Mate Preferences and Their Behavioral Manifestations

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Keywords: Human mating, sexual strategies, mate preferences, sex differences, evolutionary psychology

Acknowledgements. The authors thanks Courtney Crosby, Patrick Durkee, Anna Sedlacek, and Shelley Tayor for helpful comments on an earlier draft of this paper.

Abstract

Evolved mate preferences define a central causal process in Darwin's theory of sexual selection. Their powerful influence has been documented in all well-studied sexually reproducing species, and is central to Sexual Strategies Theory (SST) as applied to humans. This chapter takes stock of what is scientifically known about human mate preferences and their many behavioral manifestations. We discuss sex differences and sex similarities in the design features of human sexual psychology as they vary according to short-term and long-term mating temporal contexts. We review context-specific shifts in mating strategy depending on individual, social, and ecological qualities such as mate value, life history strategy, sex ratio, gender economic inequality, and cultural norms. For mate preferences to have evolved, they must be manifested in actual mating behavior in some individuals some of the time, such as those with high mate value in contexts where freedom of mate choice is permitted. We review the empirical evidence for the impact of mate preferences on actual mating decisions, as well as on tactics of mate attraction, tactics of mate retention, patterns of deception, causes of sexual regret, attraction to cues to sexual exploitability, attraction to cues to fertility, attraction to cues to resources and protection, derogation of competitors, causes of breakups, and patterns of remarriage. We conclude by articulating unresolved issues and offer a future agenda for the science of human mating. This agenda includes resolving key debates, such as competing evolutionary hypotheses about the functions of women's short-term mating; how humans invent novel cultural technologies to better implement ancient sexual strategies; and how cultural evolution may be dramatically influencing our evolved mating psychology.

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Introduction

In sexually reproducing species, no single decision is more important than the choice of a mate. Good mate choices can bring a bounty of reproductive benefits, such as genes for healthy immune functioning, physical protection, and provisioning of resources for self and offspring. Poor mate choices can usher in a cascade of costs—sexually transmitted diseases, a DNA packet with a high mutation load, reputational damage, and abandonment. These dramatic costs and benefits have imposed tremendous selection pressure over the 800 million years since the origins of sexual reproduction. The forces of selection have forged evolved strategies of mating in all known and scientifically studied sexually reproducing species. Foremost among these strategies is preferential mate choice.

Darwin's (1859) original formulation of natural selection focused on survival selection, the evolution of adaptations that gave organisms advantage in the three struggles of life—struggles with the physical environment, struggles with other species such as predators and parasites, and struggles with members of one's own species. With the evolution of sexual reproduction 800 million years ago, an entirely new form of evolution by selection came into

existence—sexual selection (Darwin, 1871). Sexual selection describes the evolution of adaptations not because of their survival advantage, but rather because of their mating advantage.

Darwin described two key processes by which mating advantage could accrue—

intrasexual competition and intersexual selection. In intrasexual competition, qualities linked with success in same-sex contests get passed with greater frequency due to the increased sexual access of the victors. Qualities linked with losing intrasexual competitions bite the evolutionary dust because the vanquished fail in the mating game and their genes die with them. Although Darwin linked intrasexual competition to physical contests, we know now that the logic is more general, and can extend to scramble competition for territories or even competition to ascend status hierarchies (Buss, 2016).

The core feature of intersexual selection, the second mechanism of sexual selection, is preferential mate choice. This process requires three key ingredients. First, there must be some consensus about the qualities desired in the other sex, although perfect agreement is not necessary. Second, desired qualities must be partly heritable. Third, the process must iterate through enough generations to effect an evolutionary change. The change comes about because those who successfully embody the desired qualities of the other sex have a mating advantage and get preferentially chosen, and hence pass on desired qualities with higher frequency. Individuals lacking desired qualities struggle to find mates and may be shut out of mating entirely, so undesirable qualities decrease in frequency over evolutionary time.

All known sexually reproducing species—including fruit flies, spiders, love bugs, frogs, hamsters, ring doves, penguins, dolphins, marmosets, baboons, and chimpanzees—have been shaped by sexual selection (Andersson, 1994; Arnqvist & Rowe, 2005). All have evolved mate preferences. All compete for desirable mates. It would defy scientific logic if humans were the

sole species on earth, among the roughly 1.3 million sexually reproducing species, whose mating psychology was entirely untouched by sexual selection, entirely lacking evolved mate preferences, and totally bypassed by the process of intrasexual competition.

Abundant scientific evidence reveals humans are no exception. We have not escaped the powerful forces of sexual selection over the six million years or so since we split from our common ancestor with chimpanzees. But because humans have evolved multiple mating strategies that have many unique features, our evolved mate preferences and forms of mate competition are complex and differ in some key respects from those of other sexually reproducing species, including closely-related primates (Gray, 2013). Before describing evolved human mating strategies, it is useful to briefly review the history of non-evolutionary theories of human mating prior to Sexual Strategies Theory (Buss & Schmitt, 1993).

Theories of Mating Prior to Sexual Strategies Theory

Although the domain of human mating largely lay in the unexplored scientific shadows prior to evolutionary perspectives, there did exist a few theories. Freud (1913/1950), for example, proposed that people seek mates who resemble their opposite-sex parents. Winch (1958) proposed people seek mates who possess qualities they themselves lack, a search for complementarity. Several theories posited that people seek mates similar to themselves (e.g., Cattell & Nesselroade, 1967). Exchange and equity theories posited that people search for those with whom the exchange of valuable resources will be in approximate equilibrium or equity (e.g., Berscheid & Walster, 1974; Clark & Reis, 1988), although what qualified as a "valuable resource" was left unspecified.

All these prior theories shared notable limitations. First, they were domain-general with regard to content, failing to specify the primary dimensions on which similarity,

complementarity, exchange, or equity might be based. This domain-generality precluded predictions based on particular content domains such as economic resources, sexual resources, coalitional resources, or parental resources. Second, they were domain-general with regard to context. For instance, they failed to specify temporal context. Short-term mating, casual sex, and extra-pair infidelities were strikingly absent, the focus being exclusively on marriage or long-term mate choice. They also contained no premises explaining why mating goals might shift according to predictable developmental, situational, and ecologically-contingent circumstances. Finally, and perhaps most importantly, all failed to provide an explanation of *why* humans would be motivated in the directions posited, be it similarity, complementarity, or equity. They lacked a causal account of the functional origins of these mating goals, the adaptive purposes for which they might have evolved. Perhaps because of this, all ignored the possibility that women and men might differ strategically in their mating psychology, and indeed none contained any sex-differentiated premises or predictions.

We highlight these limitations to provide the minimum specifications of what a cogent theory of human mating should provide. It should identify the resource-relevant domains that are important in mate selection, such as sexual, economic, and parental resources. It should go beyond a sole focus on long-term committed mating such as marriage, and specify different mating strategies humans are known to initiate, including brief sexual encounters, serial mating, and extra-pair copulations. A good theory of human mating should specify how mating strategies change according to predictable contexts, such as changes in mate value, shifts according to different sex ratios in the mating pool, shifts according to whether a short-term or a long-term mating strategy is being pursued, and so on.

It should provide an account of the *causal origins* of human mating strategies. It should generate cogent hypotheses about the functions, if any, of each feature of human mating psychology, that is the specific manner in which each feature solved an important adaptive problem. It should contain sex-differentiated components, since the process of sexual selection is the most powerful evolutionary force responsible for forging a somewhat sex-differentiated mating psychology (Andersson, 1994; Buss, 1995).

Sexual Strategies Theory (SST; Buss & Schmitt, 1993) was the first theory that attempted to correct the deficiencies of prior mating theories and provide a rough sketch of some of the key complexities of human mating psychology. This sketch has been refined over the ensuing 25 years, with additional complexities and context-specificities, as well as hundreds of empirical tests of its 9 core hypotheses and 22 empirical predictions. We outline these complexities and empirical tests after briefly describing the core premises of SST.

Core Premises of Sexual Strategies Theory

A core premise of SST is that humans have evolved a multifaceted mating psychology consisting of a complex suite of psychological adaptations, each of which evolved in response to evolutionarily recurrent adaptive challenges. Many of these challenges are subsumed under the rubric of sexual selection theory. The two broad adaptive problems humans faced were (1) exerting fitness-enhancing preferential mate choice, and (2) out-competing rivals for desirable mates.

Although in principle these are distinct challenges, they are conceptually related in two ways (Buss, 1988a). First, the mate preferences of one sex dictate the domains of intrasexual competition in the other sex. If women prioritize bravery in the face of danger, for example, that preference imposes selection pressure on men to out-compete their rivals to provide honest

indicators of bravery. Conversely, forms of intrasexual competition can influence the evolution of mate preferences. If men compete with each other in forms of same-sex combat, such as wrestling, chest-pounding duels, or club fights (Puts, 2016), the informative variance produced by winning and losing contest competitions may create or amplify women's mate preferences for formidability or athletic prowess. Although the two processes of sexual selection are distinct, they can influence each other in reciprocal causation. With this conceptual background, we now outline the key premises of SST:

Premise 1: Humans have evolved multiple mating strategies. Both women and men have evolved a menu of mating strategies that include long-term committed mating, short-term mating, serial mating, and extra-pair mating. Although variable in form and function, long-term matings tend to be characterized by high levels of commitment, pair-bonding, and emotional involvement while short-term matings such as one-night stands, brief hookups, and temporary liaisons tend to lack these features. Nonetheless, we fully recognize that these ends of the temporal continuum are rough proxies and do not fully capture the psychological complexities of the suite of mating strategies that lie along this continuum (Buss & Schmitt, 1993).

Premise 2: Each sexual strategy has specialized design features. Because different adaptive problems must be solved when pursuing these different strategies, selection has forged a complex mating psychology designed to reap the benefits and minimize the costs of each strategy.

Premise 3: Men and women are strategic similar in some domains. In all domains in which men and women have faced similar adaptive challenges in mating, such as solving the commitment problem in long-term mating, men and women will be similar in their underlying mating psychology (Buss, 1995).

Premise 4: Women and men differ in mating strategies where they have recurrently faced different adaptive problems. In domains in which men and women have faced different adaptive challenges recurrently throughout human evolutionary history, the sexes will differ in their mating psychology (Buss, 1995).

Premise 5: Sex differences in minimum obligatory parental investment and sexual selection have fashioned sex-differentiated forms of short-term mating. Because women and men differ dramatically in the minimum obligatory investment to produce a single offspring (nine months pregnancy for women; one act of sex for men), selection has favored a sex-differentiated suite of adaptations regarding short-term mating strategies and the circumstances in which they are implemented.

Premise 6: Access to fertile women historically has been a key constraint on men's reproductive success, so selection has favored a psychology of short-term mating specially-designed to overcome this constraint. This key constraint on men includes solving at least four somewhat distinct adaptive challenges: (a) motivating access to a variety of sex partners; (b) identifying which women are sexually accessible; (c) identifying fertile women; and (d) minimizing commitment and investment in each.

Premise 7: Women obtain several key adaptive benefits from short-term mating.

Women's short-term mating has been hypothesized to obtain at least four adaptive benefits: (a) securing immediate access to economic resources; (b) using short-term mating to assay prospective long-term mates; (c) obtaining genes superior to those of their regular mates; and (d) using short-term mating to switch mates (Buss et al., 2017).

Premise 8: Men and women have evolved long-term pair-bonded mating strategies that possess at least five common components. Commonalities include (a) identifying potential

partners who possess a similar mate-value trajectory as the selector; (b) identifying potential partners willing and able to commit over the long-term; (c) identifying good long-term partner qualities, including an altruistically-skewed welfare tradeoff ratio (WTR); (d) identifying potential partners with good parenting skills; and (e) identifying potential partners who are not encumbered by costly commitments, such as young needy children from former mateships.

Premise 9: Male-specific challenges of long-term mating. Men have faced at least two sex-specific adaptive challenges when committing to a long-term mating strategy: (a) identifying women high in reproductive value (i.e., future reproductive potential); (b) because fertilization occurs internally within women, men must solve the problem of paternity uncertainty so that investments get channeled to their own biological offspring.

Premise 10: Female-specific challenges of long-term mating. These include (a) identifying men who have the ability to acquire and invest resources in her and her children; (b) identifying men who are willing to acquire and invest resources in her and her children; and (c) identifying men who are able and willing to offer physical protection to her and her children from aggressive conspecifics and other hostile forces of nature.

Premise 11: The deployment of different sexual strategies, such as short-term and long-term, are highly context-dependent. These contexts include: (a) the individual's mate value; (b) the operational sex ratio in the relevant mating pool; (c) the strategies pursued by others in the mating pool; (d) the costs that might be incurred by the pursuit of each strategy, including sexually transmitted infections, reputational damage, and violence from allies, kin, or extant mates; and (e) ecological variables such as parasite prevalence, scarcity of food resources, intergroup warfare, sex-specific mortality, droughts, and other evolutionary bottlenecks.

Premise 12: Sexual strategies are evolved solutions to common and sex-differentiated challenges of human mating. The evolved psychological adaptations, including the many input contexts that differentially activate them, their information processing procedures, and their manifest behavioral output are called sexual strategies. These strategies are evolved solutions to adaptive problems, with no conscious awareness implied regarding their origins, nature, or functionality.

Because some scholars have badly misrepresented SST, erroneously characterizing it as "men are promiscuous, women are monogamous," we begin by focusing on women's short-term mating strategies in the hope that this will correct future misrepresentations.

Women's Short-Term Mating Strategies

Sexual Strategies Theory, from its inception, has emphasized that women as well as men have evolved short-term mating strategies. Mathematically, the number of heterosexual short-term matings must be identical for the sexes, given an equal sex ratio in the mating pool. Each time a man has a casual sexual encounter with a woman, a woman is simultaneously having a casual sexual encounter with a man, although of course they may construe the encounter differently. One person's one-night stand may be another person's failure to pair bond. Still, the fact is some women in some circumstances initiate and willingly engage in short-term mating—whether in the form of hooking up, friends with benefits, one-night stands, or extra-pair sexual encounters. And they do so strategically.

Because ancestral women typically could not have dramatically increased their reproductive output from adding more sex partners (unless their regular partners were infertile), a key scientific puzzle has been whether adaptations for short-term mating exist in women, and if so, what their evolved function might be. Buss and Schmitt (1993) proposed four possible

adaptive functions of women's short-term mating: immediate resources, good genes, evaluating short-term mates for long-term possibilities, and mate switching.

Although these are alternative hypotheses, they are not in competition with each other in a zero-sum scientific contest. Women in circumstances of harsh winters or severe food shortages, for example, might use short-term mating as a desperate measure to obtain calories that might make the difference between survival and starvation for herself and her children. Women in other circumstances, such as those in long-term mateships with men of low genetic quality, might use short-term mating to obtain better genes for her offspring—the hypothesis most vigorously advocated by many evolutionary scientists (e.g., Gangestad and Thornhill, 2008; Gildersleeve, Haselton, & Fales, 2014). And some women, finding themselves in a cost-inflicting mateship, a mateship that has not lived up to its initial promise, or when an incrementally better option comes along, might use short-term mating as a mate-switching tactic—a hypothesis most recently advocated Buss and colleagues (Buss et al., 2017).

What do the empirical tests show? One of the first tests was conducted by Greiling and Buss (2000) who attempted to examine predictions from all except the good genes hypothesis in four studies. They examined women's perceptions of an array of benefits from short-term mating, the likelihood of receiving those benefits, the contexts in which short-term mating occurred, and benefit perceptions by women who actively pursued short-term mating. They found some support consistent with the resource acquisition and mate switching hypotheses, although these findings cannot be viewed as decisive or definitive.

The good genes hypothesis. Most research on the possible functions of women's shortterm mating has focused on the good genes hypothesis. The primary source of evidence has been shifts in women's mate preferences at ovulation. The logic of the hypothesis is that some women pursue a dual mating strategy—obtaining investment and resources from one regular committed partner and obtaining superior genes from an affair partner. This hypothesis predicts that women will experience a mate preference shift around the brief window of ovulation, the only time in which a woman can conceive, to value hypothesized 'good genes' qualities (e.g., symmetry, masculine features, physical attractiveness); that these preference shifts will center on short-term rather than long-term mating; and that sexual desire will peak for men other than women's regular partners.

The empirical evidence for these mate preference shifts is somewhat mixed. One large meta-analysis reviewed 134 effects from 50 different studies and found some support for the predicted preference shifts, although the effect sizes tended to be small (Gildersleeve et al., 2014). A recent large-scale longitudinal study of 584 women, however, found no correlation between hormonally-assessed ovulation status and preference for masculinity in male faces, although it did find that the general preference for masculine faces was more pronounced for short-term rather than long-term mateships (Jones et al, 2018). A preregistered study of 157 women did not find women's preferences for masculine bodies increased at ovulation, as predicted by the good genes hypothesis (Junger et al., in press). Based on the studies conducted thus far, empirical support for the hypothesized good genes function of women's short-term mating is weak or mixed.

The good genes hypothesis has also been questioned on theoretical grounds (Buss & Shackelford, 2008; Buss et al., 2017). First, to the degree that women do elevate their preferences for certain features such as masculinity at ovulation, these finding could be conceptually interpreted as a shift in women's self-perceived mate value rather than a switch to a preference for good genes (Buss & Shackelford, 2008). It is known that women higher in mate

value elevate their standards, desiring higher levels for many characteristics in a mate, including hypothesized good genes indicators, good partner qualities, and resources (Buss & Shackelford, 2008). Conceptually, women are indeed higher in mate value when they are ovulating compared to when they are not ovulating, since they are maximally fecund at precisely this time in their cycle. Indirect evidence for ovulation shifts in women's mate value comes from a study of 26,000 online self-reports that tracked ovulation cycles, which found reliable increases in self-perceived desirability around ovulation—possibly a psychological tracking adaptation (Arslan et al., 2017).

Second, because all traits highly valued by women in long-term mating show moderate heritability, including intelligence, emotional stability, dependability, ambition, and industriousness, it is not clear conceptually why masculine and symmetrical features should be singled out as special cases of 'good genes' in contrast to the others. To take one compelling example, intelligence shows somewhat higher heritability than most other traits, has been directly hypothesized to be a cardinal good-genes indicator (e.g., Miller, 2000), yet there is no evidence that women elevate the importance they attach to intelligence at ovulation. In short, on both theoretical and empirical grounds, the good genes hypothesis of women's short-term mating, although potentially applicable to a small subset of women pending future tests, can be regarded as questionable theoretically and not well supported empirically. In contrast, an alternative function of women's short-term mating may be more promising—the mate switching hypothesis.

The mate switching hypothesis. There are several variants of the mate switching hypothesis of women's short-term mating. One involves cultivating a *backup mate* should something befall a woman's regular mateship, such as a partner becoming injured, dying in a

war, or simply in probabilistic anticipation of a potential breakup. This has been called the 'mate insurance' function (Buss, 2016). Another variant involves having a short-term sexual encounter to make it easier to divest herself of an existing mate. A third variant involves trading up to a partner of higher mate value, or one who offers more benefits and fewer costs than her current partner. A fourth variant involves using short-term mating as a means of assaying her mate value to evaluate whether there might exist more desirable and accessible potential partners in the mating market.

Few empirical studies have tested the mate switching hypothesis directly, but several independent findings converge on it plausibility. First, *relationship dissatisfaction* is one of the most powerful predictors of women's actual infidelity, but not men's infidelity (Glass & Wright, 1992). Second, relationship dissatisfaction predicts women's sexual interest in other men both during the fertile *and* luteal phases of the ovulation cycle (Gangestad et al., 2005). This finding is consistent with infidelity functioning for mate switching, but it cannot be explained by the good genes hypothesis, which predicts interest in other men only during the ovulation phase. Third, *women's reported expressed benefits* of extra-pair mating include (a) finding a partner more desirable than their current partner, (b) making it easier to break up with their current partner, (c) being able to replace their current partner, and (d) discovering other potential partners who might be interested in a relationship (Greiling & Buss, 2000). Fourth, the *contexts* that women report would incline them to infidelity include a partner who cannot hold down a job, meeting someone more successful than their current partner who seems interested in them, and meeting someone who is willing to spend a lot of time with them (Greiling & Buss, 2000).

Fifth, 79% of women who have affairs report *falling in love* with their affair partner, in contrast to only a third of men who have affairs (Glass & Wright, 1992)—and love is an emotion

hypothesized to come online primarily in long-term mating contexts (Buss, 1988b, in press). If the primary function of female infidelity was simply to secure superior genes from an affair partner, falling in love seems both superfluous and costly by potentially interfering with securing continued investment from a woman's regular partner.

Sixth, the *qualities women want in an affair partner* are very similar to those they want in a long-term committed mate (Kenrick, Sadalla, Groth, & Trost, 1990; Greiling & Buss, 2000). These include a minimum 70th percentile rank on being dependable, emotionally stable, successful, honest, intelligent, mature, and unselfish. These six clusters of empirical findings are consistent with the mate switching explanation for female infidelity, but appear difficult to explain with the good genes hypothesis.

Moreover, one meta-analytic study of actual misattributed paternity puts the rate at only 1.7% (Anderson, 2006). A second meta-analytic study put the figure between 3.1% and 3.7% (Voracek et al., 2008). And a large-scale study in Germany found a lower nonpaternity rate of 0.94% (Wolf et al., 2012). It is possible, of course, that misattributed paternity rates were higher in ancestral environments, and studies of more traditional cultures may shed light on this issue. For instance, among the semi-nomadic Himba of Namibia, 23% of children from arranged marriages, but none from 'love' marriages, were cases of misattributed paternity (Scelza, 2011). The vast majority of women appear to be securing both genes and investment from the same partner, which poses an empirical problem for the dual mating strategy hypothesis.

Of course, the good genes and mate switching hypotheses are not mutually exclusive or inherently contradictory. A small minority of women in delimited contexts could successfully implement a dual mating strategy and secure good genes from an affair partner, while other women who have affairs are implementing one or another variant of mate switching. We suggest

that the mate switching hypothesis provides a more parsimonious explanation for the function of infidelity for most women (for a fuller elaboration of hypotheses about mate switching adaptations, including its inputs, decision rules, and outputs, see Buss et al., 2017).

Additional functions of short-term mating for women. The mate switching and good genes hypotheses, of course, do not exclude other key possible functions of female short-term mating. Other candidates include securing immediate resources or protection from affair partners (Greiling & Buss, 2000; Symons, 1979); instilling confusion about paternity to prevent infanticide or to elicit resources from multiple mates (Hrdy, 1979); securing a fertility backup in the event that the regular mate proves infertile; seeking revenge on a current mate as a means of deterring his future infidelity; and screening men for qualities desired in a potential long-term mate (Greiling & Buss, 2000). Although these alternative hypotheses for female short-term mating have some supporting evidence in delimited circumstances (Buss, 2016; Scelza & Prall, 2018), they cannot explain the panoply of findings that support the mate switching hypothesis regarding female infidelity. They key point is that mate switching may be the most frequent or primary function of female infidelity, in contrast to the common assumption among evolutionary scientists that good genes is the primary function.

Men's Short-Term Mating Strategies

Because of the large sexual asymmetry in obligatory parental investment, a straightforward set of predictions follow from SST about sex differences in short-term mating. Buss and Schmitt (1993) originally specified four that directly pertain to sex differences in desires for *sexual variety*: 1) men will express greater desire for, or interest in, short-term mates than will women, 2) men will desire larger numbers of sex partners than will women, 3) men will be willing to engage in sexual intercourse after less time has elapsed than will women, and 4)

men will relax their mate preference standards in short-term mating contexts more than women. The cross-cultural empirical tests of this body of predictions have provided powerful support for them (e.g., Buss & Schmitt, 2011, Table 1; Lippa, 2009; Schmitt, 2017).

Sex differences in desires for sexual variety are among the most robust and well-replicated of all effects in the psychological sciences, with effect sizes often reaching *ds* of +.74. Men more than women desire a larger number of sex partners across time intervals ranging from a month to a lifetime. If married, they are more likely to desire extradyadic sex. Men are more likely to have sexual fantasies that involve short-term sex, multiple sex partners, and sex with total strangers. They are more likely to consume pornography depicting short-term sex devoid of context, emotion, and relationships. Men have more permissive attitudes toward casual sex (Petersen & Hyde, 2010) and express a more unrestricted sociosexuality than do women. These findings have been supported by two independent cross-cultural studies, with not a single cultural exception (Lippa, 2009; Schmitt, 2005). Men more than women relax their standards for low-cost short-term matings across an array of mate qualities, including personality, intelligence, and even attractiveness.

Not only are these sex differences robust across cultures, on some measures, the magnitude actually *increases* in more gender-egalitarian cultures. For example, sex differences in expressed comfortability with multiple casual sex partners are higher in Denmark, Norway, Finland, and Iceland than they are in less gender-egalitarian cultures such as Ethiopia, Nigeria, and Swaziland (Schmitt, 2014).

In short, voluminous empirical evidence supports key predictions from SST regarding predicted design features of men's short-term sexual psychology. Over the past quarter century, additional design features have been hypothesized and empirically tested, expanding SST well

beyond its original articulation. These include hypotheses about sexual regret, cues to sexual exploitability, and forms of sexual deception.

Sexual regret. Sexual emotions experienced in the aftermath of a short-term sexual encounter dovetail with the large sex differences discovered in in sexual desire. Men are less likely than women to experience the *emotion of regret* after short-term mating (Galperin et al., 2013), a finding replicated in Norway, one of the most sexually egalitarian cultures in the world (Bendixen et al., 2017; Kennair et al., in press). For example, women more than men report experiencing regret about relationships that progress "too fast" sexually, having sex with a stranger, having sex with someone who faked commitment, and having a one-night stand. Men in the USA and in Norway are more likely than women to experience regret about missed sexual opportunities. Men are less likely than women to experience regret in the aftermath of college campus 'hookups.' Women are more likely than men to say that their 'ideal outcome' of a hookup is a romantic relationship; men are more likely to say that their ideal outcome is more hookups.

Sexual exploitability. A raft of recent studies shows that men prone to seeking short-term matings are especially attracted to women who show *cues of sexual exploitability*—women who might be easily seduced or easily deceived in order to have a brief sexual encounter (Goetz et al., 2012). Cues to sexual exploitability include seeming immature, intoxicated, reckless, flirtatious, sleepy, wearing skimpy clothing, and showing an open body posture. Importantly, men do not find these sexual exploitability cues attractive at all in a potential long-term mate. And men dispositionally inclined to pursue short-term mating find these cues to be especially attractive, substantially more so than men who dispositionally pursue a long-term mating strategy (Lewis et al., 2014).

Strategic interference and sexual deception. In 1993, systematic studies of sexual deception had not yet been conducted, but SST provides a precise prediction. Men more than women will use deception as a means for obtaining short-term sexual access. This prediction follows from Strategic Interference Theory (Buss, 1989a), which suggests that 'negative' emotions such as anger and upset function to alert individuals to when their preferred mating strategy is being blocked or impeded. These emotions help to mark interfering events in memory and motivate actions that function to eliminate the current interference or to avoid future forms of interference. Empirical studies support this prediction regarding sexual deception (Haselton et al., 2005). Three empirical studies in two different cultures found that men were more likely than women to exaggerate the depth of their feelings and commitment in order to gain short-term sexual access. Moreover, women so deceived, compared to men deceived in these ways, reported that they would experience intense emotional upset, with large effect sizes (ds ranging from +.67 to +1.69).

Do men's short-term mating desires translate into actual mating behavior? Mating desires cannot evolve unless they translate into actual mating behavior some of the time. In field experiments, more men than women consent to sex when approached with requests by a stranger of the other sex—75% of men versus 0% of women (Clark & Hatfield, 1989). These findings have been robustly replicated in behavioral experiments in other cultures, including Germany, Italy, and Denmark (e.g., Hald & Hogh-Olesen, 2010; Schutzwohl et al., 2009). For instance, Hald and Høgh-Olesen (2010) replicated these findings in Denmark, with 59% of single men and 0% of single women agreeing to the proposition, "Would you go to bed with me?"

Other studies also point to the expression of men's short-term sexual desires in actual behavior. Married men are more likely than married women to desire and actually have

extramarital affairs (e.g., see Buss, 2016 for summaries). Men who have affairs are more likely than women who have affairs to have them with a larger number of affair partners. Men worldwide become patrons of prostitutes, even in the most sexually egalitarian and sexually liberal countries in the world such as Sweden, Denmark, and Norway. Indeed, 99% of those who purchases the sexual services of prostitutes are men. More men than women on college campuses seek 'hookups' and 'friends with benefits,' both of which are casual sexual encounters with little or no commitment. In sum, the large sex differences postulated by SST in the psychology of short-term mating do indeed get expressed in many ways in actual mating behavior.

Men's Long-Term Mating Strategies

Humans stand out among primate species in that males sometimes devote tremendous time and resources to parental investment (Alexander & Noonan, 1979). Among the roughly 5,416 species of mammals, only 3-5% engage in anything resembling long-term pair-bonds or committed mating. Humans do. The potential reproductive benefit human male ancestors would have reaped from long-term mating consisted primarily of monopolizing all of a woman's lifetime reproductive resources. Additional benefits include increasing the survival and reproductive success of children through paternal investment, reduction of intra-household conflict, and the formation of beneficial long-term alliances with his partner's kin (Henrich, Boyd, & Richerson, 2012).

SST (Buss & Schmitt, 1993) outlined several additional benefits and selective forces that would favor a long-term mating strategy in men, a list subsequently expanded by Buss (2015):

(1) increasing the odds of attracting a mate, especially if women require commitment before consenting to sex; (2) increased ability to attract a high mate value mate, including one of high genetic quality, if women higher in mate value require higher levels of commitment; (3)

increased paternity certainty in ensuing offspring; (4) increased survival of children through protecting, provisioning, and paternal socialization; (5) increased reproductive success of children through paternal investment or paternal arrangements of mating opportunities; (6) increased social status, since marriage in most cultures confers elevated prestige; and (7) acquiring coalitional allies through a partner's kin and other social networks.

Juxtaposed against these potential benefits is a key cost of long-term mating—the *opportunity costs of foregone sexual opportunities*. Time and resources allocated solely to a single mate preclude allocating efforts to securing short-term or even medium-term mateships. Selection likely favored in men adaptations to minimize these opportunity costs. One minimization strategy would be to seek opportunistic copulations when the costs and risks were low. A second would be to pursue a polygynous mating strategy, committing long-term to two or more women. In this context, it is noteworthy that studies reveal that polygynous men, in contrast to lower status married men with only one wife, often minimize direct paternal investment in children (e.g., Hewlett, 1991).

Successful long-term mating requires that men solve two adaptive problems that are sexspecific and at least one that is similar for men and women. The first challenge is identifying
potential mates of high *reproductive value* (Williams, 1975). This problem is made difficult by
the fact that ovulation is concealed or relatively cryptic in women, in sharp contrast to
chimpanzees, humans' closest primate cousin. Indeed, some hypothesize that the evolution of
concealed ovulation was one of the driving forces in the evolution of human long-term
committed mating (Alexander & Noonan, 1979). The second is solving the problem of *paternity uncertainty*. Selection would strongly oppose heavy male parental investment in offspring who
are unlikely to be their own. A third key problem was establishing a mutually cooperative and

mutually beneficial long-term relationship marked by some degree of division of labor—an adaptive problem similar for the sexes.

Identifying women of high reproductive value. Reproductive value, like fertility, is not a quality that can be directly ascertained in humans. Our ancestors had two primary sets of observable cues that were probabilistically correlated with reproductive value—features of physical appearance and manifest behavior. One set of cues are those correlated with relative youth. A young female of age 17, for example, has higher reproductive value than a woman of 27, 37, or 47, since she has many more years of *future* reproduction. This logic leads to an evolution-based theory of female beauty and a cogent array of specific empirical predictions. The theory of beauty, first articulated by Symons (1979), and subsequently elaborated by Buss (1987), Buss and Schmitt (1993), and many others, is graphically depicted in Figure 1.

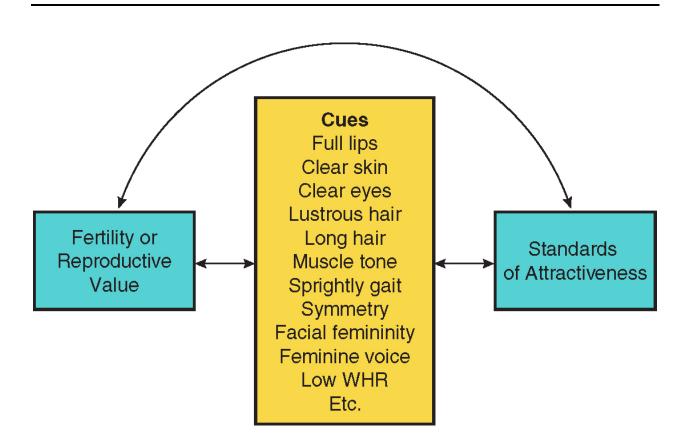


Figure 1. Evolutionary theory of female attractiveness. Ancestrally observable cues probabilistically linked with reproductive value are hypothesized to shape men's evolved long-term mate preferences and, more generally, standards of female attractiveness. Arrows depict hypothesized correlations. Modified from Buss (1987), Figure 1.

This theory of female beauty has been confirmed by independent investigators (see Sugiyama, 2005 for a review). Empirically verified cues linking reproductive value and beauty include: length and quality of women's hair; skin clarity and suppleness; feminine facial features caused by in part by estrogen production such as facial adiposity, full lips, small chin, thin jaws, and high cheekbones; a slender waist; a low waist-to-hip ratio; firm breasts; a relatively low body mass index; and many others. One study found that even men who are congenitally blind from birth prefer a lower waist-to-hip ratio (Karramens et al., 2010). Another found that a latent variable capturing reproductive value correlated almost perfectly with a latent variable capturing female body attractiveness (Andrews et al., 2017). Eye tracking laboratory studies also corroborate men's attraction to bodily cues to reproductive value (Garza et al., 2016). Cues to relative youth, in short, are powerful predictors of judgments of female attractiveness.

Another prediction is that men will prefer and seek relatively young women as long-term mates. This prediction has been confirmed in dozens of cultures (e.g., Buss, 1989b; Conroy-Beam & Buss, in press; Kenrick & Keefe, 1992). A study of 37 cultures found that men, on average, preferred as potential spouses women who were roughly three years younger than they were (see Figure 2).

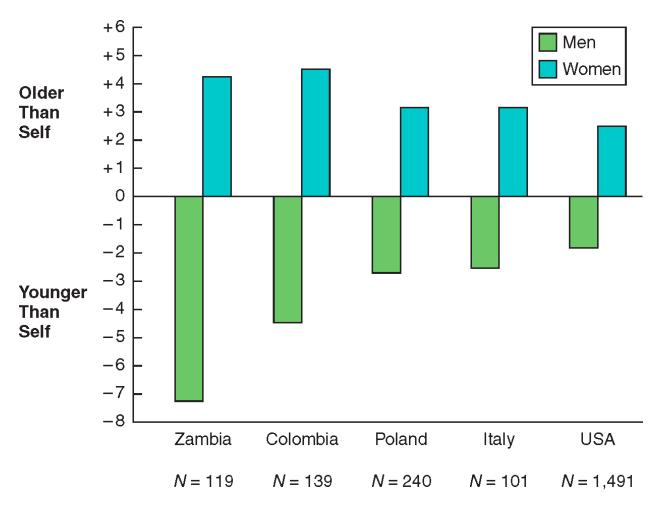


Figure 2. Scale numbers refer to the number of years younger or older preferred relative to self. Men prefer younger potential spouses in all cultures; the preference is especially strong in polygynous cultures such as Zambia, in which men are typically older before they have enough status and resources to marry.

Do age preferences get translated into actual mating behavior? Although some have questioned whether mate preferences influence actual mating behavior (e.g., Eastwick et al., 2014), the empirical data are quite strong that they do. Brides are younger than grooms across cultures, averaging roughly three years at first marriage (Buss, 1989b). As men get older, and if they divorce and remarry, men marry women increasingly younger than they are. In the United

States, the age gap is roughly three years at first marriage, five years at second marriage, and eight years at third marriage (Guttentag & Secord, 1983). These findings are robust over time as well, showing up, for example, in marriage statistics on the island of Poro a century ago (Kenrick & Keefe, 1992). In Sweden in the 1800s, church documents reveal that men who remarried following divorce married brides 10.6 years younger than they were (Low, 1991). Data from Norway from the century and a half from 1851 through 2002 reveal similar findings (Conroy-Beam & Buss, in press). The actual marriage data across cultures and over time support the hypothesis that men's age preferences translate into actual marriage decisions.

An unprecedented data set bearing on this issue came from a study of marriages in South Korea (Sohn, 2017). A subset of these marriages occur through an unusual mechanism—some men purchase brides from developing countries. Although the sample of Korean men who married Korean women (N = 1,088,457) showed the usual age gap of several years, Korean men who purchase foreign brides (N = 45,528) married dramatically younger women, reaching two decades younger for the older cohorts of men. In a mating market where men can act on their preferences, they actually select and marry women substantially younger.

Other behavioral data converge on this conclusion (Conroy-Beam & Buss, in press). In studies of online dating, men actively seek younger partners. Younger women in online dating receive a larger number of responses from men than do older women. The age of potential brides influences the amount of money spent on pre-marriage customs in cultures such as the Kipsigis in Kenya (Borgerhoff Mulder, 1990). The amount of money spent on engagement rings is higher for younger compared to older fiancées (Cronk & Dunham, 2007). Younger wives are more intensely mate guarded than older wives (Buss & Shackelford, 1997). In sum, converging lines of evidence from multiple data sources using different methods, from independent investigators,

from dozens of different cultures, and over time periods spanning centuries robustly confirm the prediction that age preferences translate into actual mating behavior.

The problem of paternity uncertainty. Because fertilization occurs internally within women, maternity is 100% certain. Men can never be sure; paternity certainty is almost always less than 100%, at least prior to very recent molecular methods of DNA testing. Estimates of actual non-paternity vary across culture and from study to study, but meta-analyses put the figures between roughly 1%–3.7% (Anderson, 2006; Voracek et al., 2008). The reproductive costs to ancestral men investing heavily in long-term mating and parenting would have been catastrophic unless they evolved adaptations that increased the probability of paternity certainty. Several such adaptations have been proposed.

Three hypothesized adaptations from SST have centered on (a) a mate preference for *virginity*, or no prior experience in sexual intercourse, (b) preference cues to that auger well for *post-mating sexual fidelity and loyalty*, and (c) the emotion of *sexual jealousy* and its mate guarding behavioral outputs.

Virginity. The first hypothesis was poorly formulated. For a mate preference to have evolved, it must involve a quality that our human ancestors could have actually observed or assessed in some direct or indirect way. Unlike qualities like age (roughly reliably assessed via appearance such as smooth versus wrinkled skin and behavior such as a sprightly versus a stooped slow gait) and physical attractiveness—qualities that can be evaluated with at least some accuracy, albeit imperfectly—virginity is not a quality that our ancestors could have observed or assessed reliably. There are no observable physical or behavioral cues to virginity. Even tests such as palpating the hymen are inherently unreliable; women vary tremendously in whether they have an intact hymen and many causes other than sexual intercourse can rupture an

otherwise intact hymen (e.g., through horseback riding). What is most relevant to men for solving the problem of paternity uncertainty may be not whether a potential mate is a virgin, but rather whether she is not pregnant by another man at the time of commitment and will remain sexually faithful after commitment or marriage. Sexual conduct prior to marriage, either through observation or reputation, might predict sexual fidelity.

Perhaps because the virginity hypothesis was conceptually problematic, empirical tests failed to produce universal support for it. As shown in Figure 3, cultures differ tremendously in both in the absolute magnitude of value placed on virginity, as well as in the presence (62% of the cultures) or absence (38% of the cultures) of a sex difference. At best, the original hypothesis about virginity can be regarded as only weakly and inconsistently supported. These findings belie the oft repeated, yet factually incorrect, claim that evolutionary psychological hypotheses are inherently unfalsifiable (see Confer et al., 2010, for a fuller discussion of this issue).

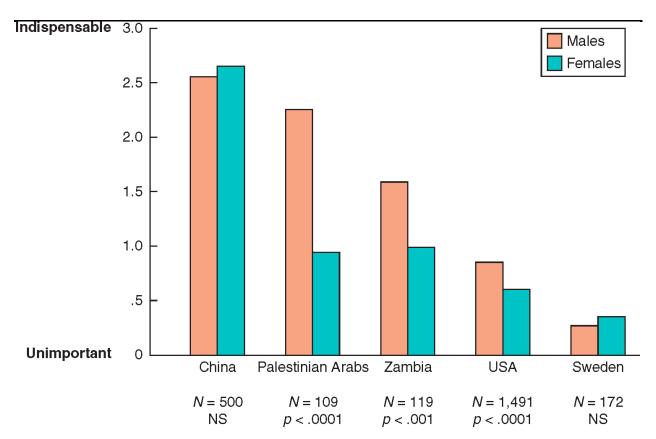


Figure 3. Importance placed on chastity (no prior sexual intercourse) in a potential spouse.

Adapted from Buss & Schmitt (1993).

Sexual fidelity. In contrast, there exists considerably more support for the value men place on sexual fidelity in a long-term mate. Men place sexual fidelity at or near the very top of the list of desired qualities in a potential spouse (Buss & Schmitt, 1993; Gil-Berman et al., 2002; Waynforth & Dunbar, 1995). On a rating scale of -3 (extremely undesirable) to +3 (extremely desirable), men give the quality 'fidelity' +2.88 and 'sexually loyal' +2.85, the two most highly valued qualities in a long-term mate out of 67 qualities evaluated (Buss & Schmitt, 1993). On the other end, men rate 'unfaithful' -2.93 and 'sleeps around a lot' -2.79, the two most undesirable qualities in a prospective long-term mate. Men apparently assess and evaluate levels of sexual activity by a woman prior to long-term commitment—behavior that would have been observable or known through social reputation in the small-group living of our ancestors. Past behavior is a good predictor of future behavior, and having a large number of sex partners prior to marriage a statistical predictor of infidelity after marriage (Buss, 2016).

Sexual jealousy. The emotion of sexual jealousy has been hypothesized as an adaptation to solve the problem of paternity uncertainty in men (Buss et al., 1992). Empirical tests have largely confirmed this hypothesis using multiple methods, including force-choice dilemmas, continuous self-report measures, experiments with memorial recall and speed of processing, laboratory experiments using cognitive load, reports after experiencing actual infidelities, and fMRI techniques (see Buss 2015, and Edlund & Sagarin, 2017 for recent summaries).

These findings have not gone unchallenged. Some have argued that they are methodological artifacts. Others have argued the findings are better explained by alternative

theories, such as attachment theory or domain-general social-cognitive theories. These challenges have all been successfully refuted. The findings are consistent across many methods, not restricted to a single method. An experiment that purported to show that the findings disappeared under cognitive load (deSteno et al., 2002) actually found that they did not (Barrett et al., 2006). And alternative theories cannot explain the many design features of male sexual jealousy that have been empirically documented (e.g., Buss & Haselton, 2005).

Mate guarding and mate retention tactics, from vigilance to violence, have been the hypothesized behavioral output of sexual jealousy adaptations (Buss & Shackelford, 1997). Hypothesized design features include increased mate guarding (a) as a function of perceived infidelity probability, (b) as a function of the youth and hence reproductive value of the female partner, and (c) as a function of mate-value discrepancies.

Although this review has focused on sex-differentiated adaptive problems men have faced in long-term mating, several adaptive problems are critical for women and men alike. These include choosing a partner who will be a good cooperator, a dependable long-term partner, and a healthy long-term partner. The high levels of sexual similarities revealed in the 37-culture study—for kindness, dependability, and good health—support these hypothesized similarities in mate selection.

Women's Long-Term Mating Strategies

Given men's evolved desires for sexual variety, most women have available to them a wide range of potential short-term mates, including many of high mate value. As most women can secure a higher mate value man in the context of short-term mating than long-term mating, why would women ever seek a long-term mate? SST identifies three potential benefits ancestral women could have accrued: (a) status and economic resources for herself and her children, (b)

physical protection for herself and her children, and (c) enhanced mating success of her children as a consequence of social and material benefits. The primary costs to women from committed long-term mating, like the primary costs for men, are the opportunity costs of relinquishing some or all short-term matings and the potential benefits they might entail.

The evolution of mate preferences for these qualities would have required at least two recurrent conditions. First, men would have to vary in their *ability* to provide such resources and in reliable cues to that ability. SST identified three such cues in potential mates—ambition, industriousness, and social status. Second, men would have to be *willing* to invest those resources in a particular woman. Although the original formulation of SST (Buss & Schmitt, 1993) did not identify potential cues to a man's willingness to commit, other research has identified the emotion of love as a powerful signal of such commitment (Buss, 1988b, in press).

Economic resources. Women's preference for men with economic resources has been abundantly supported by dozens of studies. The 37-culture study found that women valued long-term mates who had 'good financial prospects' more than did men (Buss, 1989a). The universality of this mate preference spans across cultures with different mating systems (presumptive monogamy versus polygyny), different levels of gender economic equality (e.g., Sweden versus Iran), and different religious orientations (e.g., Muslim, Jewish, Christian, atheist).

The findings have been replicated with multiple methods across dozens of cultures. In studies of the 'minimum percentile' people would accept in a long-term mate, women put earning capacity in the 70th percentile, whereas men put it in the 40th (Kenrick et al., 1990). Wang et al. (2018) asked men and women from China, the US, and Europe to rate the attractiveness of opposite sex individuals, experimentally manipulating the physical and

economic (i.e., salary) information about the targets. Across all cultures, women were roughly one thousand times more sensitive to salary when rating men than men were when rating women. An in-depth study of the Hadza, a traditional hunter-gatherer group residing in Tanzania, found that women placed great importance on a man's foraging abilities, centrally his ability to hunt and provide meat (Marlowe, 2004).

Ambition, industriousness, and social status. Sex differences in mate preferences for key predictors of economic resources are not quite as universal across cultures. The combined item 'ambition and industriousness' showed significant sex differences in 29 of the 37 cultures sampled (Buss, 1989a). Women in all cultures, however, placed a relatively high absolute value on this quality, typically giving it above a 2 on the 0–3 scale, where a 3 indicates 'indispensable.' For example, Nigerian women gave it 2.61, Chinese women 2.63, Iranian women 2.81, Estonian women 2.46, Italian women 2.07, and Swedish women 2.04.

Love and kindness as indicators of willingness to commit. The emotion of love has been hypothesized to be an evolved mate commitment device (Buss, 1988b, in press; Frank, 1988). Love turns out to be a human universal (Jankowiak, 1997). Across cultures, people sing love songs, elope with a loved one against the wishes of their parents in societies with arranged marriages, and report personal anguish and longing when separated from a loved one. Acts of commitment of reproductively-relevant resources top the list of most prototypical love acts (Buss, 1988b). These include giving up romantic relations with others, talking of marriage, and expressing a desire to have children. Reports of experiencing love powerfully predict feelings of subjective commitment, far more than feelings of sexual desire (Gonzaga et al., 2008).

Women also prioritize kindness in a long-term mate. The 37-culture study found that the variable "kind and understanding" was placed at or near the top of mate preferences in all

cultures (Buss et al., 1990). Subsequent studies have provided an important scientific advance in documenting that women prefer mates who are kind and trustworthy specifically with respect to themselves and their families, but much lower levels when kindness is directed toward other types of individuals (Lukaszewski & Roney, 2010). Like love, these target-specific mate preferences suggest a willingness to commit to a particular woman and her genetic kin rather than a domain-general trait of undifferentiated kindness.

Protection. Women and their children historically faced dangers from predators, and perhaps more profoundly from aggressive conspecifics, especially men. Hazards include physical harm and sexual assault. A long-term mate could effectively function as a bodyguard, both deterring potential assaulters and when needed directly repelling immediate threats and dangers. Qualities rendering a potential mate an effective bodyguard include physical formidability, size, athletic prowess, and bravery in the face of danger.

Women's preferences in a mate appear to embody these cues. Women judge short men to be undesirable for either a short-term or a long-term mate (Buss & Schmitt, 1993). In contrast, women find it very desirable for a potential marriage partner to be tall, physically strong, and athletic. A study of women from Britain and Sri Lanka found strong preferences for male physiques that were muscular and lean. Women prefer and find attractive men with "V-shaped" torso, that is broad shoulders relative to hips (Hughes & Gallup, 2003). Women who are especially fearful of crime show even stronger preferences for long-term mates who are physically formidable.

Tall men are consistently seen as more desirable as dates and mates than are short or average men (Courtiol, Ramond, Godelle, & Ferdy, 2010). Two studies of personal ads revealed that, among women who mentioned height, 80 percent wanted a man to be 6 feet or taller (Pierce,

1996). Personals ads placed by taller men received more responses from women than those placed by shorter men. A study of the "hits" received by 1,168 personal advertisements in Poland found that a man's height was one of the four strongest predictors of the number of women who responded to the male ads (the others being education level, age, and resources; Pawlowski & Koziel, 2002). Tall men are perceived as more dominant, are more likely to date, and are more likely to have attractive partners than shorter men (see Brewer & Riley, 2009, for a review). Women solve the problem of protection at least in part by preferring a mate who has the size, strength, and physical formidability to protect them. These physical qualities also contribute to solutions to other adaptive problems such as resource acquisition and genes for good health, since tallness is also linked with status, income, symmetrical features, and good health (Brewer & Riley, 2009).

Do women's preferences translate into actual mating behavior? In one study of speed dating, women were more likely to actually select men who indicated that they had grown up in an affluent neighborhood (Hitch et al., 2010). Another study of 382 speed daters found that women were more likely than men to select dates who had higher levels of income and education (Asendorpf et al., 2011; see also Li & Meltzer, 2015). A study of mail-order brides from Colombia, the Philippines, and Russia found that women actively sought men with higher levels of status and ambition (Minervini & McAndrew, 2006). A study of 2,956 Israelis using a computer dating service found that women, far more than men, sought mates who owned their own cars, had good economic standing, and who placed a high level of importance on their careers (Bokek-Cohen et al., 2008). In the Kipisigis of Kenya, women and their parents preferentially select men who have large plots of land (Borgerhoff Mulder, 1990). And the men

who women choose to marry, compared to same-aged men who do not marry, have consistently higher incomes (Buss, 2016).

Would women who acted on these long-term mate preferences, actually selecting men of high status and resources, have experienced greater reproductive success? There is evidence that women married to older, higher-status men have more and more surviving children (Nettle & Pollet, 2008). For instance, in a study of 1700s pre-industrial Finland, women married to wealthier men had more children and better child survival rates than women married to poorer men (Pettay et al., 2007). Fieder and Huber (2007) found marrying a man four years older was associated with maximum levels of fertility among women, which matches closely what women say is their ideal long-term mate (Buss, 1989; Kenrick & Keefe, 1992).

A cross-cultural study of the causes of divorce found that inadequate economic support, including inadequate food, housing, and clothing, was a sex-linked cause of marital dissolution (Betzig, 1989). In no society did a woman's failure to provide economic resources constitute grounds for divorce. Women's mate preferences for economic resources and social status in a long-term mate translate into actual mating behavior, from selective decisions in speed dating to real-life fertility outcomes to the causes of divorce. As with men's preferences, women's mate preferences matter in real-world mating markets.

Context-Specific Influences on Sexual Strategies

Sexual strategies are predicted to be highly sensitive to context. One aspect of this sensitivity centers on strategic shifts according to personal qualities such as mate value and life history strategy, social conditions such as operational sex ratio, ecological conditions such as parasite prevalence, and cultural conditions such as prevailing norms surrounding sexual conduct. We highlight a few of these important contextual shifts.

Women's mate value and long-term mating. Women who are young and physically attractive have more mating options and can become choosier in their selections. But does a woman's mate value influence her mate preferences? Little and colleagues had seventy-one women rate themselves on their perceptions of their own physical attractiveness and subsequently showed them photos of men's faces that varied along the masculinity–femininity dimension (Little, Penton-Voak, Burt, & Perrett, 2002). Women's self-rated attractiveness was significantly linked to attraction to masculine faces. Women who view themselves as physically attractive also show a more pronounced preference for men who display vocal masculinity, marked by a low-pitched voice (Pisanski & Feinberg, 2013).

Studies of personal ads in Canada, the United states, Croatia, and Poland find that women higher in mate value specified a longer list of traits that they sought or required in a potential mate than did women lower in mate value (Pawlowski & Dunbar, 1999). Similar results have been found in Brazil and Japan. Furthermore, women who perceive themselves as higher in mate value tended to impose higher minimum standards in what they would require of a long-term mate on a wide variety of characteristics, notably social status, intelligence, and family orientation (Regan, 1998). A Croatian study of 885 found that women high on self-perceived physical attractiveness preferred higher levels of education, intelligence, good health, good financial prospects, good looks, and favorable social status in a potential mate (Tadinac & Hromatko, 2007).

A U.S. study had interviewers evaluate 107 women for face, body, and overall attractiveness (Buss & Shackelford, 2008). Attractive women expressed a desire for higher levels of hypothesized "good genes" indicators such as masculinity, physical attractiveness, sex appeal, and physical fitness. They also expressed a greater desire for potential income of a mate, good

parenting qualities such as fondness for children, and good partner indicators such as being a loving partner. A speed dating study conducted in Germany examined actual mate choices made by women (Todd, Penke, Fasolo, & Lenton, 2007). Women high on self-perceived physical attractiveness actually chose men high on overall desirability, an aggregate score that included wealth and status, family orientation, physical appearance, attractiveness, and healthiness. Attractive women apparently want it all.

Men's mate value and long-term mating. Although most men place a premium on youth and beauty in a mate, not all men succeed in achieving their desires. Men lacking the status and resources that women want have the most difficulty attracting such women and may have to settle for less than their ideal. Evidence comes from men historically in a position to get exactly what they prefer—kings, emperors, and other men of high status. In the 1700s and 1800s, for example, wealthier men from the Krummerhörn of Germany married younger brides than did men lacking wealth (Voland & Engel, 1990). High-status men from the Norwegian farmers of 1700s to 1900s to the Kipsigis in Kenya consistently married younger brides than did their lower-status counterparts (Borgerhoff Mulder, 1988; Røskaft, Wara, & Viken, 1992).

Kings and despots routinely stocked their harems with young, attractive, nubile women and had sex with them frequently (Betzig, 1992). The Moroccan emperor Moulay Ismail the Bloodthirsty, for example, sired 888 children. His harem included 500 women. But when a woman reached the age of thirty, she was removed from the emperor's harem, sent to a lower-level leader's harem, and replaced by a younger woman. Roman, Babylonian, Egyptian, Incan, Indian, and Chinese emperors all shared the tastes of Emperor Ismail and enjoined their trustees to scour the land for young pretty women.

Marriage patterns in the United States today confirm the prediction from SST that men with resources are most able to actualize their preferences. High-status older males, such as business CEOs, rock stars, and famous actors, frequently select spouses one or two decades younger, whereas similarly high-status women do not (Conroy-Beam & Buss, in press; Kenrick & Keefe, 1992). Several sociological studies have examined the impact of a man's occupational status on the physical attractiveness of the woman he marries (see Buss, 2016, for a review). All point the same conclusion that men high in status tend to marry women younger and more physically attractive than men low in status (Von Rueden, Gurven, & Kaplan, 2010).

Men who have high status and income are aware of their ability to attract more desirable women. In a study of a computer dating service involving 1,048 German men and 1,590 German women, Karl Grammer found that as men's income goes up, they seek younger partners (see Buss, 2016). Each increment in income is accompanied by a decrease in the age of the woman sought. Men high in mate value express a stronger preference for facially feminine women—a key correlate of attractiveness (Burriss, Welling, & Puts, 2011). Finally, an experiment showed men who won a video-game competition expressed stronger preferences for women's facial femininity than men who lost the competition, suggesting that even temporary increases in status may cause men to elevate their mating standards.

Men's mate value and short-term mating strategy. One context that may affect short-term mating is mate value. The self-perceived mating success scale (Landolt, Lalumiere, & Quinsey, 1995) assesses mate value. Sample items from this scale are: "members of the opposite sex notice me"; "I receive many compliments from members of the opposite sex"; "members of the opposite sex are attracted to me"; and "relative to my peer group, I can get dates with great ease."

Scores on the mate value scale were correlated with the reported sexual history of the participants. The results were strikingly different for the sexes. High-mate-value men, relative to their lower-mate-value counterparts, tended to have sexual intercourse at an earlier age, a greater number of sex partners since puberty, more partners during the past year, more sexual invitations within the past three years, sexual intercourse more frequently, and a stronger feeling of no need to be attached to a person before having sex. High-mate-value men tend to score toward the high end of the Sociosexual Orientation Inventory (Clark, 2006), suggesting that they are pursuing a short-term mating strategy. Men who high in status and resources tend to have a larger number of sex partners, indicating success at short-term mating (Perusse, 1993).

Men with a higher shoulder-to-hip ratio (SHR) have sex at an earlier age, have more sex partners and more extra-pair copulations, and are more likely to have sex with other people's mates (Hughes & Gallup, 2003). Men with attractive faces and masculine bodies have more short-term sex partners (Rhodes, Simmons, & Peters, 2005) and express an especially strong preference for women with high facial femininity (Burriss, Welling, & Puts, 2011). Men high in handgrip strength (Gallup, White, & Gallup, 2007) and who have high circulating testosterone (van Anders, Hamilton, & Watson, 2007) tend to pursue a short-term mating strategy. Men with a mesomorphic (muscular) body build tend to have higher reproductive success, as gauged by offspring count (Genovese, 2008), which may reflect a short-term strategy.

Women's mate value and short-term mating strategy. The findings for a link between women's mate value and sexual strategy are more mixed. Some find no association between women's self-perceived mate value and the pursuit of a short-term mating strategy (e.g., Landolt et al., 1995; Mikach & Bailey, 1999). On the other hand, women with a low (attractive) WHR tend to follow a more unrestricted (short-term) mating strategy and are perceived by others to be

more promiscuous and less trustworthy (Brewer & Archer, 2007). One speculation is that bodily attractiveness, rather than facial or overall attractiveness, may be linked with a short-term mating strategy in women.

Temporal context shifts. Women's mate preferences shift as a function of temporal context. Buss and Schmitt (1993) asked women to rate sixty-seven characteristics on their desirability in short-term and long-term mates. The rating scale ranged from +3 (extremely undesirable) to +3 (extremely desirable). Women found the following qualities to be more desirable in long-term marriage contexts than in short-term sexual contexts: "ambitious and career-oriented" (average rating, 2.45 in long term versus 1.04 in short term), "college graduate" (2.38 versus 1.05), "creative" (1.90 versus 1.29), "devoted to you" (2.80 versus 0.90), "fond of children" (2.93 versus 1.21), "kind" (2.88 versus 2.50), "understanding" (2.93 versus 2.10), "responsible" (2.75 versus 1.75), and "cooperative" (2.41 versus 1.47). These findings suggest that temporal context matters a great deal for women, causing shifts in their preferences depending on whether a marriage partner or a casual sex partner is sought (Schmitt & Buss, 1996).

Sex ratio shifts. The ratio eligible men relative to eligible women is another critical context that can influence sexual strategies (Moss & Maner, 2016). Many factors affect this sex ratio, including wars, which kill larger numbers of men than women; risk-taking activities such as physical fights, which more frequently affect men; intentional homicides, in which roughly seven times more men than women die; and different remarriage rates by age, whereby with increasing age women remarry less often than men. Men shift to brief encounters when many women are sexually available because the sex ratio is in their favor and they are therefore better able to satisfy their desire for variety (Pedersen, 1991). Ache men of Paraguay, for example,

appear to be highly promiscuous because there are 50 percent more women than men (Hill & Hurtado, 1997). In the most comprehensive cross-cultural study of sex ratio and sexual strategies, involving 14,059 individuals in 48 nations, people in cultures with a surplus of women were more likely to endorse attitudes and behaviors associated with a short-term mating strategy (Schmitt, 2005). When there is a surplus of men, in contrast, both sexes appear to shift toward a long-term mating strategy marked by stable marriages and fewer divorces (Pedersen, 1991). A surplus of males also predicts polyandry— a form of mating in which one woman marries more than one man, often brothers (Starkweather & Hames, 2012).

Personality and mating strategy. One's own personality characteristics also appear to influence the pursuit of differing sexual strategies. A study of 13,243 individuals from 46 nations found that the traits of extraversion, low levels of agreeableness, and low levels of conscientiousness predicted an interest in short-term mating, attempts at poaching the mates of others, and succumbing to the lure of mate poaching by others (Schmitt & Shackelford, 2008). The "Dark Triad" of personality—the traits of narcissism, psychopathy, and Machiavellianism—also predict exploitative short-term mating strategies, including willingness to engage in sex with others while in a relationship (e.g., Schmitt et al., 2017). Narcissism, for example, predicts a preference for one-night stands (Jonason, Luevano, & Adams, 2012).

Ecological parasite prevalence. Because parasites are known to degrade physical appearance, people living in ecologies with a high prevalence of parasites should place a greater value on physical attractiveness in a mate than people living in ecologies with a low prevalence of parasites (Gangestad & Buss, 1993). To test this hypothesis, the prevalence of parasites in 29 cultures was correlated with the importance that the people in those cultures attached to physical attractiveness in a marriage partner. The results confirmed the hypothesis: The greater the

parasite prevalence, the more important was physical attractiveness (see also, Gangestad et al., 2006).

Cultural norms and rituals influence mating strategies. Cultures differ tremendously in prevailing cultural norms surrounding mating and the rituals they enact. In some, matings are arranged; in others, individuals have great latitude for choice. Some, such as the Trobriand Islanders, encourage premarital sexual experimentation and place great emphasis on the female orgasm. Others forbid premarital sex and pay little attention to female sexual pleasure. Although all cultures appear to have marriage rituals, these vary in form. Some require men to pay a 'bride price' in which resources are transferred to the woman's kin. Others expect the woman's family to provide a dowry in which resources get transferred to the man or his family. Some cultures legally permit polygamy; others forbid it. A few practice polyandry.

Although the origins of these differing cultural norms are largely unknown, it would be astonishing if they failed to influence human mating behaviour. Humans have psychological adaptations to conform, prioritize the opinions of others, and monitor the status effects of their own behaviour on their reputation within the group (Buss, 2015). Cultural variation in the importance placed on virginity is correlated with the prevalence of premarital sex. Cultures with ritual practices of clitoridectomy and other forms of genital mutilation place a low priority on female sexual pleasure. Cultures even invent novel forms of mate guarding, such as infibulation, which physically prevents sexual intercourse unless or until the threads closing the vulvar lips are cut. A key direction for future theoretical and empirical work is a fuller integration of cultural evolution with Sexual Strategies Theory.

Challenges to Sexual Strategies Theory: Can alternative theories provide cogent explanations?

Prior to Sexual Strategies Theory, no theories of mating in the social sciences were anchored in fundamentals of evolutionary biology, specified the origins of mating strategies, predicted that the temporal dimension of mating would prove crucial, or outlined context-specific shifts in mating. Importantly, no prior theories predicted sex differences in the underlying psychology of mating.

The first competing explanation for sex differences in mate preferences was proposed by Buss and Barnes (1986) prior to their cross-cultural discovery--a form of social role theory explanation they called "structural powerlessness and sex role socialization." According to this view, because women are typically excluded from power and access to resources, which are largely controlled by men, women seek mates who have power, status, and earning capacity. Women try to marry upward in socioeconomic status because this provides their primary channel for gaining access to resources. Men do not value economic resources in a mate as much as women do because they already have control over these resources and because women have fewer resources anyway.

Subsequently, Eagly and Wood (1999) also proposed a social role explanation for the sex differences in mate preferences, albeit after the robust cross-cultural sex differences had been discovered (Buss, 1989). They suggested that the reason some sex differences are universal is because gender roles stem, in part, from evolved physical differences between men and women (e.g., physical strength, ability to bear children). These physical sex differences, they argued, lead to the development of certain social structures (e.g., divisions of labor, political institutions, marital traditions) that guide gendered socialization practices and influence relationship dynamics in ways that generate psychological sex differences, including culturally-universal sex differences in mate preferences (Eagly & Wood, 1999). "As societies become more egalitarian,

men and women become more similarly positioned in the social structure and, therefore, more similar psychologically in many ways" (Eagly et al. 2004, p. 283-284). Thus, social role theory predicts as girls and boys are socialized more equally, experience more similar economic and undivided labor roles, experience lower levels of sociopolitical power differentials, and experience less patriarchy and sexism, psychological sex differences should become smaller.

The society of Bakweri from Cameroon in West Africa provides one test of social role theory by illustrating what happens when women have real power (Ardener, Ardener, & Warmington, 1960). Bakweri women hold greater personal and economic power because they have more resources and are in scarcer supply than men. Women secure resources not only through their own labors on plantations but also from casual sex, which is a lucrative source of income. There are roughly 236 men for every hundred women, an imbalance that results from the continual influx of men from other areas of the country to work on the plantations. Because of the extreme imbalance in numbers of the sexes, women have considerable latitude to exercise their choice in a mate. Women have more money than men and more potential mates to choose from. Yet Bakweri women persist in preferring mates with resources. Wives often complain about receiving insufficient support from their husbands. A lack of sufficient economic provisioning is the reason most frequently cited by women for divorce. Bakweri women change husbands if they find a man who can offer them more money and pay a larger bride-price. When women are in a position to fulfil their evolved preference for a man with resources, they do so. Having personal control of economic resources apparently does not negate this mate preference.

Buss (1989b) provided a more systematic set of tests of the social role theory explanation. In one test, he identified women who were financially successful, as measured by their salary and income, and contrasted their preferences in a mate with those of women with lower salaries and

income (Buss, 1989b). The financially successful women were well educated, tended to hold professional degrees, and had high self-esteem. Successful women turned out to place an even greater value than less professionally successful women on mates who have professional degrees, high social status, and greater intelligence and who are tall, independent, and self-confident. Women's personal income was positively correlated with the income they wanted in an ideal mate (+.31), the desire for a mate who is a college graduate (+.29), and the desire for a mate with a professional degree (+.35). Contrary to the social role/structural powerlessness hypothesis, these women expressed an *even stronger* preference for high-earning men than did women who are less financially successful.

In a second test, Buss (1989b) correlated two culture-wide indicators of gender economic inequality with the magnitude of sex differences on preferences for mates with good earning capacity across 30 cultures. Neither indicator of gender economic of educational inequality correlated significantly with the magnitude of gender difference in this mate preference.

Eagly and Wood (1999) subsequently conducted secondary analyses on Buss's (1989) data set. They constructed somewhat different indicators of the magnitude of culture-level gender equality/inequality in a subset of the cultures that Buss had studied. Only one of the four tests yielded a significant correlation with the magnitude of sex differences in the mate preference for good financial resources. None of the four tests of gender equality predicted significant cultural variation in sex differences in the importance attached to physical attractiveness. So, of the critical tests across these two key variables, only one of the eight proved to be statistically significant, suggesting rather weak support for social role theory in the domain of mate preferences on these core variables.

Subsequent studies have continued to fail to find support for social role theory of sex differences in mating strategies. Cross-cultural studies consistently find small but positive relationships between women's personal access to economic resources and preferences for mates with resources. A study of 1,670 Spanish women seeking mates through personal advertisements found that women with more resources and status were more likely to seek men with resources and status (Gil-Burmann, Pelaez, & Sanchez, 2002). A study of 288 Jordanians found that both women and men with high socioeconomic status place more, not less, value on the mate characteristics of having a college graduate degree and being ambitious-industrious (Khallad, 2005). A study of 127 individuals from Serbia concluded: "The high status of women correlated positively with their concern with a potential mate's potential socio-economic status, contrary to the prediction of the socio-structural model" (Todosijevic, Ljubinkovic, & Arancic, 2003, p. 116). Other large-scale cross-cultural studies fail to find support for the structural powerlessness hypothesis or social role theory (Lippa, 2009; Schmitt, 2012; Schmitt et al., 2009; but see also Zentner & Eagly, 2015). More generally, a common finding across many studies is that sex differences tend to be larger in more gender egalitarian cultures (e.g., Stoet & Geary, 2018; Schmitt, 2014), in direct contradiction to predictions from the social role theory.

Conclusions

To our knowledge, SST, but neither social-role theory nor any other competing theories, have yet been advanced that provide content-rich predictions concerning: (1) sex differences short-term mating psychology, such as desires for sexual variety, quickness to agree to sex, and consenting to sex with complete strangers; (2) sex differences in patterns of, and emotional reactions to, sexual deception; (3) context-dependent male attraction to cues of female sexual exploitability, (4) sex differences in the causes of sexual regret, (5) universal standards of female

facial beauty that embody cues to youth and fertility, (6) standards of female body attractiveness such as a low-waist-to-hip ratio that embody cues to youth and fertility, (7) standards of male attractiveness that embody cues to status and resource acquisition, (8) standards of male attractiveness such as height and physical formidability that embody cues to protection, (9) sex differences in, and predictors of, tactics of mate attraction, competitor derogation, and mate retention that correspond precisely to evolved mate preferences; and (10) context-dependent shifts in sexual strategies as a function of variables such as sex ratio, parasite prevalence, and mate value. SST predicts and successfully explains this diverse array of empirical findings. Any truly competing theory of human mating strategies, to be taken seriously, should provide a compelling alternative account for this large cumulative array of empirical findings.

In this concluding section, we highlight advances in SST since it 1993 formulation, and suggest directions for future theoretical development.

Men's short-term mating. Whereas Buss and Schmitt (1993) generated hypotheses about four design features of men's short-term mating strategies (e.g., time elapsed before seeking intercourse; number of sex partners desired; lowering of standards for short-term mates), subsequent theorizing and research has documented at least five additional design features. These include sexual regret over missed sexual opportunities, sexual attraction to women displaying cues to sexual exploitability, tactics of deception by feigning long-term interest for short-term sex, emotional upset about being led on sexually without subsequent follow-through, and psychological tactics for avoiding entangling mating commitments (e.g., Jonason & Buss, 2012).

Women's short-term mating. Although SST originally outlined several competing hypotheses about the function of women's short-term mating, evidence bearing on each was

virtually non-existent in 1993. Over the past quarter century, most research effort has been devoted to testing variants of the 'good genes' hypothesis. After reviewing the evidence, our judgment is that the empirical evidence for the good genes function is weak, although it cannot be ruled out for a subset of women.

Although far less studied, we suggest that the mate switching hypothesis of female shortterm mating is more promising (Buss et al., 2017). These hypotheses are not mutually exclusive. Short-term mating could serve different functions for different women in different circumstances. Some women might use short-term mating to assay potential long-term mates—a hypothesis original proposed by Buss and Schmitt (1993), but to our knowledge has remained untested empirically. Some women might use short-term mating to obtain resources, as proposed by Symons (1979) and Buss and Schmitt (1993), and more recently by Baumeister and Vohs (2012) under the rubric of 'sexual economics theory.' Modern forms of sex-for-money exchanges include internet pornography, sex-for-money internet dating sites, and men who pay to watch women live on the internet using sex cams. Do these forms of sex-for-money simply reflect an exploitation men's short-term mating psychology? Or are they modern manifestations of a proper evolved function of women's short-term mating strategy? More research is needed. For some women, short-term mating might serve no function at all, and be merely a non-adaptive byproduct of activating sexual pleasure mechanisms in the modern environment. Consequently, future research should focus on testing hypotheses about which women in which circumstances obtain which benefits, if any, by short-term mating.

Variations in short-term and long-term mating. 'Short-term mating' is not a singular phenomenon. Future research should distinguish low-commitment casual sex such as college campus hookups from low investment affairs, and distinguish those from long-term affairs that

may in essence function little differently from formal long-term mating. The apparent surge in popularity of *consensual non-monogamy* represents another interesting research avenue. Do these arrangements represent attempts to fulfill long-term and short-term mating strategies simultaneously? Do individuals who pursue consensual non-monogamy differ in critical ways from those who do not, such as possessing an unusually high sex drive or an unusually low activation threshold for sexual jealousy? There remains much to be discovered about important variations that cross-cut the temporal dimension of sexual strategies.

Men's long-term mating strategy. Men's long-term mating has been central to SST from the start. Many core elements of this strategy have been documented. These include mating priorities similar to those of women in long-term mating, such as prioritizing good partner and good parent qualities such as dependability and emotional stability. They include activation of the emotion of love, likely a key commitment device. Men's long-term mating also includes the priority that men place on cues to female reproductive value, such as youth and beauty; the priority that men place on sexual fidelity; the functional emotion of sexual jealousy; and the array of mate retention tactics that men deploy to protect their reproductive assets, including benefit-bestowal of resources and tactics to repel threats from mate poachers (Buss & Shackelford, 1997). Some scientific evidence highlights the value of SST in predicting men's mate switching or remarrying, such as divorcing an unfaithful or post-menopausal wife and remarrying women increasingly younger than they are (Conroy-Beam & Buss, in press). Much remains to be discovered, however, about the contexts that cause men to shift from a long-term to a short-term mating strategy (e.g., a sudden rise in status), or from a short-term to a long-term mating strategy (e.g., successfully attracting a woman at the high end of his mate value range).

Women's long-term mating strategy. Like men, women prioritize good partner and good parent qualities in a long-term mate—intelligence, dependability, emotional stability, adaptability, and good health. Women more than men prioritize economic resources, cues to resource acquisition such as ambition and status, and cues to a man's willingness to channel those resources specifically to her and her children. There is little evidence from recent studies conducted across the globe, from India to China to Norway, that these priorities have changed, despite increased gender equality in some countries.

There is evidence, however, of cultural evolution in women's long-term mating. Modern men and women in mainland China, for example, no longer place as much value on chastity as they did three decades ago (Chang et al., 2011). Women in some cultures, such as Japan, appear to be foregoing long-term mating entirely, choosing to focus instead on their careers. And as gender economic equality continues to increase, we can expect women to be increasingly exacting in their long-term mate preferences, and to be less intolerant of existing mates who fail to fulfill their long-term desires.

Evolved mating psychology in the modern world. Humans evolved in small groups of hunter-gatherers, numbering perhaps 50 to 150 individuals (Dunbar, 1993). Contact with other groups occurred through fusion of smaller groups into a larger group, trade between neighboring groups, efforts at exogamous mating, and small-group warfare. The entire pool of potential mates to which a typical ancestral human would have been exposed would have been perhaps a few dozen. Mating in the modern world, in sharp contrast, exposes people to hundreds of thousands of potential mates, first made possible through population explosion and large urban cities. Internet dating has expanded the mating pool to millions. Cultural technologies have been invented to implement our evolved sexual strategies.

In a real sense, cultural evolution may be taking over where organic evolution left off.

Humans create culturally novel technologies to more successfully pursue their evolved mating strategies. Specialized internet dating sites are designed to exploit different facets of our evolved mating psychology. But simultaneously, these cultural innovations may change our mating psychology in many ways, some known and some unknown, such as whether they delude us about finding a perfect mate who is maximally optimal on each of several dozen dazzling qualities. Our evolved standards of sexual morality may clash with cultural innovations, such as deciding whether viewing pornography, purchasing increasingly realistic sex dolls, or using advanced virtual reality sex technology constitutes infidelity to a long-term mate.

It is an exciting time to study human mating. Sexual Strategies Theory does not furnish the final word on human mating strategies, but does provide a foundation on which the future science of human mating can be built.

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