be used as a deadly weapon. Puts (2010) proposes that violent contests aided individual men in their competitions against other men in securing mates. Further, he proposes that males formed alliances with other males that enabled them to take over other groups or threaten members of their own group in order to acquire additional mates.

Taken as a whole, these arguments suggest that male-male competition was a more important factor than female choice in generating male testosterone-linked traits, and perhaps that contest competition had a more significant impact on whom women partnered with than did women's choices and preferences. In this view, women's preferences were not the primary force in shaping men's physical appearance. Not all reviews have come to the conclusion that the evolution of human sexual dimorphism emerged primarily from contest competitions, noting that a variety of processes could have lead to the dimorphism seen in

humans (e.g., mate choice, resource competition, intergroup violence, and female choice; Plavcan, 2012). Puts' proposal is intriguing, however, and merits further consideration.

Constraints on Female Choice by Relatives

In addition to constraints placed on women's mating choices by men, parents can strongly influence or restrict women's choices. Evidence presented by Apostolou (2007) has been particularly influential in emphasizing this point. Parents wield a great deal of power over offspring in many societies. Girls are often dependent on parents for food, protection, and access to influential social networks within the community. Parents have a direct interest in controlling the mating choices of their offspring. The fate of parental genes is at stake when offspring select mates, as is the social reputation and influence of the parents. Although some preferences between parents and offspring may overlap, others may diverge. A family with two sons and one daughter may find it beneficial to arrange a marriage with a family with two daughters and one son so that each child has a partner, even if the arranged marriage is not ideal for the single daughter. These potentially different priorities could generate conflicts between parents and offspring regarding mate choice.

In contrast to the freedom of choice experienced in Western and other industrialized cultures, arranged marriages are more common in most preindustrial societies (Murdock, 1967, 1981). For example, Apostolou (2007) claims that in 190 modern forager societies, only 4% allow individuals to select their mates free of much, or any, influence from their parents. If high levels of *parental control over mate choice* has been a long-standing pattern in human evolutionary history, it may suggest that current evolutionary models of human mating that assume free female choice are highly problematic and misleading (Apostolou, 2007). This work highlights the importance of examining the influence parents have in the mate selection process, and the traits that parents take into account when arranging or influencing their offspring's mating choices.

Evolutionary Origins of Patriarchy

Several such constraints on women's social influence were highlighted by Darwinian feminist Barbara Smuts (1995), who noted that human societies appear to exhibit greater male control over female sexuality than is typical in most nonhuman primate species. Smuts posits that this desire for control over female sexuality was one of the key factors facilitating the emergence of patriarchy, which has strongly constrained women's reproductive choices.

In particular, she proposes six factors that diminished women's reproductive choices and control over their own lives. First, patrilocal societies in which females moved away from kin led to reduced social support for women from families and

allies. Second, men's alliances became increasingly well developed across human evolutionary history, which enabled men to exert greater influence over women. Third, men's alliances allowed them to increase control over resources needed by women to survive and reproduce, making women more dependent on men. Fourth, control over resources by some men's alliances created increased variance in men's wealth and power, which left women increasingly vulnerable to the will and whims of a few powerful men. Fifth, women engaged in behaviors that promote male control over resources, such as preferring and choosing more dominant and wealthier men as partners. This pattern of choice increases pressure on men to control these resources. Last, the evolution of language enabled the creation of ideologies supporting men's dominance and supremacy, and women's subordination and inferiority. Smuts (1995) was not proposing that female choice was unimportant, but it is clear that this constellation of factors would have reduced women's ability to act on their preferences.

Resistance to Constraints on Female Choice

Research over the past few decades in evolutionary psychology on mating in Westernized cultures has led to a relative overemphasis on mate choice as a mechanism of sexual selection. In contrast, contest competition and parental influence on mate choice have been relatively underemphasized.

We present evidence, however, that women's preferences and choices can be exercised, even in the face of strict constraints. We examine methods that women use to subvert attempts at mate guarding, that daughters use to influence parental control over mating decisions, and the cultural factors that enable women's choices. The extent to which women are able to break through these constraints has implications for the importance assigned to female choice as a factor in human evolution.

Subverting Mate Guarding

The fact that men engage in *mate guarding* suggests that women engage in behaviors that require guarding against. If women were uniformly and strictly sexually monogamous, then mate guarding would only need to be exerted in limited circumstances. Men would only need to guard against rival males who were attempting to gain access to their sexual partner. If women did not at some level exert choice in mates, then there would be no other pressure on men to mate guard.

In Western societies, approximately 11–15% of women indicate that they have had extramarital sex in their current marriage. These numbers exclude, however, relationships that have ended in divorce caused by infidelity, and infidelity is frequently cited as one of the leading causes of divorce in the United States and across cultures. Estimates vary, but approximately 20–25% of heterosexual

married women will have an extramarital affair during their lifetime, and the incidence of extrapair sex is far higher for dating couples (for reviews, see Allen et al., 2005; Betzig, 1989; Tsapelas, Fisher, & Aron, 2010). In the Standard Cross-Cultural Sample, female extramarital affairs are common among foragers, horticulturalists, and pastoralists (Marlowe, 2000). These data are consistent with numerous ethnographic accounts describing female infidelity among the !Kung (Hill & Hurtado, 1996), Ache (Hill & Hurtado, 1996; Kaplan & Hill, 1985), Bari (Beckerman et al., 1998), Tsimane (Winking, Kaplan, Gurven, & Rucas, 2007), and Tiwi (Goodale, 1971).

Extramarital affairs can lead to extrapair paternity, which occurs when the purported biological father is not the actual biological father of a child. In general population samples taken primarily from European and North American cultures, the estimated human extrapair paternity rates range from 2 to 4%. This extrapair paternity rate jumps to 30% among men who specifically seek out paternity tests (for reviews, see Anderson, 2006; Voracek, Fisher, & Shackelford, 2009). It remains unknown how comparable these rates are among other populations because systematic data on nonpaternity rates are not available for nonindustrialized societies. The only known study of genetic paternity from a small-scale natural fertility (noncontraceptive using) population is from research with the Yanomamo in the 1960s, showing a nonpaternity rate of 9.1% (Neel & Weiss, 1975). The figure for the Yanomamo is at the high end of global reported prevalence rates.

Other types of data on nonindustrialized cultures are available, however, and these data shed light on the potential frequency and impact of women's extrapair mating on men's paternal certainty. Gaulin and Schlegel (1980) attempted to assess degree of paternal certainty using three variables from the Standard Cross-Cultural Sample of nonindustrialized societies. They classified societies as having low paternal confidence if the society had some form of culturally sanctioned sharing of wives, at least a moderate frequency of extramarital sex, or a lack of a double standard regarding attitudes toward extramarital sex by women versus men. Relevant data was available in 145 of the 190 societies. Based on this criteria, they estimated that 61 (45%) of the societies had low paternal confidence and 74 had high paternal confidence (55%). The actual number of societies with low paternal confidence may be higher, however, because the authors frequently treated missing data as evidence of high paternity (for example, a society with a sexual double standard, wife sharing, and no information on frequency of extramarital sex was coded as high paternal certainty; Wolfe & Gray, 1981).

Huber, Linhartova, and Cope (2004) used four measures of extramarital sexual activity from 57 nonindustrialized cultures to create a 16-level measure of paternity confidence. The measures included frequency of premarital and extramarital sex, and strength of the social deterrents to premarital and extramarital sex. In their sample, 36 of the cultures were classified as having moderate to very high frequencies of extramarital affairs and 44 were classified as having moderate to very high frequencies of premarital sex.

The aforementioned studies relied on broad ethnographic data available from many cultures. To examine the paternal uncertainty in a given society in more specific detail, Scelza (2011) collected reproductive histories from Himba women. The Himba are a seminomadic pastoral population living the northwest corner of Namibia. They are largely isolated from the market economy and rely primarily on livestock for subsistence and trade. Marriages can be arranged or can result from love matches. In this study, reproductive histories were collected from 110 women, and showed 421 births, of which 329 occurred within marriage. The women were asked to identify whether the child resulted from liaisons with an extramarital affair partner or from their husband. Nearly one-third of women indicated having at least one extrapair birth in their lifetimes (32%), which accounted for 18% of all marital births. None of the women in love marriages reported extrapair births (0 of 79), whereas for the arranged marriages, 23% of the births were described as extramarital births. The results may be somewhat skewed due to the self-report nature of the data, but these findings demonstrate the potentially high rates of extrapair paternity in some natural fertility populations.

In contrast to the view that female choice is highly constrained by parents and males, these findings collectively suggest that in many nonindustrial societies, mate choice is occurring outside the purview of parental influence and possibly outside the context of contest competitions. The results of Scelza (2011) indicate that arranged marriages may be a risk factor for extrapair paternity. It is likely that the rates of extramarital affairs and births will vary considerably according to one's culture, depending on social and ecological factors. The existing evidence, however, provides support for the claim that women are able to exercise choice, even in the face of constraints. Through extramarital affairs, women exercise a tremendous influence over the mating system and the evolutionary process by controlling reproduction (Tsapelas, Fisher, & Aron, 2010).

Subverting Parental Choice and Mate Guarding

Arranged marriages and parental influence on mate choice are common across cultures. In most of these cultures, however, women are still able to exercise substantial influence over mating choices. As Pillsworth and Barrett (2011) have shown in a broad sample of nonindustrialized cultures, women have some degree of sway on parental choices in many societies where there are arranged marriages. This influence can range from having veto power, having some input, or having substantial input on parental choice, as well as the option of entering love or arranged marriages.

Pillsworth and Barrett (2011) documented the various ways in which women among the Shuar of Ecuador, a hunter-horticulturalist society, are able to exercise choice in the face of strict constraints. Through ethnographic interviews, they identified strategies that women use to escape marriages, despite the fact that among the Shuar it is said that "marriage is forever." Corporal punishment is

regularly meted out against both women and children as way to control and constrain their options. One mechanism of escape from abusive or undesirable marriages is simply to run away. Women most frequently return to their father's home or run away with another man, although they may occasionally seek employment in one of the cities. A second method of escape is to attempt suicide. By attempting suicide, a woman gains the attention of her family. It is also a clear signal to the husband that she is unhappy, which may motivate the husband to change (either from genuine concern or from fear that her family will kill him or his kin if he is viewed to be the cause of the suicide). Women will also engage in adultery or seek a new partner. If a girl disagrees with the marriage her parents are arranging, she may elope with a different boy.

Men in this society expend a great deal of energy to attract women and woo them, even if the parents are officially the ones to approve or arrange the marriage. Failing to woo the daughter can lead to a conflict between daughter and parents, which may cause the parents to withdraw from the marriage negotiation. There is pressure on men to display traits that the daughters, not just the parents, will find attractive.

The extent to which women choose relatively more or less dominant men as partners may depend in part on the local ecological and cultural settings. Frederick and Haselton (2007) found that women perceived muscular men as more attractive and dominant, but also as more volatile. Snyder et al. (2011) proposed that women face a trade-off when choosing a man with domineering personalities and powerful body types as a mate (e.g., men described as dominant, domineering, tough-guy, strong, could win a fight if necessary). These men may provide better protection from other males, for example, but they may also be more controlling of their mates. Snyder et al. reasoned that women who perceived the world as relatively more dangerous would more strongly prefer domineering men because the benefits of a potential protector in a dangerous world outweigh the costs, whereas the costs may outweigh the benefits in a relatively safe world. Women may facultatively adjust their preferences based on actual or perceived environmental conditions.

Concluding Comments: The Future of Mating Research

Western cultures and other industrialized cultures have provided women with the opportunities to exercise a great deal of choice over their mates, perhaps more so than at any other time in recent or ancestral history. It is particularly interesting to explore how women's preferences are expressed in this context and how these preferences differ from the preferences exhibited in cultures where choices are more constrained. In general, our examination indicates that there is tremendous variability in female choice that can be exercised across different societies, which leaves some reason to suspect that this may have been true across different isolated groups in human ancestral history.

The theories of parental investment, sexual strategies, and strategic pluralism have generated a wealth of hypotheses regarding men's and women's long-term and short-term mating strategies. Much work has been done documenting the presence of sex differences, and more recent work examines the individual differences within each sex. The current focus on understanding how ecological factors, cultural ideologies, life history factors, parental influences, female choice, and contest competitions interact will provide greater insight into how evolution shaped individual and sex differences in mating preferences and choices.

The field of evolutionary psychology has generated a wealth of novel and interesting predictions using the perspectives in evolutionary biology related to sexual selection. As cultural attitudes toward female sexuality have changed, these theories have evolved by more fully incorporating notions of active female choice and reproductive decision. The current debates in evolutionary biology and animal behavior regarding the role of sex, ecological factors, developmental factors, and social factors provide evolutionary psychologists with new perspectives to draw from when generating predictions regarding human sexual behavior (e.g., Gowaty & Hubbell, 2005). One conclusion from the changing understanding of female sexuality in evolutionary biology and psychology is clear: Women have been, and will likely continue to be, active agents in shaping the course of human evolution.

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