

The evolution of human mating: Trade-offs and strategic pluralism

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Abstract: During human evolutionary history, there were “trade-offs” between expending time and energy on child-rearing and mating, so both men and women evolved conditional mating strategies guided by cues signaling the circumstances. Many short-term matings might be successful for some men; others might try to find and keep a single mate, investing their effort in rearing her offspring. Recent evidence suggests that men with features signaling genetic benefits to offspring should be preferred by women as short-term mates, but there are trade-offs between a mate’s genetic fitness and his willingness to help in child-rearing. It is these circumstances and the cues that signal them that underlie the variation in short- and long-term mating strategies between and within the sexes.

Keywords: conditional strategies; evolutionary psychology; fluctuating asymmetry; mating; reproductive strategies; sexual selection

Research on interpersonal relationships, especially romantic ones, has increased markedly in the last three decades (see Berscheid & Reis 1998) across a variety of fields, including social psychology, anthropology, ethology, sociology, developmental psychology, and personology (Berscheid 1994). Unfortunately, these diverse perspectives have not coalesced into larger, more integrative theories of how and why relationships function the way they do.

Evolutionary principles can integrate the findings on interpersonal relationships, especially concerning mating and parental behavior. In the evolutionary approach one tries to understand human psychological design – the nature, organization, and operation of domain-specific psychological mechanisms – by identifying plausible constraints from selection pressures during evolutionary history (see Buss 1995). Human behavior is highly flexible and environmentally responsive but “[psychological] designs that produce ‘plasticity’ can be retained by selection only if they have features that guide behavior into the infinitesimally small regions of relatively successful performance with sufficient frequency” (Tooby & Cosmides 1992, p. 101). To understand behavioral flexibility (i.e., the ability to adjust adaptively to specific environmental circumstances), especially in the form of cultural variation, one must understand the psychological architecture that guides social interactions.

Romantic relationships have several unique qualities that distinguish them from other types of relationships. Romantic love, for example, differs from other forms of love (Hendrick & Hendrick 1986). Sexual jealousy has features and consequences that differ from other types of jealousy (Daly & Wilson 1988; Daly et al. 1983). Specialized verbal and nonverbal courtship rituals are observed in virtually all cultures (Eibl-Eibesfeldt 1989). Certain personal

attributes (e.g., physical attractiveness) tend to assume greater importance in mating relationships than in other types of relationships (Buss 1989; Gangestad & Buss 1993 [see also Kenrick & Keefe: “Age Preferences in Mates Reflect Sex Differences in Human Reproductive Strategies” *BBS* 15(1) 1992]). Specific facial and body features predict the attractiveness of mates in nearly all cultures (Cunningham et al. 1990; Jones & Hill 1993; Perrett et al. 1994). Marriage is culturally universal (Daly & Wilson 1988). This

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all suggests that a specialized psychological architecture may underlie and guide romantic interactions. This would make sense considering the importance of mating, reproduction, and parenting throughout evolutionary history. The fact that the ties between mating and reproduction can now be severed by contraception does not imply that evolved psychological mechanisms no longer influence human mating (see Symons 1987; 1992; Thornhill 1991; Tooby & Cosmides 1992). [See also BBS multiple book review of Symons's *The Evolution of Human Sexuality*, BBS 2, 1980.]

Evolutionary theories of human mating have been heavily influenced by research on mating in other animals (see Campbell et al. 1999). These theories – especially Trivers's (1972) theory of sexual selection and parental investment – clarified the major (and slightly different) barriers that males and females in most species must surmount to increase their inclusive fitness. Trivers's work launched the strong theoretical and empirical focus on sex differences in human mating strategies, most of which has tried to explain why women, in comparison with men, tend to be more discriminating when choosing mates and more “restricted” in their sexual behavior. Recently, Buss and Schmitt (1993) have applied and extended many of Trivers's ideas in developing their Sexual Strategies Theory (SST). The focus on sex differences in human mating has been criticized, however, for not explaining why there is more variation in mating-related behaviors within sexes than between (see Gangestad & Simpson 1990) and for not considering how women's control of resources may have influenced the mating strategies of both sexes (see Gowaty 1992a; 1992b; Hrdy 1997).

In this target article, we show how evolutionary principles can extend and deepen our understanding of human mating, and how and why both sexes display both short- and long-term mating tactics in certain contexts. SST (Buss & Schmitt 1993) tries to explain why men tend to adopt short-term mating tactics more often than women. SST also emphasizes that both men and women have evolved mixed strategies involving both long- and short-term matings. After reviewing SST, we will argue that selection produced mixed strategies that depend on environmental circumstances and their cues. Men and women accordingly shift between short- and long-term mating, with considerable variation *within* each sex.

The target article has six major sections. In the first, we discuss basic concepts in evolutionary biology that are relevant to mating, paying particular attention to trade-offs and their adaptive role. In section 2, we summarize previous theoretical claims about sex differences in short-term mating in humans, including Sexual Strategies Theory. We discuss how existing theories fail to incorporate trade-offs to explain fully within-sex variation in mating tactics. In section 3, we discuss how and why genetic fitness and models of good-gene sexual selection should affect mating decisions and behavior. In the fourth section, we review recent evidence concerning good-gene sexual selection in humans. In section 5, we discuss how good-gene and good-provider sexual selection should affect how men and women make trade-offs and hence why individuals engage in different mating tactics. We also discuss how different environmental factors should affect the expression of short- and long-term mating tactics within each sex. Section 6 is a short summary of the target article.

1. Basic evolutionary concepts

1.1. Sexual selection

Sexual selection refers to discrepancies in reproduction rates among individuals resulting from the various “advantages” in mating, independent of advantages resulting from differential survival. Evolutionary biologists have traditionally studied the effects of sexual selection on two kinds of adaptations: (a) intrasexual competitive abilities, and (b) specialized signals that appeal to members of the opposite sex (Andersson 1994). In many species, the number of different mates that one sex can obtain is related directly and strongly to reproductive success, whereas this is less true of the other sex. In most mammals, the former sex is male, and the latter, female (whose reproductive output is limited by internal gestation and lactation). Thus, in most mammals, females are a limited reproductive resource for males, who compete to attract mates. Given this disparity, sexual selection pressures should have acted more strongly on the male intrasexual competitive abilities and the specialized signals appealing to female preferences than vice versa (see Cronin 1991; Trivers 1972). Empirical evidence supports these predictions in many different species (see Trivers 1985).

Theories about the signals or cues that females prefer in mates have focused on two types: (a) attributes that tend to signal qualities of a “good parent” (or a “good provider”), and (b) attributes suggesting that an individual may have “good genes” (Cronin 1991; Gangestad 1993; Miller 1998). Theories of good parenting have been fairly uncontroversial. Those involving good genes, on the other hand, have been debated extensively (see sect. 3). Consequently, most applications of sexual selection to human mating have *not* seriously considered good-gene sexual selection. Recently, however, theoretical and empirical research has indicated that both good-parenting and good-gene selection could have operated on many species (Kirkpatrick 1996; Møller 1994b), particularly those in which males provide substantial parental care (as is true of humans). In what follows, we will argue that these selectional processes are likely to have produced differential mating tactics *within* each sex.

Natural selection also has important implications for human mating. In many species, parental care by males might have evolved to increase offspring fitness directly and, thus, could have evolutionary benefits (Clutton-Brock 1991), particularly in humans (Lancaster & Lancaster 1985). Natural selection could also have led females to obtain the resources necessary to reproduce and compete for additional resources (Gowaty 1992a; Hrdy 1981). Moreover, mating can have benefits that are indirectly derived from reproduction and are not associated with sexual selection. For example, females may induce paternity uncertainty by having multiple mates, possibly leading to more protection or greater tolerance of offspring by different men (Hrdy 1981).

1.2. Adaptations

Adaptations are traits that gave individuals a gene-transmitting advantage over other individuals who had different variants of the traits found in the original environments in which the traits evolved (i.e., in the “environment of evolutionary adaptedness” or EEA; Alcock 1993). They are identified by showing that specific traits or behaviors meet the requirements of “special design” (Williams 1966), evidence that a trait shows specificity, efficiency, and economy for produc-

ing a particular beneficial effect (the “function” of the trait). In many instances, adaptive behavioral flexibility should be facilitated by domain-specific psychological mechanisms (Tooby & Cosmides 1992). These mechanisms should operate according to specific decision rules that are activated by certain environmental cues and that produce efficient, stable, persistent, and finely tuned responses (e.g., specific perceptions, arousal, behavioral reactions) designed to solve specific adaptive problems (e.g., choosing or attracting mates). These decision rules do not have to be consciously formulated or under deliberate control. During puberty, for example, individuals’ physiological adaptations “decide” to produce secondary sexual characteristics. Likewise, the basis of attraction to a potential mate, suspicions about a mate’s infidelity, or interpretations of flirtatious glances are all responses to specific environmental cues that are likely to be governed by implicit, unconscious decision rules.¹

1.3. Evolutionary functional analysis and trade-offs

Evolutionary theory existed for more than a century before Williams’s (1966) groundbreaking work on adaptations. This lag occurred because “classical Darwinists” viewed adaptations almost exclusively in terms of the benefits they bestowed on organisms; associated costs were not fully considered (Cronin 1991). Individuals must invest considerable time, effort, and energy to accomplish the major tasks that most directly affect their inclusive fitness: surviving to reproductive age, reproducing successfully, and rearing offspring to reproductive age. These factors are important not only because they put individuals at risk (and, hence, can decrease their future reproductive success, despite immediate benefits), but because individuals could have used these resources differently. Thus, adaptations have “opportunity costs” associated with them – costs that accrue from lost fitness benefits that might have been achieved by using resources in different ways. A major “modern Darwinian” insight was that one must weigh the benefits *in relation to* the costs to appreciate whether and how adaptations evolved during evolutionary history (using cost-benefit analyses: Parker & Maynard Smith 1991). The fundamental goal of evolutionary analysis is to specify the cost-benefit “trade-offs” that led individuals to allocate their time, energy, and effort to activities in ways that increased their ancestors’ inclusive fitness.

1.3.1. Parenting effort versus mating effort. Trade-offs are illustrated by the differential allocation of effort to parenting versus mating activities. Trivers (1972) defined parental investment as “any investment by the parent in an individual offspring that increases the offspring’s chance of surviving (and hence reproductive success) at the cost of the parent’s ability to invest in other [*including future*] offspring” (p. 139, emphasis ours). This definition implies a basic trade-off. Parental investment can increase the probability that offspring will survive and subsequently reproduce, yielding greater fitness. However, parental investment also has costs. Indeed, according to Trivers (1972), the amount of investment is measured in units of lost benefits of alternative investment (i.e., lost opportunities to invest in other offspring). Individuals who engage in parental effort (the sum total of parental investment in all offspring; Low 1978) could be doing other things with their limited time and energy, such as devoting greater effort to mating (e.g., at-

tempting to attract additional mates). Thus, costs include the lost benefits of potentially productive yet foregone activities (Gross & Sargent 1985).

If fitness gains arising from mating effort (through increased access to more mates) are greater for one sex, selection should tilt the balance toward more mating than parental effort in that sex compared to the other (see Low 1978). Because obtaining more mates (a component of mating effort) cannot produce large fitness gains for females in many species (e.g., Bateman 1948), the average females in those species should devote more time and energy to parental investment than the average male.² Conversely, most males in these species should devote a greater portion of their time, energy, and effort to finding and attracting mates than most females. Hence, trade-offs are implicit in the prediction that males and females should, on average, differ in the total reproductive effort they devote to mating, a prediction that is central to many theories of human mating. These same notions about trade-offs also lead to the expectation that males should *differ from one another* in the total amount of reproductive effort devoted to mating.

As an illustration, consider Burley’s (1986) innovative research on zebra finches. She found that when females mated with males who were experimentally manipulated to be more “attractive,” females increased their parental investment in the resultant offspring. As a result, males actually decreased the amount of parental effort they exerted and, at the same time, experienced greater success in extra-pair matings. Thus, when a male’s mating effort was more productive, he exerted more mating effort at the expense of reduced parental effort. This notion has not been fully incorporated into existing theories of human mating.

2. Existing theories of sexual strategies

2.1. The concept of sexual strategies

Sexual strategies (or mating strategies) are integrated sets of adaptations that organize and guide an individual’s reproductive effort. They influence how individuals select mates, how much mating effort they expend, how much parental effort they expend, and so on. As discussed in section 1.2, sexual strategies are not necessarily formulated consciously or even accessible to awareness.³ Strategies typically are defined as genetically based programs (i.e., decision rules) that individuals use to allocate their somatic and reproductive effort to specific alternative phenotypes (i.e., mating tactics) in adaptive ways. Tactics in turn are the specific actions and behaviors in which individuals engage when pursuing a given strategy. A mating strategy often involves multiple behavioral tactics (Dominey 1984).

Consider, for example, Trivers’s (1972) hypothesis that males in many biparental investing species may invest heavily in offspring, yet remain open to low-cost mating opportunities with other females. This is a *mixed* mating strategy involving multiple behavioral tactics in which each tactic is displayed with a certain frequency. If each tactic is cued by specific environmental stimuli (e.g., the prolonged absence of a mate, having short-term sex only with mates who have certain attributes, seeking short-term sex only when such efforts have paid off in the past), the strategy is *conditional*.

2.1.1. Conditional strategies. In the last two decades, evolutionary theorists have begun to acknowledge that selec-

tion pressures should not have produced a single “best” mating tactic (or mixture of tactics) for males and females in most species. Instead, selection should have fashioned considerable phenotypic diversity in mating (Gross 1996). Guided by concepts from game theory (Maynard Smith 1982 [see also Maynard Smith “Game Theory and the Evolution of Behaviour” *BBS* 7(1) 1984]) and the theory of evolutionarily stable strategies (Dawkins 1980; Parker 1984), evolutionary biologists are now documenting how having alternative mating tactics gives individuals of each sex differential reproductive fitness in various species. Although relatively little theory and research have focused on the mating behavior of human beings, hundreds of studies have confirmed that males and females in a wide range of species display alternative mating tactics that reflect conditional strategies (Gross 1996). Burley’s (1986) finding that male zebra finches’ relative allocation of parental effort and extra-pair mating effort is contingent on their attractiveness is a good illustration of a conditional strategy.

Conditional strategies have five main properties (see Gross 1996): (a) They involve different behavioral tactics that are consciously or unconsciously “chosen” by an individual; (b) the choices between tactics are “made” in response to specific features or cues in the environment, often an individual’s status or attractiveness relative to other individuals; (c) all individuals are genetically monomorphic (i.e., they are genetically designed to enact the same tactics); (d) during their evolution, the average adaptive values of different tactics were not equal except at a “switchpoint” on a continuum of environmental input (e.g., individuals’ relative status) where the costs and benefits of each tactic balanced out; and (e) during their evolution, the chosen tactic tended to yield higher fitness for the individual than other tactics given current environmental conditions. Thus, the environmental conditions moderate the fitness gains of pursuing different tactics (e.g., exerting parental effort, pursuing short-term matings), thereby affecting the optimal allocation of effort to different tactics.

If males differ in the conditions under which they engage in different tactics, they are enacting *alternate conditional strategies*. Although alternate strategies can be noncontinuously distributed in a population (e.g., if certain males never invest in offspring and always seek short-term mates), they are usually distributed continuously. This should occur if males differ in how long they tolerate their mate’s absence before pursuing other mates, or if males differ in the degree to which they expect extra-pair mates to have certain desirable attributes (Dominey 1984). Alternate strategies can reflect genetic polymorphisms (see Gross 1996). Although such polymorphisms exist in nature and may underlie certain variations in human mating strategies (see Gangestad & Simpson 1990; Wilson 1994), we focus on conditional strategies in this article.

2.2. Sex differences in sexual strategies

Most evolutionary theories of mating have focused on the different strategies purportedly adopted by men and women. Based on Trivers’s (1972) theorizing, Wilson (1978) suggested that men and women differ along an assertive-coy dimension:

The . . . conflict of interest between the sexes is a property of not only human beings but also the majority of animal species. Males are characteristically aggressive, especially toward one

another and most intensely during breeding season. In most species, *assertiveness is the most profitable male strategy*. During the full period of time it takes to bring a fetus to term, from the fertilization of the egg to the birth of the infant, one male can fertilize many females but a female can be fertilized by only one male. Thus if males are able to court one female after another, some will be big winners and others will be absolute losers, while virtually all healthy females will succeed in being fertilized. It pays males to be aggressive, hasty, fickle, and indiscriminating. In theory it is more profitable for females to be coy, to hold back until they can identify males with the best genes. In species that rear young, it is also important for the females to select males who are more likely to stay with them after insemination. . . . Human beings obey this biological principle faithfully. [p. 129; emphasis ours]

More recent theories of sex differences in mating have incorporated similar notions. Perhaps the most ambitious of these new theories is Buss and Schmitt’s (1993) Sexual Strategies Theory (see also Buss 1994b; 1998a; 1998b). Buss and Schmitt’s theory emphasizes that both men and women should have evolved tactics for obtaining long-term mates and investing in offspring. Similar to Wilson’s (1978) theory, however, SST predicts that men should have evolved to seek multiple mates in particular:

What specific adaptations should be expected in the evolved sexual psychology of men to solve the problem of gaining sexual access to a number of women? One first-line solution to the problem of number can be expected in desire: *Men may have evolved over human evolutionary history a powerful desire for sexual access to a large number of women* (cf. Symons, 1979). (Buss & Schmitt 1993, p. 208; emphasis ours.)

This prediction is based on an implicit cost-benefit analysis that involves trade-offs between different activities that were presumably optimal for men and women in evolutionary history. According to SST, men experienced, on average, a greater net benefit than women from attempting to attract multiple mates. This prediction has received empirical support in several recent studies. For example, men report desiring four times as many sex partners in the next five years as women do (Buss & Schmitt 1993).

2.3. A sex-specific universal?

Evidence indicates that men do, on average, desire and seek short-term mates more than women do. Wilson (1978), however, makes an even stronger prediction about this sex difference. He claims that males should benefit by being “aggressive, hasty, fickle, and indiscriminating.” This should hold true for *all* males in a species. Although Buss and Schmitt (1993) do not explicitly claim that all men have a “powerful desire for sexual access to a large number of women,” they do not qualify their statement to indicate that some men may not. Clearly, a mean sex difference – even a large one – does not imply a near-universal propensity in each sex. Indeed, a mean sex difference could exist even when the modal response of each sex is similar (e.g., when the distribution for one sex is more variable and skewed than for the other sex).

Sex differences in the desire for multiple sex partners and interest in engaging in short-term mating are moderate in magnitude. Buss and Schmitt (1993) report γ s (i.e., the number of within-sex standard deviations on which the means of the two sexes differ) for each effect they found. We converted this statistic to percentages of variance accounted for on each variable by sex. Sex accounts for 16%

of the variance in seeking short-term mates, 9% of the variance in the number of sex partners desired within a specified time, and 20% of the variance in the probability of consenting to sex after knowing an attractive, opposite-sex person for a given length of time. In a recent meta-analysis, Oliver and Hyde (1996) found that the mean sex difference in interest in casual sex accounted for 25% of the variance. Across different college samples, we have found that sex accounts for 8%–20% of the variance in expressed interest and willingness to engage in sex without commitment (Simpson & Gangestad 1991a).

Although these effect sizes are fairly large by conventional standards (Cohen 1977), substantial amounts of within-sex variation and overlap exist between the distributions of women and men. For example, despite the mean sex difference in the desire to have sex without commitment (Simpson & Gangestad 1991a), approximately 30% of men express *less* favorable attitudes about casual sex compared to the median attitudes of women. Substantial overlap also exists for many other measures, including interest in sex with multiple partners and optimal time before having sex (see Miller & Fishkin 1997). Generic claims that women desire certain mating arrangements whereas men desire others raise the questions “which men?” and “which women?” (Gowaty 1992b). If the within-sex variation in mating strategies is adaptive, the environmental contingencies in the EEA that led men and women to adopt short-term versus long-term mating tactics must be specified.

Sexual Strategies Theory acknowledges that both sexes can and do exhibit short-term and long-term mating tactics (i.e., that human mating strategies are mixed); indeed, this is one of SST's defining features. Buss and Schmitt (1993) also explicitly note that within-sex variation in mating tactics may be adaptive. Nonetheless, within-sex variation has received less theoretical attention than sex differences have and it remains an “unresolved issue” (Buss & Schmitt 1993) within SST (see also Buss 1998a). Moreover, to state that “[m]en who lack mechanisms such as a desire for a variety of partners . . . would have been out-reproduced by men who successfully solved [the problem of partner number] entailed by the pursuit of a short-term mating strategy” (Buss 1998a, p. 24) is to imply that evolution would not have favored a male strategy entailing *little* desire for multiple mates. However, as we shall see, *most* men may have benefited reproductively by having little interest in pursuing multiple mates. Both the desire for multiple mates and the lack of this desire should have been beneficial under certain conditions.

2.4. Cost-benefit considerations

If aggressiveness and interest in short-term mating is the “most profitable” strategy for men, why do only some men pursue short-term mates? Differential cost-benefit trade-offs should have led men to pursue more mates *on average* than women. Consequently, men should, on average, dedicate more time and energy to mating effort than women. These premises, however, do not lead to the conclusion that the best strategy for most males would involve high mating effort, whereas the best strategy for most females would entail high parental effort. A consideration of trade-offs suggests that the best strategy for men may not always – or even usually – be to devote effort to pursuing short-term mates (see Kitcher 1985 [see also BBS multiple book re-

view of Kitcher's *Vaulting Ambition: Sociobiology and the Quest for Human Nature*, BBS 10(1) 1987]; Maynard Smith 1982). Similarly, the best strategy for women may not always be to devote less effort to pursuing short-term mates than the average male.

From our perspective, the basic notion that men, on average, evolved to engage in greater mating effort than women correctly assumes that some ancestral males *could* have increased their fitness by trying to attract multiple mates. However, the more stringent notion that the best evolutionary strategy for most men should have been to pursue multiple mates assumes that most men were successful at short-term mating. This is a dubious assumption. Men's short-term mating success should have depended partly on which attributes women preferred and desired in short-term mates. Relatively few men are likely to have satisfied these preferences. Thus, for some men, one cost of engaging in short-term mating would have been the loss of opportunities to engage in parental investment (which human males also evolved to do: see Alexander & Noonan 1979; Lancaster & Lancaster 1985). If short-term mating effort generated poor payoffs for men who did not have the attributes most women desired in short-term mates, these costs should have outweighed the benefits of pursuing short-term mating. Hence, the most profitable mating strategy for the *typical* man may have been to devote most of his reproductive effort to enhancing the phenotypic quality of his offspring by investing heavily in a single mate's offspring, despite the fact that a few men with certain desirable attributes were even more successful when they adopted short-term tactics.

Consider a parallel example where the currency of profit is money rather than fitness. Suppose that brain surgeons make more money than everyone else does. Clearly, it is not the “most profitable” money-making strategy for everyone to decide to become a brain surgeon. Only so many people can become brain surgeons; hence, most people would be bound to fail. Instead, the most profitable strategy for most people would be to select careers that provide them with the most money, given their abilities and, in competitive markets, their chances of success.

If the most evolutionarily profitable strategy for men depended in part on the attributes each man possessed (e.g., his ability to attract multiple, short-term mates), what sexual strategy should have evolved in men? The answer is a conditional mating strategy (see Gross 1996; Trivers 1972). Most men would probably have profited from substantial investment in a primary mateship (or small set of mateships), investing fairly heavily in subsequent offspring. When men could obtain short-term, opportunistic matings with other women (often other men's primary mates), they could have profited by pursuing the sex-typical strategy outlined by Wilson (1978) and Buss and Schmitt (1993). However, when they could not, men should have shifted greater amounts of time, energy, and other resources to long-term mating (including mate guarding) and parental investment to attract and retain one mate and derive the benefits of parental investment. Although men may have “evolved over evolutionary history [*the capacity for*] a powerful desire for sexual access to a large number of women” (Buss & Schmitt 1993, p. 208; our addition and emphasis), the desire for short-term mating should be expressed conditionally, and it should be observed infrequently under conditions when only a few men are able to attract short-term mates. The key

adaptation should be a set of decision rules about when and how to allocate reproductive effort wisely and contingently, rather than a universal desire for short-term mating. As noted above, this is not a novel notion. Conditional strategies are a central topic in behavioral ecology (see Krebs & Davies 1993, on “making the best of a bad job”; see also Dawkins 1980; Gross 1996). However, the possible role of conditional strategies in human mating has received relatively little attention (see Buss 1998a; Buss & Schmitt 1993). We accordingly propose that evolution generated conditional strategies in *both* sexes, resulting in a plurality of mating tactics.

Trivers (1972) also noted that “the optimal [mixed strategy] is likely to differ for different males” (p. 146). Trivers was in fact the first evolutionary theorist to acknowledge that selection could have favored adaptations that led some males to devote very little time and effort to short-term mating. It is ironic that his classic article is often cited as suggesting that the most profitable strategy for males should be to pursue short-term mating almost universally.

What attributes have women evolved to desire in short-term mates? It is important to identify these attributes because they should moderate strategy choice in men. In the next section, we suggest that good-gene sexual selection may be central to answering this question. As we shall see, these selection pressures may also have important implications for understanding variation in women’s interest in short-term mating.

3. Genetic fitness and sexual selection

In many species, males provide little or no parental investment. Yet even in these species, females are selective and consistently prefer certain males over others as mates. Good-gene sexual selection (GGSS) can explain female mate preferences in species that do not have much paternal investment (Cronin 1991). According to models of “good gene” selection, females have evolved to prefer males who possess indicators of viability and good condition, that is, adaptive attributes that might be passed on to their offspring through genetic inheritance.

3.1. Genetic variation in fitness

For mate preferences based on indicators of heritable fitness to evolve, additive genetic variance must underlie fitness (i.e., fitness must be transmitted genetically across generations). Historically, GGSS has been controversial because population geneticists have assumed that selection typically reduces the heritability of fitness to nearly zero (e.g., see Kirkpatrick’s [1985; 1986] arguments against the “sexy son” [Weatherhead & Robertson 1979]). Recent empirical and theoretical developments, however, have led even the harshest critic to acknowledge that GGSS can and probably has occurred in a variety of species (see Kirkpatrick 1996).

The new empirical development is the ability to estimate the actual amount of genetic variation in fitness (or fitness components) in natural populations. The most relevant measure of genetic variation is the additive genetic coefficient of variation (CV_a), the genetic standard deviation of a trait, standardized by the trait mean and multiplied by 100 (Houle 1992).⁴ Houle has argued that the CV_a s of fitness traits (e.g., longevity, fecundity) in natural populations are

typically *greater* than those of ordinary morphological traits (e.g., height). Human fecundity, for example, has a CV_a of 15 to 20 (Burt 1995), 4 to 5 times *greater* than that of human height. Values exceeding 10 have been estimated for fitness traits in other organisms (Burt 1995; Houle 1992), compared to values around 5 for ordinary traits or traits under stabilizing selection (Houle 1992; Pomiankowski & Møller 1995). Fitness itself has been estimated to have a CV_a of between 10 and 30 in natural populations of many species (Burt 1995).

New theoretical developments are based on the notion that the amount of genetic variance in fitness within a population is the result of two opposing forces: natural selection (which removes genetic variation) and forces that degrade an organism’s fitness, such as mutations and environmental change (both of which enhance genetic variation: Fisher 1958). As long as deleterious mutations and environmental change are negligible, natural selection should keep genetic variance near zero. Recently, population geneticists have begun to model and estimate the amount of genetic variance in fitness that can be maintained by mutations alone. The genome-wide mutation rate (i.e., the number of new deleterious mutations per organism) is about 1 in *Drosophila*, a rate that explains at least half of its estimated genetic variance in fitness (a CV_a of 6–17; Charlesworth 1990; Charlesworth & Hughes 1998). The genome-wide mutation rate in humans is probably higher, given our larger genome (Charlesworth 1990). Thus, mutations probably account for a human CV_a of fitness of 10 or more. Hence, mutations alone might produce more genetic variance in fitness than is observed in most ordinary traits.

Recent theory has also drawn attention to phenomena that induce rapid change in the selective environments of organisms. Pathogens are one set of the strong selective forces operating on long-lived organisms such as humans. Because parasites evolve in response to their hosts’ defenses against them, no set of host defenses is evolutionarily stable; these defenses are always being challenged by changing parasites. These rapid shifts in the selective environments of hosts ensure not only that hosts will never be free of maladaptations caused by parasites, but that they will vary in their ability to resist parasites. Hence, host-parasite coevolution maintains genetic variance in host fitness (Anderson & May 1982; Haldane 1949; Hamilton 1982; Tooby 1982).

It is important to emphasize that alleles that are good genes at one point in time need not be intrinsically better than alternative alleles. Host-parasite coevolution imposes changing selection pressures on host genes, maintaining heritable fitness in individuals. Thus, an allele that is a good gene today might be selected against in future generations, and an allele that is currently selected against could become a “good gene” in the future. Because no gene is inherently better than an alternative one, the population does not become more fit through selection.

In combination, mutation and host-parasite coevolution can maintain a substantial amount of genetic variance; as a result, fitness traits contain relatively large amounts of genetic variance in natural populations. Moreover, recent theoretical models indicate that large amounts of genetic variance in fitness not only can but *do* produce GGSS (Kirkpatrick 1996; see also Andersson 1986; Charlesworth 1988; Grafen 1990; Heywood 1989; Iwasa et al. 1991; Pomiankowski 1987).

3.2. Markers of heritable fitness

The degree to which individuals harbor mildly deleterious alleles or are less pathogen-resistant must be inferred from phenotypic markers (e.g., “advertisements”: Zahavi 1975). GGSS must operate through honest signaling, which explains why only certain features tend to be valid indicators of individuals’ underlying conditions and, potentially, their genetic fitness (Grafen 1990; Zahavi 1975). If an attribute is a marker of heritable fitness, sexual selection should favor new genes that simulate the valued feature, even in individuals who do not actually have high fitness. Thus, “cheaters” – individuals who display the selected phenotypic traits or behaviors but do not have high fitness – may invade the population. Over time, selection should eliminate these attributes as valid cues of heritable fitness, and preferences for them should diminish. Under certain conditions, however, an attribute’s link with heritable fitness can remain honest and stable. In particular, an attribute can remain an “honest” advertisement when individuals who have deleterious alleles or who are less pathogen-resistant cannot develop or maintain the attribute without incurring substantial costs. Attributes that meet this criterion are those that conditionally “handicap” individuals who have mutations or are less pathogen-resistant.

Both mutations (Pomiankowski et al. 1991) and pathogens (Hamilton & Zuk 1982) divert an individual’s energy and resources. Hence, honestly advertised traits tend to be energetically costly because individuals who have mutations or are less pathogen-resistant cannot develop such traits without diverting valuable resources from competing demands (e.g., sustaining their immune systems: Folstad & Karter 1992). In peacocks and other birds with extravagant features, costly handicaps include exaggerated sexual ornaments and colorful plumage (Zuk et al. 1990). In many mammals, they include large size and increased musculature resulting in sexual dimorphism for size in polygynous species, including primates (Alexander et al. 1979).

This type of selection can be understood in terms of cost-benefit analysis. A costly trait confers certain benefits. For example, males who have the trait may be preferred as mates. However, having such a trait also involves costs because the resources used to develop the trait could have been used for other purposes. At some point, the marginal gains of investing in the costly trait begin to diminish, and individuals should no longer be selected to invest in the trait beyond that point. The benefits of sexual selection can be maintained if males with different levels of heritable fitness maximize their benefits relative to their costs (i.e., maximize their outcomes) at different levels of the costly trait (Grafen 1990).

Trivers (1972) proposed that intrasexual competitive abilities may have evolved to be valid cues of heritable fitness. Successful intrasexual competition, such as winning physical fights, requires developing the potentially costly attributes used in competition (e.g., muscularity) and the expenditure of considerable energy during competition. Just as highly viable males should be more capable of enduring “handicapping” traits than less viable males, they should also be able to devote more energy to developing the physical tools needed for successful intrasexual competition. Females may in turn have evolved to pay attention to the outcomes of intrasexual competition to assess male fitness (Andersson 1994).

3.3. Tests of good-gene sexual selection

To test GGSS, researchers should show that direct indicators of individuals’ genetic fitness are associated with their attractiveness as a mate (particularly as a short-term mate). Unfortunately, perfect indicators of fitness do not exist. Tests of good-gene selection must therefore rely on indirect, fallible markers of genetic fitness. The best available measure may be fluctuating asymmetry.

Fluctuating asymmetry (FA) reflects the degree to which individuals deviate from absolute perfect symmetry on bilateral features (e.g., in humans, both ears, both feet; in other species, bilateral fins, bilateral tail feathers) for which the signed right versus left differences have a population mean close to zero and are nearly normally distributed (Møller & Swaddle 1997; Van Valen 1962). Asymmetry is believed to reflect deviations in developmental design resulting from the disruptive effects of environmental or genetic abnormalities encountered during the lifespan (i.e., developmental instability: see Lerner 1954; Palmer & Strobeck 1986; Parsons 1990; Soule 1982; Thoday 1955; Waddington 1957). Because these disturbances lower reproductive fitness, pronounced asymmetry reflects maladaptation (Møller & Swaddle 1997). Recent meta-analyses and reviews have shown that greater asymmetry is associated with lower fecundity, slower growth, and poorer survival in many species (Leung & Forbes 1996; Møller 1997; Thornhill & Møller 1997; see also Clarke 1998, and a subsequent analysis by Møller 1999). FA should be a good marker of genetic fitness because an individual’s degree of asymmetry should be affected primarily by (1) mutations (that cause lower metabolic efficiency and imprecise development), and (2) diseases (that reflect an individual’s pathogen-resistance; Møller 1992). Consequently, FA probably reflects both genetic and nongenetic variation in fitness. Because sexual selection should lead females to mate with males who have phenotypic traits that signal greater fitness, the association between FA and mating success has been studied in many species. A recent meta-analysis of these studies reveals that, on average, more symmetrical individuals have greater mating success (Møller & Thornhill 1998a).

GGSS is of course not the only form of selection that could explain these findings. In some species, more symmetrical males may provide greater material benefits (e.g., more direct and better parental care or more physical protection of young). In addition, females may find less symmetrical males less attractive to avoid contracting infectious diseases from them. However, three novel sets of findings suggest that GGSS may have occurred in humans.

First, a recent meta-analysis indicates that, across many species, symmetry is partly heritable (Møller & Thornhill 1997). Modeling the relationship between asymmetry and underlying developmental imprecision in these data, Gangestad and Thornhill (1999a) have estimated that the additive genetic coefficient of variation of developmental imprecision is approximately 15 to 20, about the same size as other fitness traits and much *greater* than ordinary morphological traits (e.g., height: see Houle 1992). If part of this genetic variance is associated with fitness, the favored status of symmetrical males may in part reflect the operation of good-gene selection (Kirkpatrick 1996).⁵

Second, in some species in which symmetry predicts male mating success, more symmetrical males are favored as extra-pair mates, even when they provide little or no ma-

terial benefits. For example, although male and female European barn swallows mate seasonally and rear offspring together, their rate of extra-pair paternity is approximately 35% (Møller 1994b). More symmetrical male barn swallows are the main beneficiaries of extra-pair mating, yet they do not provide material benefits that enhance the reproductive success of their female mates (see Møller 1994b).

Third, in some species, more symmetrical males also provide fewer material benefits to their primary mates. For example, more symmetrical male barn swallows spend less time feeding their offspring than do less symmetrical males, and they do not compensate for their lack of time with greater feeding efficiency. In a recent review of 18 bird species, Møller and Thornhill (1998b) have documented an association between extra-pair paternity and the extent to which attractive males engage in direct parental care. Specifically, when the rate of extra-pair paternity is high (and, thus, when males can benefit more from trying to attract extra-pair mates), attractive males perform a smaller proportion of offspring feedings than less attractive males. Exerting greater extra-pair mating effort should yield larger payoffs for more attractive males, and this is evident in the time they fail to spend engaging in a competing activity: providing direct parental care. We suggest that this type of trade-off also occurs in humans. Over evolutionary history, men who had indicators of genotypic quality should have experienced larger gains in fitness payoffs than men who lacked these indicators. Moreover, men should have evolved to “decide” conditionally to allocate more versus less effort to mating or parenting, depending on the degree to which they possess these features.

4. GGSS in humans?

New evidence indicates that GGSS might have operated on ancestral humans. Most of this evidence indicates that FA is systematically associated with male mating success in humans. Although FA is not the only valid marker of heritable fitness, it currently appears to be the best marker. As we discuss below, other, more visible features (such as physicality, social dominance, and intrasexual competition tactics) are likely to be the proximate cues that “advertise” an individual’s genetic fitness. We focus on FA because rival models of selection do not capture the complex relations predicted from developmental imprecision.

4.1. FA and sexual behavior

If women evolved to prefer men who exhibited indicators of genetic fitness, more symmetrical men should have more lifetime sexual partners (see also Perusse 1993; 1994). Thornhill and Gangestad (1994) measured the symmetry of men and women on seven bilateral features (foot, ankle, hand, wrist, elbow, ear width, and ear length) using digital body calipers. They then aggregated these measures (each standardized by feature size) to form a global index of FA. With the effects of age partialled out, more symmetrical men reported more lifetime partners than less symmetrical men, $r = -.32$. Controlling for potential artifacts (e.g., height, ethnicity, marital status) strengthened this effect, partial $r = -.38$. These effects have also been estimated in several other studies. The weighted correlation in a sample of more than 500 men is $-.21$ ($p < .0001$), and the latent

correlation between developmental imprecision and male partner number is approximately $-.38$ (Gangestad & Thornhill 1999a). Waynforth (1998) has found a similar correlation ($-.23$) in a sample of Mayan men in Belize and has also documented that more symmetrical men have higher fertility. Because women should be less inclined to convert intrasexual competitive advantages into increased numbers of mates (see Trivers 1972), no relation between women’s FA and their number of lifetime sex partners was predicted, and none has been consistently found in several studies (see Gangestad & Thornhill 1997a).

Given that these studies are based on self-report data, the findings could be explained by a tendency for more symmetrical men to exaggerate their past sexual behavior. In one study, therefore, men’s scores on narcissism (a measure that reflects self-aggrandizement tendencies: John & Robins 1994) were partialled out. Controlling for narcissism did not attenuate the relation between men’s FA and their number of lifetime sex partners, partial $r = -.27$ (Gangestad & Thornhill 1997b).

4.2. Men’s extra-pair sex and FA

Extra-pair sex (i.e., sex outside a current, ongoing relationship) is one form of short-term, opportunistic mating. If women evolved to desire men with greater heritable fitness (independent of the investment and resources these men provided), more symmetrical men should have more extra-pair partners (see Bensch & Thornhill 1979; Smith 1984). Gangestad and Thornhill (1997b) found that men’s FA does predict their number of extra-pair sex partners, $r = -.17$ (reflecting a latent correlation between extra-pair partners and developmental imprecision of about $-.36$; Gangestad & Thornhill 1999a). Once potential artifacts were controlled (e.g., social status, socioeconomic status [SES] in family of origin, anticipated future salary), the correlation between FA and extra-pair sex increased slightly. Neither men’s social status nor their resources (as indexed by their SES and their anticipated future salary) predicted their frequency of extra-pair sex. Although Perusse (1993) has found that men with higher status report having more sex partners than men with lower status, this effect did not hold for married men in his sample. Thus, it is unclear whether men with higher status (e.g., wealthier men) have more extra-pair mates than men with lower status.

4.3. Women’s extra-pair sex and FA

More symmetrical men should also be preferred as women’s extra-pair mates (i.e., mates chosen by women who already have primary mates, regardless of whether the man has a primary mate). Gangestad and Thornhill (1997b) found that men’s FA predicted the number of times they were chosen as extra-pair partners by women who were simultaneously involved in other, ongoing relationships, $r = -.26$ (reflecting a latent correlation between developmental imprecision and these partners estimated to be $-.60$; Gangestad & Thornhill 1999a).

4.4. FA and associated traits

What personal attributes should mediate the link between men’s FA and their number of lifetime sex partners? One possibility is physical attractiveness (Feingold 1990), which

Buss and Schmitt (1993) have found is important to women when they evaluate short-term mates and Scheib (1999) has found is particularly important to women choosing extra-pair mates. In fact, a man's attractiveness in short-term mating contexts is just as important to women as a woman's attractiveness is to men when men evaluate long-term mates. Buss and Schmitt (1993) claim that this finding is consistent with the notion that attractiveness might have been an indicator of genetic fitness in ancestral environments, but they say little about this possibility.

If preferences for attractiveness evolved in response to GGSS, attractiveness should be correlated with markers of heritable fitness (such as FA). Gangestad et al. (1994) measured individuals' FA and then had coders rate their physical attractiveness from facial photographs. After controlling for potential artifacts (e.g., age, height), FA significantly predicted men's facial attractiveness, $r = -.33$, but not women's, $r = -.17$, *ns*. That is, more symmetrical men were rated as more physically attractive. This sex difference has been replicated (Thornhill & Gangestad 1994), but has not been found consistently (Gangestad & Thornhill 1997a). Across several studies, the correlation between facial attractiveness and body FA is significant but rather small (see Gangestad & Thornhill 1997a). Studies of the association between facial symmetry and facial attractiveness have similarly yielded mixed but positive results overall (e.g., Grammer & Thornhill 1994; Kowner 1996; Mealey et al. 1999; Scheib et al. 1999; see also Møller & Thornhill 1998). Gangestad and Thornhill (1999a) have estimated that the latent correlation between developmental imprecision and male facial attractiveness is about $-.28$.

Because facial attractiveness mediates only part of the relation between men's FA and their sexual history, Gangestad and Thornhill (1997a; 1998a) tested three other potential mediators, namely, three sexually dimorphic traits involved in intrasexual competition: (1) *Body mass* – Humans show moderate sexual dimorphism, consistent with their purported ancestral polygyny (Alexander et al. 1979); (2) *Physicality* – A measure of men's muscularity, robustness, and vigor, as rated by both men and their romantic partners; and (3) *Social dominance* – A measure based on the California Adult Q-Sort. Once again, a relation was found between men's FA and their number of lifetime partners, $r = -.29$ (estimated by causal modeling). In addition, all three traits associated with intrasexual competition were predicted by men's FA, estimated r s = $-.31$, $-.39$, and $-.39$, for body mass, physicality, and social dominance, respectively. The indirect effects mediated through these traits accounted for more than 70% of the total effect of FA on the lifetime number of partners. As expected, women's FA did not predict their number of lifetime partners, and it did not correlate with any of the 3 intrasexual competitive traits, average $r = -.06$.

The fact that men's FA covaries with traits that should have facilitated intrasexual competition in ancestral environments (i.e., physical intimidation of competitors) is consistent with other research showing that more symmetrical men engage in fights with other men more often, particularly fights they initiate (Furrow et al. 1998). Besides affecting the outcomes of intrasexual competition, these traits may serve as cues that women use to evaluate men as potential short-term mates. This would explain why all three traits mediate the link between men's FA and their sexual history.

Because men who have traits that facilitate intrasexual competitive success should benefit by comparing themselves directly with their competitors, Simpson et al. (1999) predicted that, when competing for a woman, more symmetrical men would use direct competition tactics (e.g., directly comparing themselves with, and derogating, their competitors). After measuring their FA, Simpson et al. had men compete with other men for a lunch date with an attractive woman. Each man was asked a series of questions over a video system by a female interviewer (actually a videotaped experimental assistant) located in another room. After the interview was finished, the female asked each man to tell the "competitor" (ostensibly located in a different room) why she should choose him instead of the competitor. Each interaction was videotaped and coded for specific intrasexual competition tactics. Relative to less symmetrical men, more symmetrical men were more likely to directly compare themselves with and belittle the competitor, $r = .49$. These results support the hypothesis that more symmetrical men should engage in direct intrasexual competition tactics. They also provide further evidence about the proximate cues that may "advertise" genotypic quality (indexed by men's FA).

Finally, intellectual ability may be a marker of developmental precision and health. In two studies, Furrow et al. (1997) found an association between a measure of fluid intelligence (Cattell's Culture-Fair Intelligence Test) and FA, mean $r = -.23$ (the estimated latent correlation with developmental imprecision was $-.56$; Gangestad & Thornhill 1999a). The size of this effect did not differ across the sexes.

4.5. Evidence for women preferring symmetrical men for their gametes

The fact that more symmetrical men have more mates might not be explained by GGSS exclusively. More symmetrical men could be advantaged because of the superior material benefits more viable males typically provided in the EEA or because they have success in intrasexual competition (Kirkpatrick & Ryan 1991). However, additional evidence (reviewed in sects. 4.5.1–3) suggests that these alternative selectional processes cannot fully explain the greater short-term mating success of more symmetrical men. This evidence suggests that women's preferences for more symmetrical men may be specifically "designed" to favor their gametes.

4.5.1. Female orgasm and sperm retention. Baker and Bellis (1995) have conjectured that women's orgasms evolved to manipulate sperm competition via differential sperm retention. If male extra-pair mates in the EEA provided advantages to offspring above and beyond the investment and tangible resources they offered (through good genes or genetic diversification; see Smith 1984), selection could have favored adaptations that biased sperm competition in favor of conceptions with extra-pair mates who had higher genetic fitness. Baker and Bellis (1995) report that women who have both an in-pair (primary) partner and an extra-pair partner have patterns of orgasms that facilitate the retention of sperm from the extra-pair partner.

If Baker and Bellis are right, indicators of a partner's genetic fitness should be cues that lead women to have more frequent sperm-retaining orgasms during extra-pair sex. Thornhill et al. (1995) correlated women's frequency of or-

gasm during sexual intercourse with their current mate's FA, while controlling for his SES, anticipated future salary, age, and observer-rated physical attractiveness. Women experienced more orgasms if their partner was more symmetrical, $r = -.27$. More important, high sperm-retention orgasms (i.e., those occurring close to ejaculation; Baker & Bellis 1995) were significantly correlated with the men's degree of symmetry. Aside from their partner's physical attractiveness, no other male feature correlated with the frequency of female orgasms. Analyses on a larger sample have replicated this effect (Møller et al. 1999). These findings are consistent with GGSS and difficult to explain in terms of other theories. (For evidence that female orgasm favors dominant males in Japanese macaques, see Troisi & Carosi 1998.)

4.5.2. Women's olfactory preferences across their reproductive cycle. If women tend to choose extra-pair partners for their gametes, compared to sex with their primary partners, women's extra-pair sex should occur during the most fertile time of their reproductive cycles. Bellis and Baker (1990) found precisely this pattern in a sample of British women. If women's patterns of extra-pair sex thus favor the sperm of extra-pair mates, this effect might be mediated by women's preferences for specific attributes valued in extra-pair partners, especially those associated with symmetry.

Olfactory cues affect mate preferences strongly in many species (Alcock 1993). Based on evidence that women's olfactory sensitivities and preferences change across the menstrual cycle (Grammer 1993), Gangestad and Thornhill (1998b) hypothesized that women should find the smell of more symmetrical men more appealing during ovulation. Men were measured for FA and then asked to wear a non-scented T-shirt for two nights. Women smelled each shirt (blind to all other characteristics of the men), and rated how attractive they found the odor of each shirt. Women's fertility was estimated from their probability of conception when they participated in the study, based on medical data (Jöchle 1973). Women taking oral contraceptives were excluded from the analyses. The shirts worn by more symmetrical men were rated as smelling better than those worn by less symmetrical men, but only among women who were in the fertile phase of their reproductive cycle, $r = -.30$. Indeed, women's probability of fertility correlated .54 with their preferences for the scents of more symmetrical men. This effect has been replicated in a larger, separate sample (Thornhill & Gangestad 1999), where the correlation between fertility risk and preference for the scents of symmetrical men was .42. Statistically controlling for a number of factors (e.g., men's number of showers) increased the effect size.⁶ These results confirm a very specific prediction that can be derived only from GGSS and provide further evidence about the proximate cues that may "advertise" male symmetry.

4.5.3. Women's long-term and short-term mate preferences. Buss and Schmitt (1993) claim that the characteristics women prefer in long-term and short-term mates are quite similar. According to SST, women use short-term mating to evaluate men as potential long-term partners or for mate-switching. Women's long-term and short-term mate preferences are *not* identical, however. As discussed earlier, even Buss and Schmitt (1993) have found that women place greater emphasis on men's physical attrac-

tiveness and physical prowess when evaluating them for possible short-term relationships. Scheib (1999) found that women place greater emphasis on physical attractiveness when evaluating men as extra-pair partners.

Gangestad et al. (1999a) examined women's mate preferences by asking them to rate men who had been videotaped during an interview conducted by an attractive woman. After observing each man, women rated his attractiveness as a potential long-term mate and short-term mate (either as a one-time sex partner or as an extra-pair mate). Women's sociosexual orientation (based on their Sociosexual Orientation Inventory [SOI] score; Simpson & Gangestad 1991a) was measured as well. Women with an unrestricted sociosexual orientation are more willing to have short-term relationships (i.e., they are more interested in short-term mating). Women with a restricted sociosexual orientation, in contrast, are less willing to have sex without commitment and emotional closeness (i.e., they are more interested in long-term mating; see Simpson & Gangestad 1991a; 1992).

Compared to restricted women raters, unrestricted women raters preferred more symmetrical men, particularly for short-term relationships. Indeed, unrestricted women's short-term mate attractiveness ratings correlated .40 with men's symmetry. Correlations between restricted and unrestricted women's ratings of long-term mate attractiveness and men's symmetry, as well as correlations between restricted women's ratings of short-term mate attractiveness and men's symmetry, were all nonsignificant. These findings indicate that more symmetrical men have (or display) features that are preferred in short-term mates by those women who are most willing and likely to engage in short-term mating – unrestricted women. They also clarify how women's preferences may produce greater sexual success in more symmetrical men. These results would not be expected if more symmetrical men offered superior material benefits in long-term relationships.⁷

5. Strategic pluralism

According to the model we have presented, men's allocation of effort to short-term mating during evolutionary history should have been contingent on their ability to satisfy the short-term mate preferences of women. Women's short-term mate preferences, in turn, should have been influenced by GGSS. Thus, men's tendency to engage in short-term mating should be a direct function of their genetic fitness (indexed by FA), whereas men's propensity to invest in single, exclusive long-term relationships should be inversely related to their genetic fitness.

5.1. FA and attitudes toward engaging in casual sex

Simpson and Gangestad (1991a) developed the Sociosexual Orientation Inventory (SOI) to measure individual differences in willingness to engage in sex without closeness and commitment. If asymmetrical men have less desire to engage in short-term sex, as our model of conditional strategies predicts, men's FA should correlate negatively with the SOI. As predicted, the mean correlation across several samples is $-.20$. Men's SOI scores do not correlate with either the SES of their family of origin or their expected salary in five years.

5.2. FA and investment in an exclusive relationship

In a sample of long-term dating couples, Gangestad and Thornhill (1999b) tested whether more symmetrical men tend to make less of an investment in their ongoing relationships. Partners answered questions about their own and their partners' behavior in their relationships and then completed the Relationship-Specific Investment Inventory (RSI; Ellis 1998). The RSI measures 10 sets of acts pertinent to the partner and relationship maintenance: Being Expressive/Nurturing, Being Committed, Giving Time, Being Sexually Proceptive, Investing Money, Being Honest, Providing Physical Protection, Being Attentive in Social Contexts, Having a Good Relationship with the Partner's Family, and Not Sexualizing Others. Some of these acts (e.g., giving time and attention to the partner) detract from mating efforts outside the relationship. These acts, therefore, should correlate negatively with men's symmetry.

Path analyses tested models in which both self-reports and partner reports were treated as markers of men's investment. When men's resource potential (indexed by their anticipated future salary), women's rated physical attractiveness, and women's level of investment in the relationship were controlled, more symmetrical men provided less investment than did less symmetrical men, $\beta = .26$. More symmetrical men were particularly less honest with their partners, sexualized other women more, and spent less time with their partners. This pattern of lower investment should facilitate efforts to mate with women outside the current relationship.

The one component of investment that symmetrical men provided more of was physical protection, particularly their reported ability (as opposed to their reported willingness) to provide their current partner with greater physical protection. Because the ability to provide physical protection may involve the development of attributes that are also useful in intrasexual competition, providing this form of investment is not likely to interfere with men's short-term mating. If men who possess markers of good genes do "compensate" their partners with some kind of material benefits, the most likely candidate is physical protection. Hrdy (1981) and Smuts (1985) have claimed that physical aggression from men other than fathers may have been one of the major dangers to offspring in the EEA. To reduce these threats, women may have either mated with multiple partners to confuse paternity or developed male-female friendships, particularly with socially and physically dominant men. Mesnick (1997) and Wilson and Mesnick (1997) have recently argued that women may have evolved to prefer protective males primarily to receive protection from other aggressive males, which could have enhanced women's fitness directly.

5.3. Variation in women's mating strategies

Thus far we have concentrated on adaptive variation in men's sexual tactics. However, women also vary considerably in their openness to, and willingness to engage in, short-term mating (Simpson & Gangestad 1991a). We now address adaptive reasons for this variation.

According to the model we have presented, the attributes that made men valuable as short-term mates in the EEA may have differed from those that made them valuable as long-term mates. Short-term or extra-pair mates should have offered genetic benefits that were often un-

available from long-term mates. Moreover, long-term mates who offered more genetic benefits may have provided fewer material benefits. Because of variation in their circumstances (discussed in sects. 5.6 and 5.7), women should have differed in the extent to which they could have benefited from obtaining genetic versus material benefits. If some women could have appreciably improved their fitness by mating with men who offered better genetic benefits, these women should either have preferred long-term mates who had markers of genetic fitness or they should have engaged in short-term mating (especially opportunistic extra-pair matings) with males who had such indicators, even if it meant "trading-off" or risking the loss of material benefits they could have garnered from a long-term mate. Conversely, if other women could have enhanced their fitness by obtaining mates who provided (or could provide) superior material benefits, these women should have pursued long-term mates who were able and willing to provide the material benefits they most needed. Such women should have refrained from extra-pair mating, sacrificing some genetic benefits they might otherwise have obtained. The differential value of genetic versus material benefits across women should accordingly have produced adaptive variation in women's mating tactics.⁸ (For a related discussion on avian mating, see Petrie & Kempanaers 1998.)

5.4. Evidence that differential valuation of men's attributes predicts women's mating

In section 4.5.3 we described a study examining women's preferences for men's symmetry in long-term and short-term mating contexts (Gangestad et al. 1999a). It showed that women with a less restricted sociosexual orientation (i.e., more willing to have short-term sexual relationships) found symmetrical men more attractive, particularly as short-term mates. These results indicate that variation in women's willingness to engage in short-term mating is associated with – and perhaps driven by – their stronger preference for indicators of genetic fitness in men.

Several additional lines of evidence also suggest that women who engage in short-term mating especially prefer men who display indicators of genetic fitness. First, women who are willing to engage in short-term mating (i.e., unrestricted women) care more about a man's physical attractiveness than do women who are less willing to engage in short-term mating (Simpson & Gangestad 1992). Second, when given a choice between dating a romantic partner who is very attractive but not highly reliable/loyal versus one who is highly reliable/loyal but only average in attractiveness, women who are more willing to engage in short-term mating (unrestricted women) tend to choose the more attractive/less reliable male, whereas women who are less willing to engage in short-term mating (restricted women) tend to choose the less attractive/more reliable one (Simpson & Gangestad 1992).

5.5. Environmental factors and sexual strategies

Our model suggests that women should vary in their "exchange rate" between a partner's genetic fitness (indexed by FA) and his investment, whereas men should vary in their "exchange rate" between short-term mating effort and long-term parental investment. Environmental factors

should influence women's assessments of the exchange rate between a prospective male's parenting qualities and his heritable fitness. In environments where biparental care was crucial to infant survival, male parenting qualities should have had more beneficial effects (Andersson 1994). Conversely, in environments with prevalent pathogens, male genetic fitness may have had more beneficial effects (because of both the importance of pathogen resistance and the decreased marginal value of heavy parental investment when mortality rates are high; see Kaplan 1996). If ancestral women were repeatedly exposed to these contrasting environments, they should have evolved to make trade-offs between investment qualities and indicators of good genes contingent on specific environmental conditions. Factors that influenced this exchange rate may have differentiated (a) populations of individuals, producing differences in the mating systems across different groups of women (i.e., within different cultures; see Tooby & Cosmides, 1992, on "evoked culture"), and (b) women within a population, producing differences in the mating preferences and behaviors of women in a given group of people.⁹

5.6. Environmental factors producing differences between populations

5.6.1. Factors influencing the value of men's genetic quality. Several factors may have affected the value of men's genetic fitness. According to principles of host-parasite coevolution (Hamilton 1982), pathogen prevalence should have been one critical factor. In environments where pathogens were prevalent, women should have benefited more from mating with men who had good genetic qualities that made them more pathogen resistant. Although additional work is needed, several lines of research are consistent with this notion.

First, besides conveying information about female fertility, physical attractiveness may also contain cues about a person's health, pathogen resistance, and perhaps genetic fitness (Symons 1979). Gangestad and Buss (1993) tested whether preferences for attractive mates might have evolved through parasite-driven sexual selection. Men and women from 29 countries around the world rated the importance of several mate attributes, including their preference for a "good-looking" mate (see Buss 1989). Pathogen pressure at each geographical location was estimated from information about the prevalence of eight different parasites (see Low 1990a). Across the 29 countries, both men and women in regions containing more pathogens placed greater importance on a prospective mate's attractiveness, even when latitude, geographical region, and mean income were controlled, partial $r = .76$. This finding does not of course demonstrate that host-parasite coevolution necessarily influenced sexual selection in humans. Attractiveness could have been more important in regions with more parasites because of direct selection against mating with diseased individuals (Kirkpatrick & Ryan 1991).

Second, women in pathogen-prevalent environments should be more willing to trade off features associated with exclusive parental care. Indeed, across the 29 cultures, parasite prevalence correlated negatively with the mean ranked importance of 4 attributes relevant to direct and exclusive parental care: "dependable character," "pleasing disposition," "emotional stability and maturity," and "desire for home and children," $r = -.41$ (Gangestad 1993). Thus,

individuals place less weight on these attributes in environments containing more pathogens. Whether these findings reflect the increased value of physical attractiveness or an independent devaluation of these male attributes remains unclear.

Third, in environments where pathogens are more prevalent, women should trade off indicators of good genes for exclusive paternal investment. In other words, a higher degree of polygyny should be seen in pathogen-prevalent environments (see Gangestad 1993). Low (1990a) correlated the degree of polygyny with parasite-prevalence in nearly 200 societies of the Standard Cross-Cultural Sample (Low 1988; 1990a; Murdock & White 1969). With latitude and geographical region held constant, polygyny was more common in societies where pathogens were more prevalent.¹⁰ Hence, variation in parasite prevalence might be partially responsible for the variation in desired mate attributes and associated mating strategies across cultures (see Tooby & Cosmides 1992).

5.6.2. Factors influencing the value of men's parental effort. Several factors should also have played a part in determining the influence of men's parental effort on infant mortality and their later reproductive success. For example, in environments where the primary causes of infant mortality were infectious diseases (rather than inadequate parental care), paternal effort should have had less impact on offspring fitness. In contrast, when infant viability was strongly tied to biparental care (e.g., when women could not provide for all the nutritional needs for their offspring), paternal care should have had a greater impact on offspring fitness.

Women's access to resources should also have influenced their need for – and the value of – male parental investment (Gowaty 1992a; 1992b). Because parental investment often has diminishing marginal returns (see Cashdan 1993), men's resources may have been less important when women had sufficient resources of their own. Hence, polygyny should be more prevalent in societies in which women have more access to resources. Low (1990b) correlated indicators of women's ability to care for both themselves and their infants independently with measures of polygyny across nearly 200 cultures in the Standard Cross-Cultural Sample. As predicted, polygyny is more common in cultures where women have more control over resources.

We do not know how women's control over resources in ancestral environments affected their mate preferences, but their participation in current economies does predict the importance women place on physical attractiveness in men. In the cultures surveyed by Buss (1989), women's mean preference for physical attractiveness in a mate was positively correlated with the proportion of women who were involved in the economy. However, women's preferences for qualities related to parental care did *not* correlate with their economic participation (Gangestad 1993).

Across the cultures surveyed by Buss (1989), Eagly and Wood (1999) have found that women's preference for men's earning potential is predicted by a measure of women's "empowerment" (United Nations Gender Empowerment Measure; United Nations Development Programme 1995). As women's empowerment (indexed by their earnings, their representation in legislative government, and their involvement in professional positions) increases relative to men in cultures, women place increasingly less value on the earn-

ings of a mate. However, women do not place less emphasis on men's physical attractiveness (nor do men place less emphasis on women's attractiveness) as women's empowerment increases. Although Eagly and Wood interpret these findings in terms of domain-general behavioral processes and responses to gender roles, they are also consistent with an ecologically contingent, conditional mating strategy in which women moderate their mating tactics and preferences in response to specific environmental inputs (e.g., women's control of resources; see Low 1990b).

5.6.3. Effects on men's tactic choice. How women evaluate men and how they make trade-offs should influence which mating tactics men adopt. In environments where male parenting qualities are needed and valued, women should be less likely to engage in short-term and extra-pair mating. In response to this, men should devote greater effort to parental investment, and variance in men's reproductive success should be reduced (i.e., a larger proportion of men should have offspring). On the other hand, in environments where men's genetic fitness is needed and valued, women should be more willing to pursue short-term mating. Consequently, men should devote greater effort to short-term and extra-pair mating, and variance in men's reproductive success should increase (see Low 1990a; 1990b).

In environments where biparental care is not as crucial, even men with lower genetic fitness might benefit from channeling some of their effort to short-term and extra-pair mating (perhaps by attempting to "deceptively" advertise genetic quality). Under these circumstances, men's increased efforts to display their "quality" could result in an escalated war of attrition (Maynard Smith 1982), which could be facilitated by testosterone-based somatic growth and aggressive behavioral displays. Thus, the fiercest intra-sexual competition among men may not occur over resources relevant to parental investment, as SST might predict. Rather, it may occur when status displays that signal a male's genetic fitness are contested (see Daly & Wilson, 1988, for a discussion of how men's face-saving tactics often lead to homicide).

5.7. Environmental factors producing differences within populations

5.7.1. Differences caused by differential exposure to cues signaling the value of parenting. If some women are exposed to environments that require paternal investment whereas others are not, within-population differences in mating preferences and tactics should emerge. Belsky et al. (1991) have proposed that patterns of parental care experienced during childhood may affect adult mating tactics (see also Chisholm 1996; Simpson 1999). Insufficient parental responsiveness to their needs as infants (possibly caused by harsh, demanding environments) should lead individuals to adopt short-term mating tactics better suited for environments in which stable pair-bonds are not needed or anticipated. Conversely, adequate parental responsiveness should result in long-term adult mating tactics more appropriate for environments in which biparental care and stable pair-bonds are needed and expected.

5.7.2. Differences due to women's phenotypic qualities. Women's personal characteristics may also lead them to

value different qualities in mates. In many circumstances, parental investment has decreasing marginal returns: the more investment an offspring has received, the less beneficial the next "dose" (see, e.g., Cashdan, 1993; for important exceptions, see Kaplan 1996). Especially when men's and women's investments in offspring are similar (rather than complementary) in form, women who can make more of an investment on their own show less of a need for additional paternal investment. Consequently, women may have evolved to focus more on a man's genetic fitness when their own access to independent resources increased (Gowaty 1992a), making them more willing to engage in short-term mating.

Correlations between women's sociosexual orientation and their personality traits provide indirect support for these conjectures. Unrestricted women (who are more likely to engage in short-term mating) tend to be more socially dominant, more extroverted, and less harm-avoidant (Gangestad & Simpson 1990). Each of these traits should facilitate the acquisition and maintenance of independent resources. Hrdy (1981) and Gowaty (1992a) have suggested that women's access to resources through cooperation, competition, and social influence should have been an integral component of their fitness in the EEA. These personality traits may have helped unrestricted women acquire their own resources and, thus, pursue short-term mating tactics.

Based on these notions, one might expect the value women ascribe to their mates' resources to diminish as their own access to resources increases. This association has not been found: Women with high-paying jobs tend to value resources as much as or more than women with lower paying jobs do (e.g., Buss 1989; Townsend 1989; Wiederman & Allgeier 1992). These findings contrast with those of Eagly and Wood (1999), who found that, across cultures, women's access to resources and power is associated with a lower rated importance of mates' financial success. Because what women learn about the value of a mate's resources is shared within a culture, the effects of women's access to resources within a culture may differ from the effects of women's access to resources across cultures (see Eagly & Wood 1999). Another possibility is that Eagly and Wood's finding is not the result of women's access to monetary resources (only one component of the Gender Empowerment Measure they used) but to their access to power. Power and the ability to affect outcomes through social influence may have been important facets of women's circumstances for which they evolved contingent strategies, whereas their ability to accumulate wealth in modern cash economies may not have been.

In sum, environmental factors should influence women's mating tactics. Pathogen prevalence, for example, should increase the value women place on men's genetic quality, whereas the need for biparental care should increase the value they place on men's parental effort, particularly for women who do not have independent access to resources. Depending on environmental conditions, therefore, women should make trade-offs between male genetic quality and parental investment in adaptive, ecologically contingent ways. Women should vary in the exchange rate between men's genetic quality and their long-term investment, whereas men should vary in the exchange rate between short- and long-term mating. As a result, most men should adjust their mating strategies in response to what women value.

6. Summary and conclusions

Mating tactics are highly variable in both men and women and have evolved to be contingent on environmental factors. Complete theories of mating strategies must account for these individual differences and contextual effects. We have proposed that these phenomena cannot be fully understood without considering the nature of the trade-offs that underlie mating decisions in humans. We suggest that good gene sexual selection, in concert with good-parenting sexual selection, may have generated the variation and contextual effects associated with the short- and long-term mating tactics witnessed in both sexes.

Given the demands of biparental care during evolutionary history, both men and women were selected to use long-term mating tactics and invest in offspring. However, they were also selected to use ecologically contingent, conditional mating strategies, dedicating some effort to short-term and extra-pair mating under specific conditions. Women may have evolved to trade off evidence of a man's genetic fitness for evidence of his ability and willingness to invest in offspring. The specific mating tactics and preferences women adopted, however, depended on the nature and quality of their local environment. If the local environment was difficult and demanded biparental care, women placed more weight on the investment potential of prospective mates and less weight on indicators of their genetic fitness. As a result, a larger proportion of women adopted long-term mating tactics almost exclusively. If, on the other hand, the pathogens were prevalent in the local environment (or the environment signaled the importance of the genetic fitness of offspring), women placed more weight on indicators of the genetic fitness of prospective mates. In such environments, a larger proportion of women were willing to engage in short-term, extra-pair matings, allowing them to gain genetic benefits from men who provided less parental investment at the risk of losing parental investment from their primary mates. The mating tactics and preferences of women accordingly reflected the nature and quality of the environments in which they lived.

Whereas women "tracked" their environment, men tracked and adjusted their mating tactics and preferences to the behavior of women (Thiessen 1994). If most women expected heavy paternal investment, most men (especially those who displayed less fitness) offered more and perhaps exclusive parental investment, dedicating a greater portion of their effort to long-term mating tactics and parental investment. As a result, variance in men's mating success was reduced. If women's "demand" for genetic benefits increased, some men (especially those advertising such benefits) dedicated more effort to short-term, extra-pair mating tactics, thereby increasing variance in mating success among men. Only a small proportion of men (i.e., those who displayed the most fitness) were able to carry out short-term tactics successfully at all times, regardless of the environmental factors to which women were responding.

Many of the unique predictions derived from this model have been supported by recent empirical data. Although our notions extend our understanding of the strategic plurality of human mating in many ways, this account of the ties between evolutionary theory and human mating strategies remains far from complete.

NOTES

1. Not all environment-response linkages are evolved. Many are learned. Learning, however, can reflect a set of implicit, evolved decision rules (see Mayr 1974).

2. In certain species, males engage in more parental effort than females, in which case sexual selection pressures operate more strongly on females than males (Trivers 1972). The selection pressures that lead to different amounts of parental effort for the sexes are not yet fully understood (for one treatment, see Parker et al. 1972). Moreover, as we will discuss, there are circumstances in which mating with multiple mates can benefit females even in species in which they invest in offspring more than males do (see also Hrdy 1981).

3. These effect sizes may be attenuated by unreliable measurement, particularly for single-item measures. Our 3-item measure of attitudes toward casual sex has a reliability of nearly .8 (Simpson & Gangestad 1991). If sex accounts for 8%–20% of the variance in this measure, it should explain 10%–25% of the variance in an error-free measure. Single items in this domain may have as little as 50% reliable variance (estimated using the Spearman-Brown formula; Anastasi & Urbani 1998). Hence, sex may account for 20%–40% of the reliable variance underlying single-item measures of optimal number of future sex partners and willingness to have sex with an unknown partner. Naturally, the reliable variance in these measures may not all be valid, as some may reflect differences in social desirability responding. The sex difference in Clark and Hatfield's (1989) naturalistic field study of willingness to engage in unsolicited sex with a stranger (using a measure less susceptible to social desirability than lab measures) was one of the largest effects ever documented, accounting for about 60% of the variance. One possible reason this sex difference is so large is that men are willing to accept unsolicited sex even when they are not exerting effort to obtain short-term mates. The robustness of this result needs to be replicated, however. Moreover, this sex difference may partly reflect differences between men and women in the fear of physical harm from opposite-sex strangers rather than differences in interest in short-term mating per se (see Hrdy 1997). Overall, although sex accounts for a large amount of the variance in measures of interest in and willingness to actively pursue short-term mating, it appears to explain less variance – in some cases substantially less – than occurs *within* each sex. (For comparison purposes, sex accounts for about 50% of the variance in adult height.) Moreover, the distributions of men's and women's interest in pursuing short-term, opportunistic matings appear to overlap substantially.

4. The CV_a is evolutionarily relevant because the potential rate of evolution ("evolvability" or the proportionate change in a character's mean in the population per generation) is a function of the absolute amount of genetic variance (specifically, the square of the CV_a). The sheer amount of environmental variance in a trait does not affect the rate of the trait's evolution. The heritability of a trait is its genetic variance divided by total (genetic plus environmental) variance. Because this measure standardizes a trait's genetic variance (relevant to its evolvability) in relation to its environmental variance (not relevant to its evolvability), heritability is a less evolutionarily relevant index than the CV_a . Fitness characters tend to have lower heritabilities (around .25 on average; Mousseau & Roff 1987) than ordinary morphological traits do, but not because they have low genetic variance. Rather, they tend to have very high genetic variance, as well as very high environmental variance. Because fitness characters have very high genetic variance, they have more potential to evolve than ordinary morphological traits do, despite lower heritabilities (Houle 1992).

5. The fluctuating asymmetry of an individual trait (e.g., ear width) is often a very weak indicator of underlying developmental imprecision (Gangestad & Thornhill 1999a). Even the composite FA measure (which consists of 10 aggregated traits, and was used in many of the human studies we cite) is estimated to correlate only about .5 with underlying developmental imprecision. This makes the modest associations between FA and other

traits (e.g., mating success; Møller & Thornhill 1998) all the more impressive.

6. It could be argued that women find more symmetrical men more appealing because they are looking for long-term mates who will provide them (and subsequent offspring) with greater material benefits. Even though more symmetrical men may be more capable of providing certain benefits (e.g., physical protection), the reproductive cycle studies indicate that women find the smell of more symmetrical men more desirable *primarily* when they are ovulating (that is, when gaining material benefits is not an issue). From the standpoint of adaptive design, these data strongly suggest that women find symmetrical men more attractive than less symmetrical men for reasons beyond potential resource acquisition.

7. We are not suggesting that obtaining “good genes” from certain men is the *only* possible fitness benefit of short-term mating available to women. Buss and Schmitt (1993), for example, have proposed that some women may use short-term mating to evaluate and attract long-term mates. The evidence we present, however, provides support for the former function.

8. Because women also vary in their relative mate value, they should differ in the amount of benefit they receive from men. Certain highly valued women may be able to obtain both high material benefits and high genetic benefits. For most women, however, the genetic benefits and exclusive investment benefits that can be obtained from mates should correlate negatively within the most desirable set of mates a woman can attract (Gangestad 1993).

9. Previously, we suggested that women’s relative evaluation of genetic benefits and material benefits may partly reflect genetically polymorphic, alternate strategies (see Gangestad & Simpson 1990). Although this possibility remains plausible, variation in women’s mating strategies may be more strongly governed by environmental conditions that moderate the relative value of genetic versus material benefits.

10. Low (1990a) suggests that healthy men in pathogen-prevalent regions may have multiple mates because they can provide better paternal care. We suggest that men who have better fitness indicators should invest less in their offspring than men with poorer indicators.

Strategic Pluralism Theory (SPT) provides a much needed correction for the overly simple idea that evolution will have a predictable and consistent effect on human mating strategies. Under this simplistic view, men are expected to be promiscuous and to compete for women, whereas women should select mates from numerous competitors and value monogamy. Instead, SPT proposes that mating strategies will vary according to environmental conditions. Such variation accounts for a range of mate preferences and mating strategies being used by both men and women, and leads us to expect women to compete for men as well as vice versa. I believe the authors make a convincing case for SPT, providing evidence that is particularly remarkable when one considers that cultural influences on mating are certain to overlay, and could mask, any evolutionary tendencies. Still, there are additional complexities that, if incorporated within SPT, may make this theory an even better predictor of mating tactics and preferences.

As a prelude to these comments, it should be noted that sexual selection should not always be biased towards either “good-parenting” or “good-genes,” in part because these are not negatively correlated traits. For instance, size and strength are cues to good-genes in males but also indicate good-parenting as in the greater ability to defend infants. It appears that there are two somewhat distinct sets of “signs” or “cues” that can be used to evaluate these traits (e.g., fluctuating asymmetry for good-genes but not for good-parenting) and would suffice to allow a pluralism of strategies. Nonetheless, males should always value *both* traits, to some extent, since both signal increased probability of genetic transmission (i.e., more viable offspring and better parental care). While good-parenting cues may be irrelevant to a female pursuing short-term mating, the ideal long-term partners would be high on both traits.

Whereas SPT is quite cognizant of individual differences in potential mates (especially their genetic fitness and, in the case of males, their likely parental investment), the theory as presented is insufficiently attentive to important individual differences among the “selectors” (i.e., the individuals expressing mate or mating preferences). Specifically, the competence of “selectors” should modify the valuation of traits in potential mates and the strategy pursued. “Competence” is used here in a broad sense to refer to health, physical prowess, cognitive ability, and other traits that determine individuals’ ability to fend for themselves and their offspring. The more competent a woman is in this sense, the more risk she can take in the form of extra-pair mating, because losing a mate due to detection of infidelity is less likely to harm her children. Likewise, the parental contributions of mate(s) will have less value for more competent women, so such women are likely to place a relatively high value on genetic fitness rather than on good-parenting. More competent males, by virtue of being able to be good providers with less cost (e.g., proportionately less expenditure of resources) and/or being better at deception, may be more likely to pursue short-term mates while at the same time maintaining long-term mating(s). Similarly, in good environments, males with highly competent female partners will be able to put more effort towards additional sexual relationships without reducing overall parental investment to a harmful level (cf. Cashdan 1993).

Age is a detectable factor that will be correlated with competence. Given the very long period of dependency in human offspring, younger women are more likely to live long enough to raise a child. Older women become increasingly less likely to survive childbirth and to have various reproductive complications (cf. Ales et al. 1990). In addition, older women and men are more likely to have reduced competence due to a longer period of exposure to parasites, accidents, and other risks. Thus, aging should tend to modify the optimal mating strategy of women, making them increasingly concerned with paternal ability and investment. More generally, the fewer additional offspring a woman can, or is likely, to produce, and the more challenging the conditions for successfully rearing children, the more that woman should be concerned with the good-parenting indicators in potential mates. This shift is

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Variation in optimal human mating strategies: Effects of individual differences in competence and self-regulatory mechanisms

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Abstract: Several suggestions are made for revision of Strategic Pluralism Theory (SPT). One revision requires recognition of the impact of individual differences in cognitive and behavioral competence on optimal mating strategy. In addition, SPT may need to incorporate certain self-regulatory processes such as the impact of widespread valuation of mates with one trait on their availability.

analogous to that seen along the continuum of *r*- to *K*-selection in inter-species comparisons (Pianka 1970).

In addition to the variations in individuals' competence, other factors should be added to SPT as presented in the target article. One such factor is the support/resources provided by one's social web. For instance, females with additional support for child-care from their mothers or others may safely reduce the time and effort expended on child rearing (Fairbanks 1993) or, perhaps, place reduced value on good-parenting when selecting mates.

Another missing factor is the self-regulatory processes that are likely to influence optimal strategies. For example, if adverse environmental conditions increase the desirability of men with signs of good-parenting, there will be more competition for such men. Assuming a balanced sex ratio in the population, men high on parental caregiving will become scarce (already mated) while there should be lowered competition for men with apparently good genes. Consequently, the optimal strategy for some women will change as the population of unmated males shifts, with men higher on good-genes becoming more available. The end result for SPT, however, is unclear. For one thing, these self-regulatory mechanisms are likely to affect behavior but should not alter preferences. Women should still *prefer* men high on good-parenting but may not be able to *select* ("catch" or find) one. More important, the strategy pursued by one sex should tend to alter that used by the other. In this case, if most women are putting a high valuation on good-parenting, more males can be expected to display good-parenting since for many males this will be a more effective mating strategy. (For the opposite case, note that it is not possible to alter one's signs of good-genes, with the exception of grooming and related activities that have limited effectiveness.) Certainly some complex web of self-regulatory processes can be expected that includes both intra- and inter-sexual adjustments.

As Gangestad & Simpson conclude, SPT is incomplete. The fact that they were able to find a wide variety of empirical data to support their version of SPT may indicate that their model tends to incorporate at least some of the most powerful operative forces. Nonetheless, the future will produce more complex models with better empirical support.

Strategic pluralism: Men and women start from a different point

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Abstract: Gangestad & Simpson's (G&S's) analysis of strategic pluralism is welcomed as a balance to the current emphasis on between-sex variation. It could have been clarified by acknowledging the extent to which males and females represent fundamentally different mating strategies, since this affects how we view within-sex strategic variation. The distinction between conditional and alternative strategies could also have been highlighted.

Both evolutionary and standard social science accounts of sex differences in social behavior (e.g., Archer 1996; Eagly 1995) tend to overlook within-sex variations. Gangestad & Simpson's (G&S's) target article provides a welcome counterweight to this by considering variations among men and women as alternative or conditional reproductive strategies. It is an important contribution that has implications for a number of research areas, such as personality, mate selection, and psychological sex differences. This commentary concerns three points: the emphasis on between versus within sex variations; the distinctions between types of alternative strategy; and the characterization of reproductive strategies as short or long-term.

To highlight within-sex variation, G&S sought to play down sex

differences. For example, the effect sizes quoted for sex differences in preference for multiple sex partners were expressed as proportions of the variance accounted for. Meta-analysts (e.g., Eagly 1995; Rosenthal 1990) have argued that this is a misleading way of expressing magnitude of effects, not only because it is (as indicated in note 3) subject to measurement error, but also because relatively small proportions of the variance in important attributes can have large effects in practice. When converted into the statistic more commonly used in meta-analyses, effect size (*g*), the differences cited ranged from .58 to 1.01, all of which are regarded as large effects for the social sciences generally (Cohen 1988). As acknowledged, these effect sizes were found in questionnaire studies, where they are likely to be attenuated by social desirability and measurement. Again, as acknowledged (in note 3), the more ecologically valid study of Clark and Hatfield (1989) found a massive sex difference in preference for multiple sex partners. In order to emphasise within-sex variation, it is not necessary to play down sex differences by citing them in terms of proportion of the variance accounted for. Sex is after all another alternative reproductive strategy, and there are clear principles why we would expect men and women to be different in their reproductive and social behavior.

The answer to the question posed in section 2.4 (why all men do not pursue short-term matings) was answered by Symons (1979) thus: because women do not let them. On this view, it is not that most men adopt a long-term strategy in preference to a short-term strategy; it is that most men do not have the opportunity to pursue short-term strategies, but they would if they could. The brain surgeon analogy does not fit this example, since being a brain surgeon requires talent and training, whereas switching from a long to a short term strategy only requires opportunity.

In G&S's discussions of within-sex strategies, it was not always clear whether these were situation-dependent (conditional) strategies, or – as their brain surgeon analogy implied – stable individual differences (alternative strategies). Alternative strategies include the two sexes, and the morphological specializations found within the male sex in some species (such as ruffs: van Rhijn 1974). It would have been helpful to have distinguished between the two at all times. For example, it was clear that women's short-term mating strategies were considered as conditional strategies, as was men's FA, but in other cases alternative, situation-dependent, strategies seem to have been intended.

G&S refer to long and short term strategies as if these are equivalent in the two sexes. The use of these terms also suggests that it is only the duration of staying with the mate that is important, whereas time is only relevant because it is associated with parental investment. It is the degree of parental investment that distinguishes reproductive strategies (Trivers 1972). Therefore high and low investing strategies would be more appropriate labels than short and long term. When considered in these terms, it is clear that the two sexes cannot be regarded as equivalent. A female mammal may be able to engage in a short-term mating in the sense that she can then have nothing further to do with the male, but this does not necessarily represent low parental investment by this female. If she is impregnated, it will have been a mating with a high future parental investment. In this sense, only a male can truly walk away cost-free. By referring to such matings as short-term for the female, G&S were defining the female's strategy in terms of the investment of the male with whom she is mating. Perhaps this was intended; if so, it is worth further exploration, because it represents an important way in which the two sexes differ that would have implications for characterising within-sex variations. Male and female are themselves specialised reproductive strategies, and any consideration of further specializations within each sex would benefit from using this as a starting-point.

Accounting for female strategic variation

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Abstract: Gangestad & Simpson's theory accounts for the existence of male strategic variation admirably well, although it does not specify the precise nature of the adaptation linking male developmental stability to strategic pluralism. In contrast, female strategic variation remains elusive. Empirical data suggest that genetic variation partly underlies such variation, but the causes of female strategic differences largely remain unexplained.

Gangestad & Simpson (G&S) offer a compelling but ultimately incomplete theory of strategic variation in human sexual life histories. The theory is particularly well explicated for men: Men vary in their genetic quality, largely due to mutational pressure in the context of parasite resistance dynamics, which impede allelic fixation. Men with good genes have low levels of developmental instability, and some indicators of developmental instability are detectable. Women prefer men with low levels of developmental instability, and hence such men have more mating opportunities and can invest less in particular women. By G&S's theory, then, genes do not influence strategic variation via direct pathways (i.e., by affecting the neural substrates of sociosexuality independent of developmental instability). Such "direct pathway" genes may exist, but they are not the kind of genes that G&S are concerned with. Indeed, much of the genetic variation implicated by their theory can in different contexts cause either lesser or greater developmental instability, and hence can lead to either greater or lesser mating effort.

Although the theory is impressive in its demonstrated ability to link ideas from evolutionary genetics with individual differences psychology, it leaves unanswered important questions about sexual strategies. For example, the theory does not provide much guidance about the ontogeny of male strategic differences. Men must possess an evolved program that allows them to adjust their sexual strategies on the basis of information that is correlated with developmental instability. The specific content of the program is unclear, however. For example, the program might run only once, prior to birth, with the brain somehow inferring developmental stability and directing development accordingly – males with developmental stability directed toward mating effort and those with developmental instability directed toward investment in their partners. A more plausible alternative is that males continuously and unconsciously monitor their ability to succeed in a high mating-effort strategy. If so, then we would expect men's psychology and behavior to track relevant changes. For example, when men win lotteries or earn millions on the stock market, their mating opportunities surely increase. Do their psychological preferences change accordingly? The inability of G&S's theory to answer such questions does not make the theory less likely to be true, because the theory appears to be mute with respect to ontogeny. Nevertheless, it is an important limitation of the theory.

Another limitation of the theory is its inability to explain female strategic variation. According to the theory, women seek both investment and good genes. However, men with the best genes offer less investment than other men do, and most women are thus forced to make trade-offs. This fits in well with their theory of male strategic variation – so far so good. However, this observation does not necessarily lead to female strategic variation. For example, women might have evolved a uniform mechanism to assess men's investment ability and genetic quality, to calculate strategic trade-offs, and to place men on a single dimension of mate value. By this scenario, all women would have similar preferences and would not vary in their willingness to trade investment for genetic quality.

This is not our world, however. With respect to sociosexuality, or willingness to engage in casual sex (Simpson & Gangestad 1991a), women appear to be specialists rather than generalists.

For example, we recently compared Australian women in the top and bottom quintiles of a measure of sociosexuality (Bailey et al., in press). Those in the top quintile were much more likely than those in the bottom quintile to have had sex with someone they had met the same day (59% versus 6%), and they were also much more likely to have been sexually unfaithful to a steady partner (48% versus 3%). Furthermore, women who require less emotional commitment from their sex partners are more demanding in other respects, such as partners' physical attractiveness (Mikach & Bailey 1999; Simpson & Gangestad 1992). This observation is consistent with the idea that some women trade commitment for good genes, but it leaves unanswered the question of why women vary in the trade-offs they are willing to make.

According to G&S's theory, male sociosexual variation is inevitable, because not all men can win the genetic lottery. But an analogous account of female sociosexual variation – which G&S do not attempt – is neither theoretically coherent nor empirically supported. It is unclear whether the optimal strategy of women with good genes should differ from that of other women, and no correlates of women's FA have been established. In their target article, G&S focus instead on environmental explanations of female sexual strategies. However, the most sensible hypothesis, that women with adequate resources can best trade investment for good genes, is not supported by their review.

In an earlier article, Gangestad and Simpson (1990) proposed that female sociosexual variation is maintained via frequency-dependent selection. By this account, women with unrestricted versus restricted approaches to casual sex have specialized to exploit different niches. Furthermore, the value of pursuing each strategy plausibly depends on the relative frequency of women who also pursue it. Consistent with this hypothesis, female sociosexuality appears to be moderately heritable (Bailey et al., in press). The likelihood of strategic heritable variation is controversial, however, because recombination prevents fortuitous combinations of genes from persisting long enough for polygenic morphs to evolve (Tooby & Cosmides 1990a). A two-strategy system with a binary genetic switch can evolve more easily. Such a system implies that restricted and unrestricted strategies should be typologically distinct, but this has not yet been demonstrated.

My focus on the incompleteness of G&S's theory should not obscure the fact that the theory is an important advance. The theory is well articulated and has generated some surprising findings. Furthermore, it helps resolve a paradox that has been embarrassing for evolutionary psychology, namely, the existence of heritable variation in sexual strategies (Bailey 1997). This resolution is more successful for men than for women, however.

Choice of mating tactics and constrained optimality

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Abstract: Gangestad & Simpson's arguments may be rendered more substantial and precise by capitalizing on research and theory on choice between reinforced response alternatives. An analysis in terms of feedback functions shows that the effects of individual differences in attractiveness may be understood as constraints on optimality and may be reconciled with the previous research and theory that the authors criticize.

Gangestad & Simpson (G&S) present a lucid and persuasive argument that male and female mating strategies should vary with individual differences and environmental differences. Although their general argument is well made, they could improve the characterization of the factors affecting mating strategy by: (1) distinguishing more carefully between the effects of individual differences and environmental variation; (2) capitalizing on research

and theory concerning the type of choice entailed in mating strategies, and (3) reconciling their view with other views within the context of optimality theory.

Although one may treat individual differences and environmental differences in ways that look equivalent mathematically, that is only true when one examines the behavior of individuals. In the explanation given below, which focuses on individuals, the various factors determining possible fitness could all be incorporated into one multivariate function. Since environmental variation is also important to understanding the behavior of groups, however, the two should be treated separately. Given a particular environment, one still may expect variation in individual behavior because of individual differences, particularly in attractiveness.

G&S appear to be unaware of a large and rich body of research and theory on choice that applies to their conception of mating strategies (see Williams 1988, for overview; Baum 1981). If, as they suggest, a strategy consists of a mix of tactics, with different mixes providing different payoffs, this is modeled by concurrent reinforcement of two response alternatives. In research on concurrent performance, two response alternatives produce reinforcement and the relative frequency of choosing the two is related to the relative reinforcement obtained from the two (Baum 1979; Herrnstein 1961). G&S's account parallels such a situation, with the two alternatives being the two types of tactics and the payoffs being in reproductive success.

If L and S are the frequencies of an individual's pursuing long-term tactics and short-term tactics, then the possibilities for a given environment (prevalence of parasites, climate, etc.) still depend on the individual's attractiveness. Figure 1 shows the way an individual's reproductive success might vary depending on strategy, defined as the proportion (p) of L out of all mating effort, $L + S$. If all mating effort is directed toward long-term tactics ($p = 1$), reproductive success attains the value shown to the extreme right. If all the effort is given to short-term mating ($p = 0$), reproductive success attains the value shown to the extreme left, assumed here to be less than the other extreme, in keeping with the authors' hypotheses. A mix, however, produces higher reproductive success than either extreme, because the highest points on the curves lie between the extremes. Two curves are shown, one for a more attractive individual and one for a less attractive individual. The curve for the more attractive individual attains its optimum at a lesser proportion of long-term tactics, as theory and research would predict. The curve for the more attractive individual also reaches greater reproductive success at its optimum. These curves, also known as feedback functions (Baum 1973; 1981), show what is possible in the environment. An individual's actual performance would appear as a point on one of the functions. Theory predicts the point will be close to the optimum.

Two features emerge from Figure 1. First, attractiveness functions as a constraint. Each feedback function is the result of cutting through a three-dimensional surface at a certain level of attractiveness. The possibilities for the less attractive individual differ from the possibilities for the more attractive individual. Second, the more attractive individual's feedback function cuts closer to the global optimum for the entire surface, allowing that individual to attain an optimum close to that overall optimum for the environment. That global optimum includes more short-term mating than the less attractive individual optimally engages in. Thus, G&S's ideas may be reconciled with those of Trivers and others in that the overall optimum still tends toward a higher proportion of short-term tactics for attractive males. The authors' point is just that less attractive males' possibilities are constrained to make more long-term mating optimal.

A similar analysis would apply to females. If the possibilities shown in Figure 1 were for two females, particularly human females, they might tell a qualitatively similar story to that for males. If two females behaved optimally, the more attractive female might attain higher reproductive success in a certain environment (say, a parasite-ridden environment) than a less attractive female and might attain that success at a lower proportion of long-term

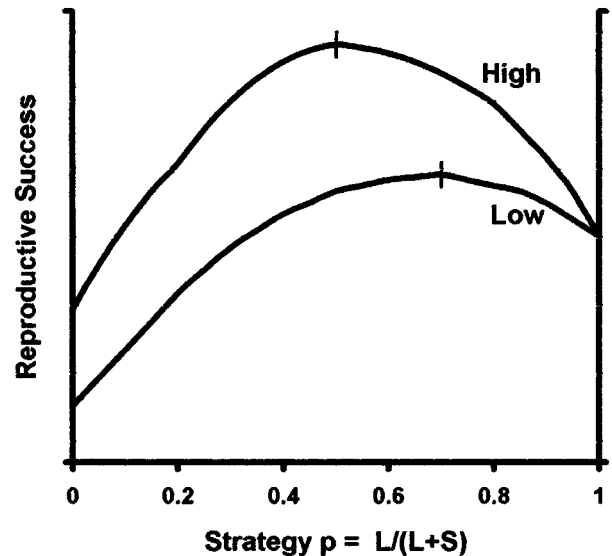


Figure 1 (Baum). Reproductive success as a function of strategy, expressed as proportion of long-term tactics (L) relative to long- and short-term (S) mating effort overall. The curve labeled “High” shows the possibilities for a more attractive individual. The curve labeled “Low” shows the possibilities for a less attractive individual. Crosses indicate optimal strategies. The optimal strategy for the more attractive individual includes more short-term tactics and is higher overall than that for the less attractive individual.

mating tactics. Males and females would differ quantitatively, however, because more short-term mating tactics would always be better for males than females. Males' feedback functions would lie to the left of those for females.

In summary, although G&S's points are well taken, they may be represented more precisely and reconciled with earlier research and theory if they are seen within the larger context of optimality theory and particularly constrained optimization.

Mating and marriage, husbands and lovers

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Abstract: Human mating strategies are contingent on individual prospects. Gangestad & Simpson provide a useful framework to explore these differing prospects, but do not take sufficient account of what is known ethnographically about mating decisions. Women often do not select their own long term mates. Men often have two or more long term mates, and can invest in the offspring of short term matings also.

Gangestad & Simpson's (G&S's) insistence that there is not one best male and one best female mating strategy in human beings, but instead a range of optimal strategies, contingent on individual characteristics and on the natural and social environment, is important and timely. However, although this sophisticated target article organizes a large number of data from several domains, there remain other domains whose findings are relevant to its model that “suggests that women should vary in their ‘exchange rate’ between a partner's genetic fitness (indexed by FA [fluctuating asymmetry]) and his investment, whereas men should vary in their ‘exchange rate’ between short-term mating effort and long-term parental investment” (sect. 5.5, first sentence). I concentrate here on two ethnographic considerations pertinent to the model, and particularly to its assumptions (1) that a woman's choices govern

who her long term mate will be; and (2) that a man is either a long term investor in a single woman and her children or a short term mate of many women, and that these strategies are mutually exclusive. The ethnographic findings are: (1) that humans do not only mate; they marry; and (2) that there is a complicated relationship between long term and short term mating tactics, particularly for men, rather than a strict tradeoff.

1. *Marriage*: With one possible exception (Cai 1997), all known human societies have the institution of marriage. There is every reason to believe that it is a very old custom, relevant to our evolution. In all but a few ethnographically famous but statistically unimportant cases, this institution links one or more men with one or more women in a socially sanctioned relationship that includes rights of sexual access and some obligations of support for the children born to the marriage. The importance of this support is culturally variable.

The greatest difficulty for the G&S thesis relating male FA to female mate preference is that in many, probably most tribal societies – those societies most similar to the social EEA in which our mating preferences evolved – ethnographers repeatedly record that women alone do not choose their husbands. Their parents choose for them to a greater or a lesser degree. Although it would probably be possible to construct a scale ranging from complete parental control of marriage choices to complete autonomy of the marrying woman, and to locate a large number of tribal societies along this continuum, that useful task remains to be done. If it were done we could begin to ask which circumstances lead to parental control and which to bridal autonomy. What we do know now is that the selection of the husband, the long term mate who has primary responsibility for provisioning the children (except in some matrilineal, matrilocal societies, where that responsibility may fall primarily on the woman's father and brothers) is often made without regard to the woman's perception of the desirability of her new husband, or at least without primary regard for her opinion.

To my knowledge, no one has yet attempted a study of the preferences of the parents of nubile women for the long term mates of their daughters with respect to FA, but such a study is clearly called for. Because tribal parents typically have several children to marry off, and because a marriage is usually a political event, with each marriage altering the marital possibilities of the unmarried siblings of the bride, it is not clear that a woman's parents, maximizing their fitness summed over all their offspring, would optimally have the same preferences as any individual daughter, even if they attended to all the same cues.

There is an additional attribute of marriage underdeveloped by G&S. The majority of societies regard polygyny (multiple wives) as the ideal form of marriage. Most men never achieve it, but the major mating strategy tradeoff in polygynous societies is not between a "single, exclusive long-term relationship" (sect. 5) with substantial paternal investment and many short term matings with little or no investment; but rather between a single long-term relationship with substantial paternal investment and two or more such relationships.

To put it baldly, the presumption that matings with multiple women exclude long-term relationships with substantial investment in both the women and the children is inadequate – as is the idea that a man's investment in his children is a simple reflection of the exclusivity of his "investment" in his relationship with his wife. The Relationship-Specific Investment Inventory is a catalog of contemporary American middle class fashions in "relationship counseling" that does not speak to the question of men's investment in children, even in our own culture.

2. *Relationship between long term and short term matings*: In general in the tribal world, long-term mates are husbands and short-term mates are lovers. Although a woman's parents often choose her husband, the woman herself, with only sporadic exceptions, chooses her lovers. It is an important difference. It is also important to recognize that in the great majority of tribal societies, the great majority of fertile women and mature men are married

most of the time. A woman does not choose between one long-term and one or more short-term mates; she has a husband and chooses among potential lovers. A man does not decide whether to be a long-term or a short-term strategist; he has a wife or wives and decides how much effort to put into courting additional (mainly married) women.

Among the Bari of Venezuela (where, in general, a woman chooses her husband subject to a veto by her parents) most married women take lovers around the time of at least one of their pregnancies (Beckerman et al. 1998). These lovers are acknowledged as secondary fathers of the children born of those pregnancies and are supposed to give them fish and game. Children with secondary fathers have higher survivorship to age 15 than children with only a single father. In field interviews, older Bari women repeatedly volunteered that in traditional times "the girls always fell in love with the best hunters." They were speaking of both husbands and lovers. The two points here are that being a good hunter (almost certainly an indication of superior health, stamina, and sensory acuity) was a trait desired in both long- and short-term mates; and that in this case the short-term mates also often supplied resources. This situation appears to have been rather common among lowland South American peoples. In such cases, men who were secondary fathers for other men's wives' children did not usually give up their long term investment in their own wives and primary children.

Although clearly there must be limiting conditions where so much time, effort and resources goes into short-term mating that nothing is left over for long-term investment, and vice versa, the more common situation may be the one sketched here, in which well favored men pursue both strategies successfully. One would expect that this dual strategy would become even more common in the presence of resources that can be accumulated and inherited.

Fixed versus flexible strategists: Individual differences in facultative responsiveness?

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Abstract: Gangestad & Simpson's central premise regarding individual differences is applied to their facultative-argument based on mating-strategy, for individual differences in susceptibility to contextual effects. Some individuals may be relatively fixed strategists who are rather unresponsive to context when it comes to mating, whereas others, perhaps most, may be, as G&S propose, flexible strategists.

Individual differences in mating, like so much other behavior, most certainly exist, as Gangestad & Simpson (G&S) convincingly argue in their target article. But perhaps the implications of the ubiquity of individual differences in general have not been sufficiently considered in their target article. That is, although G&S make a compelling case for the contingent nature of mating behavior with respect to both males and females, they seem to have failed to entertain the possibility of individual differences in susceptibility to the very conditional effects around which they base their argument. In advancing this proposition, it is my intent not so much to criticize G&S as stand on their shoulders to extend their insightful analysis.

On average, it may make good evolutionary and biological sense for males and females to respond facultatively to variation in mating context, but such an average effect could mask underlying variation in responsiveness to contextual conditions, a possibility that goes unmentioned in G&S's otherwise thoughtful target article. In advancing this proposition, I mean to apply to their analysis the very argument which G&S used to appreciatively critique existing models of mating. That is, just because there exist mean differences in mating strategies across contexts, it does not follow that

there is no variation in the degree to which individuals prove responsive to contextual conditions.

It could be useful to think in terms of fixed and flexible strategists or, at least, in terms of variation in flexibility of strategy. Whereas some males or females, perhaps even most, may inherit the capacity to adjust their mating strategy flexibly, in line with G&S's analysis, others may have inherited a far less flexible and more fixed mating strategy. It may be problematic to assume, as G&S implicitly appear to do, that all males and females are flexible strategists, or at least equally flexible strategists in the domain of mating. As I have argued elsewhere with respect to the effects of rearing on infant-mother attachment security (Belsky 1997b), early problem behavior (Belsky et al. 1998), and mating and parenting in adulthood (Belsky 1997a), it might be useful to think in terms of variation in susceptibility to contextual effects in the case of facultative mating strategies. Thus, some individuals may be less facultatively responsive than others – and for just the same reason that G&S argue in favor of facultative responsiveness in general – namely, reproductive fitness.

I take no issue with the notion that mating strategy should vary with contextual conditions, whether those conditions be defined in terms of men's genetic quality or capacity for long-term parental investment in the case of women or, in the case of men, in terms of women's long- or short-term mating strategy. But it would seem that in some cases at least, reproductive payoffs would be greater (on average) across generations when particular individuals stick to a single, inflexible (or relatively inflexible) strategy. Consider in this regard the male who inherits the very developmental stability that G&S argue is central to female mating strategy. Were highly stable males who were heritably resistant to environmental threats to their low fluctuating asymmetry genetically committed to a short-term mating strategy, it is not difficult to envision that across generations such fixed strategists would experience greater reproductive success than if they varied their mating tactics in accord with contextual conditions. Although there certainly would have been times when such a fixed strategy did not pay off, those may be the exceptions rather than the rule. In the case of some men, behaving facultatively would not have been adaptive on average, and so for men with the genes in question, a fixed rather than flexible strategy would be persistently practiced. In other words, evolution may have maintained in the gene pool, genes that promote fixed – or relatively fixed – as well as flexible mating strategies.

Can a similar argument be advanced in the case of women? It is certainly not difficult to imagine that a female of high mate value due principally to genetic factors could also have inherited genes that reduced her facultative responsiveness to mating conditions because across time the payoff of a fixed (long-term) mating strategy may have been so great as to outweigh the rare, periodic gain achieved by varying such usually sound mating tactics. Indeed, attractive healthy women might have been so assured of securing high value mates across human evolutionary history that the rare costs associated with not engaging in short-term mating under propitious conditions would not outweigh the much larger and highly reliable (even if not perfect) gain from always seeking long-term investment. Were that the case, one might again expect genes that fostered fixed mating strategies as well as facultative ones.

To summarize, in the same way that mean differences in male-female mating strategies most assuredly mask the within-gender variation that, as Gangestad & Simpson compellingly argue, has evolved due to its adaptive value, mean male and female differences in mating behavior across context may mask variation in the degree to which both males and females show facultative responsiveness to mating conditions. In the case of some and probably most males and females, facultative responsiveness makes great evolutionary sense. But in the case of others, a fixed or at least less flexible strategy may be the order of the day, week, life, and even lineage. When average reproductive payoffs for flexibility were less, as they may have been for extremely symmetrical men or ex-

tremely healthy and beautiful women, fixed rather than flexible mating tactics should have evolved. It is accordingly useful to consider for whom the flexibility would, on average, have been more expensive reproductively, in addition to the average benefits of flexible mating behavior.

Individual differences in evolutionary perspective: The games people play

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Abstract: The emphasis on individual differences in evolutionary theories is important and has not received adequate attention. Strategic Pluralism makes a major contribution by addressing these issues, but like other evolutionary models (e.g., game theory) does not articulate the specific mechanisms underlying strategy selection. Specification of such mechanisms is an essential next step in the development of these models.

Gangestad & Simpson's (G&S's) Strategic Pluralism model provides a thoughtful account of individual differences from an evolutionary perspective. As argued elsewhere, the assumption that evolutionary approaches predict strict universals in preferences and behaviors is simplistic and at odds with the well-documented variability in human behavior (Berry 2000; Buss & Greiling 1999). The target article provides a sophisticated account of individual differences via the concept of evolved conditional adaptations – evolved preferences that shift as a function of characteristics of the environment. For example, G&S note that highly attractive men are more successful in short-term mating contexts than are less attractive men. Men's conditional adaptations, they argue, therefore alter their preferences and behaviors as a function of their own attractiveness. Highly attractive men put relatively more effort into short-term mating, whereas less attractive men devote relatively more effort to long-term strategies. Such “conditional strategies” seem likely to produce individual differences in human behavior.

What exactly is a conditional strategy? If such strategies reflect conscious decisions that individuals make to enhance reproductive success, a more complete understanding of these strategies will depend on a clearer picture of the evolution of human cognition. However, if such strategies are not conscious choices, they are reminiscent of explanations of nonhuman animal mating strategies based on game theory (Dawkins 1980; Maynard Smith 1974). These explanations assume an individual's reproductive success depends on the behaviors of other members of the population. For the example of male attractiveness considered here, game theory might assume that all males are predisposed to seek short-term mating strategies, but only attractive males will succeed with this strategy. Attractive males succeed with this approach because women are more likely to seek short-term mating situations with attractive men. After all, if women did not also engage in short-term matings, men should have evolved strategies that would procure the best long-term mates, regardless of whether the men are attractive or not. Thus, the strategies that men evolved were undoubtedly influenced by the strategies that evolved in women (and vice versa). Given a short-term strategy is less likely to work for unattractive males, they adopt a long-term strategy that is more likely to produce successful results. Game theory supposes that these conditional strategies are inherited programs that influence mating behavior by providing alternative strategies for different situations. Alternative strategies allow less fit individuals (in our case, less attractive males) to increase their chances of reproductive success.

G&S's model is similar to game theory explanations of mating behavior in another respect. Neither theory adequately specifies

the nature of the underlying mechanisms involved in strategy selection. The concept of conditional adaptation could benefit from greater attention to the underlying mechanisms that evaluate characteristics of the environment and shift a person's desires and preferences as a function of those characteristics. G&S do not fully articulate how contextual factors produce these shifts in mating strategies. One might argue that until intervening processes are proposed and described in deeper detail, the term "conditional strategy" is reduced to a description of behavior, rather than an explanatory concept. We hasten to add that most discussions of evolutionary bases of human behavior – including our own (Berry 2000; Kuczaj 1998) – have been vague about underlying mechanisms. The field of evolutionary psychology could benefit greatly from more attention to this issue.

How might a man's attractiveness as a mate become linked with his preferred mating strategy? If attractive men can increase reproductive success via short-term strategies, and less attractive men attain the greatest reproductive success via long-term strategies, one possibility is that selection yielded two types of men: Attractive men who prefer short-term approaches, and unattractive men who prefer long-term strategies. (This is analogous to Gangestad & Simpson's [1990] proposed explanation of individual differences in female sociosexuality.) If we assume that attractiveness, fitness, and strategies are inherited in such a way that attractive men possess one strategy and unattractive men another (and this is, of course, a big assumption), then evolution has produced individual differences in men's mating preferences that are linked to their attractiveness. However, note that this really is not an example of a conditional adaptation – a single adaptation that produces different preferences as a function of other variables. Instead, this explanation posits the evolution of different adaptations in different individuals. The mechanism of strategy choice in such a case is genetic, with one's attractiveness being paired with a strategy that optimizes mating success for one's appearance. Strategy choice, then, is neither conscious nor a function of the environment, but instead genetically determined.

There are, of course, alternative possibilities. Perhaps all men desire many low-investment sexual partners. However, attractive men typically attract such partners, whereas unattractive men rarely do. Thus, attractive men are likely to succeed via this strategy, but unattractive men are not. If unattractive men can successfully secure one sexual partner by adopting a long-term strategy, and they adopt such an approach, they will have at least one partner. In contrast, if unattractive males adopt a short-term approach, they are more likely to have no partners (unless, perhaps, there are no attractive males available). Thus, in this scenario, unattractive men adopt a long-term strategy not because they prefer one partner to many, but because one is better than none. This explanation predicts a pattern of behavior identical to what has been documented empirically. However, it does not describe a conditional adaptation as described by G&S, who posit actual differences in preferences as a function of a man's attractiveness. Instead, this is an example of a single sex-typical evolved preference – a desire for many partners – the realization of which is constrained by women's reactions to a man's attractiveness, and is more consistent with the notion of conditional strategies in game theory.

As this brief description illustrates, it is difficult to specify the underlying processes that are involved in strategy selection. However, continued efforts to do so are imperative if we are to move from describing behaviors to explaining them.

A comprehensive theory of human mating must explain between-sex and within-sex differences in mating strategies

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Abstract: Gangestad & Simpson make a major contribution by highlighting the importance of mate choice for good genes, the costs of alternative strategies, and tradeoffs inherent in human mating. By downplaying sex differences and ignoring the nongenetic adaptive benefits of short term mating, however, they undermine their goal of "strategic pluralism" by presenting a theory devoid of many documented complexities of human mating.

We concur with Gangestad & Simpson's (G&S's) central claims that good genes are important in human mate selection and that there are tradeoffs in human mating – ideas present in prior theories of human mating, although not as explicitly as they deserve to be. Their work on fluctuating asymmetry is innovative and makes a substantial contribution to knowledge.

Despite our admiration for their work, we found several problems with their current formulation – their distorted presentation of Sexual Strategies Theory (SST), their treatment of sex differences in human mating strategies, and their neglect of potential nongenetic adaptive benefits of short-term mating.

Sexual strategies theory. In setting up the foundation and background for their own formulation, G&S appear to downplay the widely documented sex differences in human mating. They do this in part by presenting a distorted and selective depiction of SST (Buss 1994b; 2000; Buss & Schmitt 1993), using a double standard when comparing sex differences to within-sex effects, and failing to acknowledge explicitly the profoundly sex-differentiated nature of their own proposal.

Although G&S occasionally insert a qualifier, most readers will come away from their article believing that SST is all about men pursuing short-term and women pursuing long-term mating strategies. In contrast, SST proposes that both men and women have evolved a complex menu of mating strategies, including both short-term and long-term strategies, and that the combination each individual selects from this menu depends on a variety of contexts, such as operational sex ratio, mate value, physical attractiveness, quality of available alternatives, parental and kin influences, local cultural norms, reputational consequences, and many others (Buss 1994b; 2000; Buss & Schmitt 1993; Greiling & Buss, in press). G&S's version of "strategic pluralism," as we elaborate below, turns out to be considerably narrower than that of SST.

Double standard of evaluating results. To set the stage for their theory, G&S attempt to minimize the existence of empirical findings of sex differences. They do this by converting effect sizes into indices of explained variance. To take one concrete example, Buss and Schmitt (1993) found an effect size of 1.00 for sex differences in how much time would elapse before seeking sexual intercourse. Men and women differ by a full standard deviation, which greatly exceeds the magnitude of the vast majority of the "strongest" findings in psychology. In an apparent effort to diminish the importance of sex differences, G&S translate the effect size into a percentage of variance accounted for of 20%. When it comes to their own key findings, however, they choose to report correlations instead, and fail to report the percentage of variance accounted for. For one of their key theoretically predicted findings – the link between FA and attractiveness – they report a mean correlation across studies of $-.20$. This translates into merely 4% of the variance accounted for! A key sex difference that the authors take pains to minimize, in other words, accounts for *five times more variance* than does an effect that appears to be a theoretical lynchpin of their theory. We find this "double standard," using one set of statistical indicators for findings they try to downplay and a different set for their own preferred findings, to be of

dubious merit for the goal of a balanced portrayal of the empirical evidence.

Within-sex and between-sex differences. Perhaps more important, it is not necessary to minimize the existence of well documented sex differences in human mating to highlight the importance of within-sex variation. Both can be, and are, important. Men have roughly ten times the circulating testosterone as women, for example, but within-sex variation in testosterone is large and covaries with an important suite of psychological variables within each sex (Mazur & Booth 1998). Similarly, men and women differ profoundly in certain mate preferences and in their desires for partner variety, yet there are also substantial within-sex variations in these qualities. It is not necessary to downplay one in order to make an argument for the other.

Minimizing sex differences may play well to a politically correct crowd, but G&S's own proposed theory is in fact highly sex-differentiated. In essence, they propose that women seeking short-term mating pursue men with good genes, whereas men seeking short-term mating are going for increased opportunities to inseminate a variety of women. They further propose that women seeking long-term mating pursue men who will provide parental care, whereas men seeking long-term mating are portrayed as "genetic losers" who lack the genetic fitness to succeed in short-term mating (we concur with the former, but not the latter, contention). Eliding over these and other stark sex differences contained in their own theory may make it more palatable for some, but there is no getting around the fact that one cornerstone of their theory involves sex differences.

Women's short-term mating. Although G&S present their theory as one of "strategic pluralism," we find their proposal to be narrower or less pluralistic than is warranted. While focusing exclusively on the "genetic" benefits to women of short-term mating, they effectively ignore a host of other plausible hypotheses about the adaptive benefits to women. Studies of women's desires in short-term mating, women's perceptions of the benefits of short-term mating, and the contexts in which women pursue short-term mating lend plausibility to several hypothesized functions: to acquire immediate economic benefits, enact mate switching, cultivate a potential back-up ("mate insurance"), or to evaluate potential long-term mates (Buss 2000; Greiling & Buss, in press). These studies, of course, are limited in a variety of ways and are by no means definitive. Nonetheless, we believe that a comprehensive theory of strategic pluralism must include these neglected components of women's short-term sexual strategies rather than focus narrowly on genetic benefits.

Conclusion. In sum, a theory that accounts for within-sex variation need not, and cannot, ignore the large and well-documented sex differences in sexual strategies. It must explicitly acknowledge the sex-differentiated functions of short-term and long-term mating contained in the theory. And it should not focus narrowly on good-genes benefits to the exclusion of a range of other plausible functions of short-term mating.

The trade-off between frequency of intercourse and sexual partner accumulation may reflect evolutionary adaptations

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Abstract: The adaptive trade-offs between long- and short-term matings may be mediated or at least reflected partially by the trade-offs between the relative reinforcement obtained through a greater frequency of intercourse (typically greater among cohabitants) versus a greater frequency of partner change. The differing correlates of each approach and meshing with the Sexual Strategies Theory of Gangestad & Simpson are discussed.

One means by which trade-offs between short- and long-term matings may be guided is through individual differences in the relative reinforcement value of a greater long-term frequency of intercourse (FSI; reportedly most easily obtained through relatively long-term cohabitation; Brody 1997) versus an accumulation of a greater lifetime number of sexual partners (LNSP) through a series of short-term matings. Mixed strategies are not uncommon, but for the purposes of this exposition the LNSP and FSI focussed approaches will be contrasted. Although FSI and LNSP were correlated in some studies (especially those using young samples in which age at first intercourse is an important factor), they have stronger associations with separate clusters of variables. LNSP is associated with novelty seeking, habituation or boredom proneness, and impulsiveness. FSI is associated with measures of physical sensitivity (consistent with a simple operant model of greater frequency of enjoyed activities), pairbonding, health, consistency of female orgasm, and hormonal/autonomic factors (reviewed in Brody 1997). Another factor is the individual relative appeal (or aversiveness) of the intimacy or social propriety associated with longer-term relationships. Thus, individual differences in personality and related psychophysiology may affect the relative behavioral reward of LNSP and FSI focussed strategies.

Gangestad & Simpson (G&S) found that women in their samples were more likely to report desiring men with low fluctuating asymmetry, and that those men were characterised by being more muscular, violent (and given the results of the Gangestad & Thornhill 1998b study, perhaps more redolent). One might conjecture that those women who are more attracted to pairings with such men might be less sensitive or cultivated (or more attuned to the dramatic and impulsive) and less inclined to the long-term FSI approach. Given that women who use oral contraception have greater mean FSI than those who do not, excluding pill users from Gangestad and Thornhill's (1998b) study of women's olfactory appraisal of the shirts of men of varying fluctuating asymmetry (though understandable given the endocrinologic variables that were utilized) may have biased the sample toward those women more inclined to a short-term relationship niche.

The one published study cited by G&S examining the relationship between sexual reward (orgasm) and fluctuating asymmetry (Thornhill et al. 1995) also gives rise to methodological concerns. The possibility of a bias in the direction of over-reporting (rather than actually experiencing) a greater rate of orgasm by the women with more symmetrical (more violent) partners must be considered, especially given that the correlation between partners reported FSI was quite modest. However, it is also possible a greater FSI (as noted above, FSI is associated with greater female orgasm consistency, at least in nonprostitute women) is experienced by women with more aggressive partners. Apt and Hurlbert (1993) found that abusive relationships involved a greater FSI than controls, an exception to the general association of greater FSI with better partnership (Brody 1997).

G&S posit that environments with a high level of pathogens may increase the drive to seek indicators of good genes and also encourage short-term mating strategies, whereas venues with low levels of pathogens favor long-term mating. When environments are compared at an international level, FSI is associated with life expectancy ($r = .61$), per capita gross domestic product ($r = .83$), and an index of political freedom ($r = .75$; all $p < .01$; Brody 1997). At least life expectancy is inversely related to pathogen prevalence (perhaps the pathogenic influences of a repressive regime or barren economy should be considered in addition to threats posed by microorganisms). There are many possible explanations for such correlations (such as the same strengths that make for superior technological development also facilitate a more enduring sexuality). However, the associations between FSI and measures of a less threatening environment are largely consistent with FSI being a proximal influence on the trade-offs predicted by the Sexual Strategies Theory of Gangestad & Simpson.

Eating their cake and having it too: Or, how women maximize reproductive success by simultaneous mating and dating

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Abstract: Data support the claim from the target article that women, both cross-culturally and historically, have employed a variety of mating strategies, marrying but also engaging in short-term unions. But those strategies appear to be practiced simultaneously and not conditionally as Gangestad & Simpson propose, a finding consistent with assumed constraints on the potential reproductive success of females.

In their target article, Gangestad & Simpson (G&S) review a set of by now well publicized findings to the effect that both males and females are attracted to members of the opposite sex who display body symmetry. What is new here is the additional idea that men and women practice *mixed* or *conditional* mating tactics tailored to specific environmental circumstances. The key prediction is that females will shift from long-term to short-term mating tactics when environmental circumstances, especially the prevalence of pathogens, place a premium on the good genes (correlated with body symmetry) of the partner. In fact, both theory and data do support the general idea that women employ a variety of mating strategies and probably did so in our environment of evolutionary adaptedness (EEA). I wish to argue, however, that those strategies are not likely to be conditional in the way that G&S suppose.

The claim that females adopt a number of mating tactics is supported by the fact that, across time and place, women have married but also engaged in premarital and extramarital sex. Premarital sex is uncommon in only 20% of 113 cultures from the Standard Cross-Cultural Sample and extramarital sex is uncommon in only 28% of 52 Standard Sample cultures (Broude & Greene 1976). Buss (1999) reports that between 20% and 50% of women engage in extramarital affairs in the United States, and conservative estimates based on measures of genetic relatedness indicate that 10% of children are fathered by someone other than the mother's husband (Allman 1994). Indeed, short-term sexual activity on the part of females is a logical requirement of standard sexual selection theory. If males promote their fitness by engaging in short-term mating, then women must be engaging in the same kind of activity. Otherwise, with whom are the males mating? Further, human beings exhibit a variety of physiological characteristics viewed as consistent with the idea that neither men nor women are or have in the past been exclusively monogamous.

Both long-term and short-term mating, then, do appear on theoretical and empirical grounds to be female mating strategies. It is the idea that these are *conditional* mating strategies that I wish to question. Partly, the theory seems to me to be implausible on sheerly logical grounds. G&S are arguing that women make decisions about mating strategies on the basis of environmental cues. The strategy of engaging in short-term matings should kick in when the environment favors mating with men with good genes. The primary environmental cue that G&S emphasize is the prevalence of pathogens. The idea that behavior is triggered by environmental circumstances is entirely reasonable and has gained considerable currency since Barkow et al. (1992) introduced the notion of Darwinian algorithms into the evolutionary psychological literature. But how would seeking out a male with good genes count as a good mating strategy when pathogens are prevalent? Here is the problem: pathogen prevalence could, theoretically, be a one-shot short-term, a long-term, or a recurring environmental challenge. If pathogen prevalence is a one-shot short-term event, then the fitness-enhancing trait of disease resistance passed on to a woman's offspring will become obsolete, perhaps even by the time the baby is born if the pathogen threat is sufficiently transient. Short-term mating strategies in which women are choosing good-gene men, then, are only likely to promote inclusive fitness if pathogen prevalence is a chronic problem in the environment.

But if that is the case, then the strategy is no longer conditional in the sense that G&S mean it, any more than we would say that my breathing is conditional on the environment's providing air. If pathogens are always in the environment, the women should always be seeking good-gene matings. The same goes if pathogene presence is a fluctuating but recurring phenomenon. In this case also, women should be trying to mate with good-gene males throughout their reproductive lives.

The idea that women practice conditional mating strategies is also challenged by the data. The fact is that, cross-culturally and historically, virtually all women marry. Contemporary society is anomalous in this regard. Further, in a world-wide sample of 69 cultures, the mean age of marriage for females is 16.29 years (unpublished codes, Palfrey House, Harvard University). Long-term mating does not look like a conditional strategy. Rather, it looks like a universally practiced adaptation. But so are women engaging in short-term matings. As I have indicated, extramarital sex on the part of wives is common across cultures, in spite of the potential repercussions. Indeed, while G&S speculate that women might forego extra-mate pairings except as a conditional strategy because they fear risking disruption of the long-term pair bond with their husbands, wives across cultures appear to be willing to take the risk. This is reflected in the absence of a significant association between punishments for extramarital sex across cultures and actual incidences of extramarital sexual activity (Broude 1980).

The data, in short, are not consistent with the idea that women are adopting conditional mating strategies. Rather, it appears that they engage in a variety of mating strategies *simultaneously*. Across time and place, women tend to marry *and* have short-term affairs at the same time. This makes good sense from the perspective of evolutionary theory. Women benefit from the investment of a long-term mate but, because of the limitations on their reproductive capacity, cannot wait forever to attract G&S's prototypic good-gene male as a husband. Rather, they compromise and marry what is available. But a woman with an investing husband at home as her insurance policy can seek out short-term matings with a good-gene male. Thus, women seem to engage in mating strategies that allow them to eat their cake and have it too.

Scientific truth and perceived truth about sexual human nature: Implications for therapists

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Abstract: Therapists and their patients must deal with the negative sequelae of short term mating strategies. Implications for therapy of Gangestad & Simpson's strategic pluralism theory are compared with those of Buss's sexual strategies theory and Eagly's social role theory. Naive theories held by therapists and patients, as well as prevailing societal views, are posited as influential in determining the course and outcome of therapy.

John McPhee, in his collection of essays *The control of nature* (1990), provides several descriptions of attempts by civil engineers to control the physical environment; his documentation of the fragility of our successes is humbling. Although much of government, law, religion, and more recently, psychotherapy, is concerned with influencing human nature, including its sexual aspects, social engineers have arguably fared worse than have civil engineers.

Therapists are among the many who deal daily with the negative sequelae often associated with short-term mating strategies, including the birth of unwanted children, abortion, sexually transmitted diseases, rape, murder, and divorce. For many countries in

Western societies, the dominant paradigm for understanding and controlling human sexuality derived from religion. Humans were assumed to have a base nature, and only through the socialization of religion could any semblance of order be maintained. In some contemporary cultures, this paradigm continues to guide attempts to control sexual behavior. In other cultures, religion-based control systems have been supplanted by secular legal, educational, medical, and psychological systems, all of which are fed by the theories and data of science.

From our perspective as professional applied psychologists, we are concerned with how alternative scientific theories may be useful in understanding sexual behavior, especially the kinds of behaviors that lead to negative consequences, and further, how therapeutic efforts may be affected. Gangestad & Simpson's (G&S's) account of how sexual strategies may have evolved is framed primarily as a modification and extension of Buss and Schmidt's (1993) Sexual Strategies Theory (SST) and both contrast with socialization theories such as Eagly's (Eagly 1987; Eagly & Wood 1999), who proposes that culture is largely responsible for the differences in how males and females act with regard to mating.

As therapists, we are often not as concerned with the actual mechanisms supporting sexual behavior, but how patients and therapists construe the causes of their behaviors. As Heider (1958) argued, we are all "naive" psychologists, and our informal theories may serve to guide (and justify) much of our behavior. A standard therapeutic assumption drawing from Eagly's work might be that sexual behavior is largely learned, responsive to contemporary social structures, and thus malleable to a great degree. Although the socialization that shapes the sexual behavior of males and females is extremely powerful, therapists and clients who view sexual behavior as largely socialized may nevertheless view aberrant sexual behavior as potentially amenable to treatment. On the other hand, as G&S emphasize, Buss and Schmitt's (1993) SST can lead to the conclusion that "men may have evolved over human evolutionary history a powerful desire for sexual access to a large number of women" (Buss & Schmitt 1993, p. 208). Although SST does acknowledge that both genders should possess evolved methods for finding long-term mates, "men, more than women, are predicted to have evolved a greater desire for casual sex" (Buss 1999, p. 162). Although Buss (1999) takes care to note that a characteristic arising as a result of evolutionary processes does not preclude that characteristic from changing within an individual, a belief in SST would lead many therapists and clients to view sexual desires and sexual behavior as largely immutable, or at least highly resistant to modification. If men have "evolved a greater desire for casual sex," can society (or their female partners) blame them if they sometimes act upon that desire? And are efforts to modify that desire action a waste of time? G&S seem to offer a synthesis of the "strong nature" position of Buss and the "strong nurture" position of Eagly, in that although evolved mechanisms are the primary focus, their modification of SST does not polarize males and females to a high degree, and there is some recognition that contemporary environmental factors may be responsible for the engagement of ST and LT strategies in both sexes. As G&S acknowledge, there are many questions unanswered by the present version of their theory, including better specification of conditions that may call forth the mating logic they propose for each gender. These explications may eventually yield a theory that better informs the practice of therapy related to sexual behavior.

For therapy to be effective, considering the naive theories held by patient and therapist may be as important as knowing what actual mechanisms are responsible for the troubling behaviors in question. Concordance of theory between patient and therapist would seem to be crucial, and the prevailing views of society at large are also important. Pessimistically enough, for some kinds of sexual behaviors that concern us, none of this information may result in therapy being any more effective as a mechanism of prevention or damage control than anything else has been throughout recorded history.

Putting people before parasites and places

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Abstract: The strategic pluralism model depends upon pathogen prevalence and environmental hardship being independent. Evidence is presented that they are positively correlated. The rise in short-term mating strategy in the United States is better explained by changes in the operational sex ratio than by increases in pathogen prevalence. Nonetheless, in highlighting the advantages of a high-investment strategy to less attractive males, Gangestad & Simpson's model helps to clarify the dynamics of frequency-dependent selection.

According to Gangestad & Simpson (G&S), variability in female mating strategies derives from women's different responses to pathogen prevalence and harsh environmental conditions. The relationship between the two is critical both theoretically and empirically.

Before addressing this, it is necessary to clarify the meaning of harsh environments. Gangestad & Simpson define them tautologically as "environments in which biparental care and stable pair-bonds are needed and expected" (sect. 5.7.1). Effectively, however, they treat them as characterised by resource scarcity where "women could not provide for all the nutritional needs of their offspring" (sect. 5.6.2). Such harsh environments also incite competition for scarce resources (Clutton-Brock 1991, p. 257) leading to high crime rates and other forms of social pathology which exacerbate environmental challenges.

If parasites and harsh environment are negatively correlated across geographical sites, then one female strategy would be universal since women everywhere would benefit from making the same choice. If they are negatively correlated within a geographical site, for example, as a function of social class, then women of the same class should all select the same strategy. If they are positively correlated (either between or within ecological niches), the distinction between them evaporates and there is no possibility of making differential predictions. Unless niche-independent genetic differences in strategy choice are invoked, the viability of the theory depends upon a near zero correlation between environmental harshness and pathogen prevalence.

From an empirical viewpoint, there is much evidence that the two are positively correlated and associated with poverty. Across and within nations, indicators of parasite prevalence (infant mortality rate, probability of dying before their fifth birthday, the percentage of infants immunised, mortality from diarrhoeal and respiratory infections, malaria, measles, tuberculosis) and harsh environment (gross domestic product, death from accidental causes, life expectancy, percentage of poor, national health expenditure as a proportion of GNP, proportion of children whose weight-for-age is acceptable by international standards) go hand in hand (World Health Organisation 1999).

The rate of single-parent families has risen dramatically in Western countries. In the United States between 1970 and 1990, premarital births rose from 9% to 22% of births to white women and from 42% to 70% to African-Americans (Weinraub & Gringlas 1995). According to G&S such a rise would be attributed to higher pathogen prevalence yet this period has seen a rise in immunisation programs and in pre- and post-natal care. What has altered in post-war years is the operational sex ratio (Guttentag & Secord 1983; Pedersen 1991). Changes in attitudes to casual sex, single parenthood, and divorce are strongly related to the relative paucity of males, which puts them in a strong market position to impose their preferred mating strategy. This situation is most marked in the lowest social classes where the pool of eligible males is further reduced by male unemployment, drug addiction, and imprisonment (Campbell 1995). If this argument is correct, then female mating strategies are frequency dependent and driven by the availability and preferred strategy of males and females, rather than by ecological factors in the environment.

Dawkins (1989) has proposed a mathematical model of this process evaluating the pay-off of a successfully-raised offspring against the costs of wasting time in prolonged courtship and raising the child. In a monogamous population, men and women do equally well – they halve the cost of child rearing by sharing it, and both pay the price of courtship and reap the same reward. If an unrestricted female comes on the scene, she avoids the price of courtship but still halves the cost of child-rearing and gains the reward. But as unrestricted females become more common, the male's optimal strategy changes to promiscuity, earning him a child while paying no cost in waiting or child-rearing. But now the unrestricted female pays the entire cost of child-rearing alone (although not the costs of delayed mating) leaving her in serious deficit. A restricted female now starts to do better. Although she encounters mainly promiscuous males, at least she does not lose – she will refuse to mate and so will not suffer the costly experiences of her unrestricted rival. As the number of restricted females rises, promiscuous males will find it harder to find partners and will accede to monogamy.

What this model incorporates, but is ignored by G&S, is the substantial cost of child-rearing to the woman pursuing a short-term strategy. For their model to succeed, they must show that a short-term strategy leads to greater reproductive success than a long-term strategy despite the doubled cost of child-rearing. But mortality rates for father-absent children exceed those of two-parent families (see Geary 1998). Parents in single-parent families experience greater stress, resulting in reduced parental effectiveness and poorer child outcomes (Weinraub & Gringlas 1995). Conditions of poverty, disproportionately experienced by single-parent families (Hobbs & Lippman 1990), are associated with child abuse (Pelton 1978; Steinberg et al. 1981).

But the insights afforded by G&S offer a solution to a significant problem with Dawkins' model – the swing back from promiscuity to monogamy. Under promiscuity, Dawkins argues, the restricted female does better than her unrestricted competitor because she does not pay the cost of raising a child alone. True, but the restricted female also produces no (or very few) offspring if there are few monogamous males in the population. She wastes a great deal of time meeting and rejecting promiscuous males and a woman's reproductive life is a relatively short one. This can hardly be considered a good outcome from the point of view of inclusive fitness. Dawkins glosses over this difficulty and assumes that eventually monogamous females predominate. Once they do, he argues, males waste too much time looking for an unrestricted female and so are forced into monogamy. Although he admits the time-wasting cost for promiscuous males, he ignores the same cost for monogamous females – despite female's shorter reproductive life. Gangestad & Simpson, however, provide a clear rationale for why some males should be available to a monogamous female even when male promiscuity is prevalent. Less symmetrical and attractive males can maximise their reproductive success by capitalising upon a female desire for monogamy. In a previous paper, Gangestad & Simpson (1990) invoked frequency dependent selection as an explanation of the incontestable flexibility of human mating strategies. It is a pity that it has all but disappeared from the present model.

Current versus future, not genes versus parenting

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Abstract: Gangestad & Simpson's model of the evolution of within-sex differences in reproductive strategies requires a degree of female choice that probably did not exist because of male coercion. We argue as well that the tradeoff between current and future reproduction accounts for more of the within-sex differences in reproductive strategies than the "good-genes-good parenting" tradeoff they propose.

Gangestad & Simpson's (G&S's) model of within-sex differences in reproductive strategies is based on the widely-accepted deductive principle and inductive generalization that female mammals tend to "track" their environments for the resources they require for parental investment while male mammals "track" females for opportunities to mate.¹ It follows, for them, that when female reproductive success (RS) is determined primarily by resources available through males, then females are expected to favor males who are "good parents." On the other hand, when female RS does not depend on resources available through males they should favor males who have "good genes." Variation in female reproductive strategies is thus expected to be contingent on the optimal tradeoff between their capacity to benefit reproductively from "good genes" versus "good parenting." Consequently, "men's tendency to engage in short-term mating should be a direct function of their genetic fitness (indexed by FA), while men's propensity to invest in single, exclusive long-term relationships should be inversely related to their genetic fitness" (sect. 5, para. 1). Although G&S present considerable data that seems consistent with their model, we feel that the model itself may be flawed and that other interpretations are possible. We are not convinced that there really is a tradeoff between "good genes" and "good parenting" or that it is not subsumed in the already well-known tradeoff between current and future reproduction.

A major problem for their model is that there is more to sexual selection than female choice: there is also male coercion (of females and other males). "Good genes" sexual selection cannot occur when there is no female choice, and the evidence for female choice amongst nonhuman primates is weak. Sarah Hrdy even argues that "there is no evidence from nonhuman primates to indicate . . . 'female choice for genes'" (1997, p. 16; emphasis added) and that "male-male competition for rank is more important than female choice in determining male reproductive success" (ibid.). Therefore, if hominid females were unable to exert much choice in sexual matters because of male coercion, then "good genes sexual selection" would not have been very important and we would not expect "men's tendency to engage in short-term mating [to] be a direct function of their genetic fitness."

On the other hand, female choice was surely a defining feature of the EEA² and what drove the evolution of the capacity for contingent differences in male reproductive strategies that we see today. It just wasn't for "good genes" (as reflected simply in FA, that is). The evolution of prolonged helplessness in hominid children opened the way for an *alternative* male reproductive strategy. When hominid children evolved the capacity to benefit from more "good parenting" than mothers alone could provide, males were no longer *obligated* to reproduce exclusively by coercing females and competing with other males (e.g., Hrdy 1997; 1999; Smuts 1992; 1995; Smuts & Gubernick 1992). When "good parenting" by males began to make a difference in female RS, sexual selection (female-female competition) would have favored a greater capacity for females to choose mates carefully and wisely. Perhaps this is why there is more evidence for female choice for "good genes" in humans than nonhuman primates – if there is. But even if there is, there is no reason to think that "good genes" wouldn't also be involved in "good parenting." Do "bad genes" cause males to be-

come “good parents”? Do “good genes” cause males to become philanderers? If hominid females were increasingly able to choose males who were “good parents,” and if “good parenting” at least partly involved “good genes,” then G&S’s distinction between “good genes sexual selection” and “good parenting sexual selection” would seem to be muddled, and we would not expect “men’s propensity to invest in single, exclusive long-term relationships [to] be inversely related to their genetic fitness.”

What’s more, current life history models and data suggest just the opposite: men’s (and women’s) propensity to invest in single, exclusive long-term relationships is expected to be *directly* related to their genetic fitness – at least to the extent that their genetic fitness contributes to their probability of survival, adaptive growth and development, and ultimate capacity for leaving descendants. Research at the intersection of life history theory and attachment theory suggests that the development of within-sex differences in both male and female reproductive strategies are contingent on our evolved (genetic) capacity to be adaptively affected by early experiences of risk and uncertainty (e.g., Chisholm 1999a; Hill et al. 1994). Under conditions of low risk and uncertainty, when the probability of survival, adaptive growth and development, and leaving descendants is high, the optimal reproductive strategy will generally be to maximize offspring *quality* (e.g., by investing in “single, exclusive long-term relationships”) rather than quantity. This is because maximizing offspring quality tends to reduce intergenerational variance in reproductive success, which results in greater long-term fitness than maximizing offspring quantity in each generation. On the other hand, under conditions of high risk and uncertainty, when the probability of survival, adaptive growth and development, and leaving descendants is low, the optimal reproductive strategy will generally be to maximize offspring *quantity* (e.g., by engaging in short-term sexual relations with several partners). This is because maximizing offspring quantity maximizes the probability of leaving *any* descendants at all in risky and uncertain environments. It may be evolutionarily rational to sacrifice offspring quality for increased quantity when such a tradeoff reduces the probability of lineage extinction in risky and uncertain environments (for the full argument see Chisholm 1999b). The current-future tradeoff, as it is known, may thus account for within-sex differences in reproductive strategies better than the tradeoff between “good genes” and “good parenting.”

NOTES

1. G&S credit Thiessen (1994) for this insight but it was originally Richard Wrangham’s (1980).
2. G&S credit Alcock (1993) for this concept but it was originally John Bowlby’s (1969, p. 50).

More women (and men) that never evolved

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Abstract: We are not convinced by Gangestad & Simpson that differential mating strategies within each sex would be greater than such strategies between sexes. The target article does not provide actual evidence of human males who do not desire mating with multiple females, or evidence that the benefits for females of short-term matings with multiple males have ever outweighed the associated costs.

We are in full agreement with Gangestad & Simpson (G&S) that recent advances in the identification of “good gene” markers (e.g., symmetry) are an important contribution to theories of human mating. Unfortunately, rather than integrating such information into the cogent existing theories of the differences between males and females, the authors appear to attempt to overthrow such the-

ories by exaggerating the differences within each sex. Although their new theory may have certain ideological appeal, we are not convinced that the differences in sexual desires within each sex are greater than those between each sex.

The claim of greater within sex-variation hinges on the evidence of “unrestricted” women with what was previously thought to be “male-like” desires for short-term matings, and “restricted” men who lack the “powerful desire for sexual access to a large number of women” previously considered to be universal among human males. In support of these claims, G&S cite surveys asking such questions as how many sexual partners individuals expect to have in the future. From this evidence, they conclude that both males and females have evolved to pursue both, or perhaps favor either, long-term and/or short-term mating “tactics” (see Gangestad & Simpson 1990; Simpson & Gangestad 1991a, for a full review). There are, however, problems with using this type of evidence to measure the within and between sex variations in terms of the evolved desires motivating the sexual behavior.

Short-term matings must be interpreted within the context in which they occur. This context includes whether either the male or female actually desire a short-term, as opposed to long-term, relationship. As G&S mention, the research of Buss and Schmitt (1993) indicates that females may use short-term matings as a way of attracting long-term mates. Further, short-term matings that occur in novel environments (e.g., interactions initiated in anonymous single bars under the influence of alcohol and involving birth control) are not necessarily evidence of evolved short-term mating tactics in ancestral environments that lacked these features.

Answers to survey questions (e.g., Simpson & Gangestad 1991a) are also problematic as measures of sexual desire because even if the answers are assumed to accurately reflect the subject’s thoughts and feelings, the reasons for these thoughts and feelings must still be considered when interpreting the results because these reasons are likely to vary greatly between males and females. For example, identical self-reports of the number of sex partners expected by a male and female may mean very different things because of the tremendous difference between males and females in their ability to actually engage in sex with desired partners (see Symons 1979). Answers concerning attitudes about impersonal sex are even more problematic as measures of one’s own sexual desires. What is needed to support G&S’s claim that some men lack a powerful desire for sexual access to a large number of women but is not provided, is evidence of males who fail to be sexually aroused by the thought of, or the visual depictions of, short-term sexual encounters with numerous attractive females.

G&S also fail to provide ethnographic evidence demonstrating “that women anywhere normally tie up multiple male parental investments by confusing the issue of paternity” (Symons 1982, p. 299), or that women regularly lived in environments where male parental investment was ever so unimportant as to be outweighed by the benefits of short-term matings for good genes, and again no such evidence exists. They also fail to consider reasons for doubting that such tactics would have evolved. Although the authors stress that “one must weigh the benefits *in relation* to the costs to appreciate whether and how adaptations evolved during evolutionary history” (sect. 1.3; emphasis in original), they consider only the possible benefits in suggesting the plausibility of Hrdy’s (1981) hypothesis that “females may induce paternity uncertainty by having multiple mates, possibly leading to more protection or greater tolerance of offspring by different men” (sect. 1.1). What they fail to fully consider is that marriage is a cultural universal and “human sexual impulses were molded in a milieu in which adulterous wives risked being abandoned, beaten, and even killed (Symons 1982, p. 299). Research among the Ache has supported the view that although multiple matings by women may lead to greater tolerance of offspring “the price to be paid if extramarital affairs are discovered . . . can be quite high” (Hill & Kaplan 1988, pp. 298–99). Given such risks incurred by “unrestricted” females and their offspring, the genetic benefits gained by such tactics would have

had to have been tremendous to have offset the benefits obtained via long term mating strategies, including male parental investment and male kinship ties. G&S fail to provide any evidence of genetic benefits that would sufficiently justify such a trade-off.

In conclusion, new knowledge about the markers of genetic quality is important because genetic quality almost certainly influences mating opportunities. Some females obviously engaged in short-term sex with males during our evolutionary history, and they may have been more likely to do so with males showing markers of genetic quality. Males also probably vary to some degree in their desires for multiple partners, and a male's genetic quality may certainly influence his actual numbers of partners. However, none of these observations are particularly new, and none of them are incompatible with conventional evolutionary models of human sexuality (Buss 1994b; Trivers 1972) or the claim that "with respect to sexuality, there is a female human nature and a male human nature, and these natures are extraordinarily different" (Symons 1979, p. v).

Adaptive flexibility, testosterone, and mating fitness: Are low FA individuals the pinnacle of evolution?

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Abstract: The expansion of human evolutionary theory into the domain of personal and environmental determinants of mating strategies is applauded. Questions are raised about the relation between fluctuating asymmetry (FA), testosterone, and body size and their effects on male behavior and outcomes. Low FA males' short-term mating pattern is considered in the context of an evolved tendency for closer and longer human relationships.

The Gangestad & Simpson (G&S) team have contributed some of the most creative and intriguing work in evolutionary social psychology, and the current article continues that tradition.

First, the target article extends the analysis of how male and female mating strategies involve flexible trade-offs due to various contingencies. Others suggested that individuals engage in trade-offs of desirable mate qualities in a potential partner, such as youthfulness versus maturity (Cunningham et al. 1997) and agreeableness versus dominance (Jensen-Campbell et al. 1995). G&S went beyond individual decision-making to explore how ecological variables, such as parasite prevalence and resources, influence the importance placed on various mate selection qualities. The capacity of both genders to employ various mate selection strategies adaptively is a useful correction to a literature that tends to overemphasize male interest in physical appearance and female interest in wealth.

Second, G&S suggested that one of the most important variables affecting individual mating strategies is the individual's attractiveness to the opposite sex, which is linked to fluctuating asymmetry (FA). The impact of mutations and disease on FA, and the effect of FA on mating success, is clear in the animal literature. The human parallels are fascinating: males with low FA appear to have a higher number of lifetime sexual partners, including extra-pair partners; they more reliably stimulate female orgasms; smell more attractive to females who are in the fertile phase of their menstrual cycle; and boast about themselves while belittling their competitors to obtain a date.

Most human variation in FA is difficult to see, raising the question of the mediators of the relation between FA, behavior, and mating outcomes. Although FA is correlated with facial physical attractiveness and intelligence, the correlations seemed too small to carry all of the effects (Shackelford & Larsen 1997). Behavioral

effects were generally stronger for males than females, and remarkably similar to the behaviors associated with testosterone levels. High testosterone males are more aggressive and have a higher number of sexual partners (Dabbs & Morris 1990). Testosterone tends to produce a rugged, masculine appearance, one component of male physical attractiveness (Cunningham et al. 1990). In addition, females at midcycle prefer the appearance of more masculine faces, compared to other times in their cycle (Penton-Voak et al. 1999).

Could a portion of the relation of FA to behavior be mediated by testosterone levels? Gangestad et al. (1994) suggested that possibility by noting that, because high testosterone levels tend to suppress immune functioning and increase the risk of disease, and low FA individuals may have robust immune systems, they may be more capable than others of sustaining a high testosterone level. A relation between FA and testosterone would be congruent with the relation between low FA and both physicality (muscularity, robustness, and vigor) and social dominance.

The inverse relation between male FA and body mass (Manning 1995) also might follow from a testosterone (or growth hormone) interpretation, but raises a measurement question about the relation between FA and size. FA is typically calculated as the difference between right and left side features, divided by the average of the left and right measurements to standardize relative to total characteristic size. This is an appropriate calibration, but it also means that asymmetries of the same absolute magnitude at birth may produce lower FA scores for larger than for smaller people in adulthood, depending on the growth process.

Low FA indicates the accurate translation of genotype into phenotype. Relations with other forms of fitness, such as size and muscularity, require further analyses. Females are known to prefer males who exemplify sexual dimorphism, who are tall, large-chested and mesomorphic (Beck et al. 1976; Graziano et al. 1978; Shepard & Strathman 1989). The effect of height was partialled out in some of the cited studies, while body mass and mesomorphy were addressed less frequently (Gangestad & Thornhill 1997a). A simple way to consider this question is: Would women prefer a man who is short and thin, with a receding chin, but who has symmetrical body features (low FA), over a tall, mesomorphic man, with a square chin, who has asymmetrical features (high FA)? In evaluating that issue, it would be interesting to know if the effect of asymmetry is linear across all FA scores, or if there is a threshold effect, with little impact across lower FA scores, but marked impact as FA becomes extreme.

As a third focus, G&S suggest that pathogen prevalence inclines women toward a "good gene" mate selection strategy, whereas the need for paternal investment inclines women toward a "good provider" mate selection strategy. That is a provocative extrapolation from the animal literature. But conceptualizing long-term relationships primarily in terms of material benefits to the offspring or mate may obscure some of the species-typical mate dynamics of homo sapiens.

To sustain a long life-span, allowing individuals to provide continuing care and encouragement to children, grandchildren, and other kin, it is valuable to have an emotionally supportive mate (Cunningham & Barbee, in press). Our research indicated that both males and females seek partners who exchange high levels of emotional support and communication, and that is rated as more desirable in a long-term mate than either good genes or good provider qualities (Cunningham et al. 1999).

If low FA males are the most physically fit and desirable, then they could be said to be the pinnacle of human evolution. Is there any way to reconcile our belief that humans have generally been evolving toward closer, longer relationships, with the reported tendency of the highly fit, low FA males to pursue a short-term mating strategy and sexually unrestricted life style? Do only those males who are less fit exemplify loyalty and supportiveness (cf. Simpson et al. 1999)?

Perhaps some of the observed differences between low and high FA people were owing to a minority of high testosterone,

highly unrestricted males. Perhaps most low FA individuals are relatively agreeable, empathic, and disinclined to cheat on their partners. That might be determined by examining outcomes based on modal responses rather than group means (cf. Miller & Fishkin 1997). Another possibility is that low FA males employ a mixed strategy, pursuing short-term mating at one point in their lives, and a more committed long-term strategy with greater maturity. Or, on a more misandronistic note, perhaps low FA males act the way all males would if they were unconstrained: seeking closeness, support, and loyalty from their partner, but retaining the possibility of pursuing an unrestricted lifestyle if they meet a desirable new mate.

Regardless of those concerns, G&S have provided insightful illumination of the complex terrain of environmental challenges and sexual opportunities, while making an engaging case that the fittest individuals have the most choices in that domain.

Mating systems and fluctuating asymmetry: Firm foundations?

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Abstract: Gangestad & Simpson review sexual selection theory and discuss their work on fluctuating asymmetry and mate preference in humans. We question some aspects of their account and mention problems with the data. We also suggest that more theoretical work on complex but realistic mating systems is required.

We are glad that Gangestad & Simpson (G&S) go beyond the naive view that all humans of a given sex should behave in one way. They have made a serious attempt to relate human sexual behaviour to evolutionary models of nonhuman behaviour, an approach with which we are sympathetic. However, we do not feel that the base from which they extrapolate to humans is as well founded as they imply, either in terms of the theoretical predictions, or the empirical patterns observed in nonhuman studies. Many of the ideas in their target article lead to important research questions that have not been tackled adequately in theory or experiment with nonhuman animals, far less our own species, and thus result in a challenging research programme for sociobiology as a whole.

In the first part of the target article, G&S outline sexual selection theory, but their account is selective. There are two noteworthy omissions from the list of possible models of preference. One is Fisher's runaway process. This is perhaps not surprising – interest in this process seems to have waned. What is surprising is that there is also nothing on sensory biases. This is the idea that male attractiveness may depend on properties of the sensory system of females that are adaptive in other contexts or are not adaptive at all (Ryan 1990; 1997). Preference for symmetry in the context of mate choice may be the result of a sensory bias in favour of symmetrical forms (Ryan 1997; Swaddle & Cuthill 1994). G&S emphasise good genes as a basis for extrapair matings, but Enquist et al. (1998) have argued that such matings can be maintained without the need to invoke good genes.

A complete account of mating preferences and patterns of care involves several levels of interaction. For example, an animal's decision about whether to divorce its partner depends on the quality of available mates, which in turn depends on divorce decisions (McNamara et al. 1999a). Although G&S are not very explicit about these interdependencies, they do touch on them in their discussion of the interaction between male and female patterns of choice (e.g., sect. 5.5). Situations as complex as those considered by G&S are relatively unexplored from a theoretical perspective. Theory has only recently been developed to investigate the effect

of quality differences in negotiations over parental effort (McNamara et al. 1999b). Our point is that no simple prediction can be made about the optimal allocation of parental resources to mating and parental effort, as a function of self and partner quality, when quality is based on variables such as parenting ability, heritable disease resistance, and current energetic reserves.

A simple example may make this clear. In section 1.1, G&S mention the idea that by having many mates a female may reduce the probability that a given male is the father and that as a result males may be more tolerant or protective towards offspring (Hrdy 1981). But under some circumstances, reduced probability of paternity may reduce paternal care (e.g., Houston 1995; Westneat & Sherman 1993). Even in the absence of quality differences, the relationship between paternity and the total help that the female receives may depend on details of the fitness functions (Houston et al. 1997). The effects of paternity, parental ability, and energy reserves on evolutionarily stable levels of care have not been explored.

Although G&S paint a convincing picture that fluctuating asymmetry (FA) serves as an all-embracing measure of individual quality, there are problems. First, there are serious doubts that it does; second, even if it does, this may not be particularly useful to students of sexual selection. Meta-analyses of the literature on symmetry have been vigorously criticised (Houle 1997; Palmer 1999). There have been over 100 studies of the relationship between symmetry and attractiveness, but only a handful are experimental manipulations which rule out confounding variables, and even these give equivocal results (Swaddle 2000, pp. 339–59). The best that can be said of FA and relationship to either attractiveness or viability in non-human animals is “not proven,” and recent research on human facial attractiveness would actually suggest that symmetry is not the primary determinant (Scheib et al. 1999). However, even if there proves to be a consistent relationship between symmetry and fitness, the very sensitivity of FA to so many factors affecting development may make it unsuitable for the research programme G&S's article suggests. If asymmetry is a general indicator of fitness, it may have limited usefulness as an indicator of specific qualities. The possibility that males and females chose mates for specific qualities (good parent, heritable disease resistance), dependent upon their own phenotypes and genotypes, is perhaps the most exciting line of future research suggested by Gangestad & Simpson's target article; but this will require more sensitive markers of the many facets of *quality* than FA.

A few tips on hypothesis testing

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Abstract: Gangestad & Simpson's account of the role of good-gene sexual selection in conditional human mating strategies is reasonably convincing, but could be more so with a little more attention to (1), dropping unnecessary sub hypotheses and especially (2) the inclusion of alternative evolutionary explanations.

Gangestad & Simpson (G&S) have provided us with a carefully constructed account of human mating strategies. They have built a monument to the validity of using good-gene sexual selection theory to explain conditional human mating strategies. They provide us with a profusion of data consistent with their conclusions. All of this makes for a lengthy, detailed, and consistent story.

Although they have already done so much, there are at least two more things they need to do if they want to insure that their conclusions are built upon a solid foundation. Both concern their treatment of hypotheses.

Take the hypothesis in section 5.7.1 about the relationship be-

tween women's mating tactics and the need for biparental care to raise children. Ask yourself the following question: If the hypothesis that women raised in single parent households adopt short-term mating strategies because they have been provided with cues that long-term stable pair-bonds are unnecessary was proved false, where would that leave the validity of good gene sexual selection (GGSS)? For that matter, where would it leave the more local prediction about the relation between women's childhood experiences and adult mating tactics? If your answer is: in the same place they would be if it were true, then you've gotten my first point. Whether the adoption of short-term mating tactics by women in this situation is owing to them thinking they do not need paternal care, or thinking they are in an environment where long-term stable pair-bonds are rare is certainly an interesting question, but it is irrelevant to the point G&S need to make, which is simply that women's mating tactics do vary, and vary along dimensions consistent with GGSS.

On the other hand, if this behavior turns out to be the nonadaptive outcome of a usually adaptive developmental mechanism, it is time to worry. This brings me to my second point, which concerns the explication of alternative hypotheses. G&S's conclusions would be much tighter if they spent more time, or even any time, trying to generate and test their theory against alternative evolutionary hypotheses. For example, they mention the relationship between men's physicality and fluctuating asymmetry (sects. 4.4 and 5.2) two factors which they claim are highly correlated. They also cite several authors (Hrdy 1981; Mesnick 1997; Smuts 1985; Wilson & Mesnick 1997) for the idea that women may have evolved to prefer men who could provide them with protection from other, aggressive men, but they take this argument no farther. Wouldn't the argument that women's short and long term mate preferences have evolved as a means of minimizing physical danger to themselves and their children be a reasonable alternative hypothesis to GGSS? Given the relationship between physicality measures and fluctuating asymmetry, wouldn't this alternative hypothesis also be consistent with their data? Perhaps physicality is not simply a mediating factor of symmetry; perhaps it is the central factor. Until they address it, and others like it, directly pitting them against GGSS; it's hard to take GGSS as a proven, or even uniquely supported, theory of human mate choice.

Just one more small point, unrelated to the preceding discussion, yet something I cannot let slip by. Most of the evidence they provide is correlational, and, given their subject matter, providing anything experimental would certainly be difficult. Although they do a good job of interpreting their results, a few confluations of correlation with causation do slip through (e.g., their discussion of extra-pair paternity in birds (sect. 3.3, para. 7).

I would hate this criticism to leave the impression that I believe G&S's work to be neither valuable nor important. Mate choice is one of the best studied topics in evolutionary psychology, and their treatment of it in this paper, and especially their focus on conditional mating strategies, is a major contribution to it. It is, in fact, precisely for this reason that I feel the need to urge them to take what is already very good and make it even better.

Do Don Juans have better genes than family men?

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Abstract: An alternative interpretation of Gangestad & Simpson's findings features the assumption that only a subgroup of those men who are low in fluctuating asymmetry are typically available for short-term mating. In general, these philandering men do not offer higher genetic quality than men who are securely attached to long-term mates.

In their theory of human mating, Gangestad & Simpson (G&S) attempt to account for a wider variety of phenomena than have other evolutionary psychologists. Nonetheless, because their theory neglects important determinants of mating that are not a product of genetically based programs, they go beyond existing evidence in arguing for trade-offs between mates' genetic fitness and their proclivity to become family men who are securely attached to their wives and children.

Because humans' environment of evolutionary adaptedness (EEA) encompassed highly variable conditions that impinged in differing ways on hominids' reproductive behavior (e.g., Irons 1998), humans manifest a wide range of different solutions to the problems of reproduction and survival. Humans' reproductive behavior is marked by behavioral flexibility, and many aspects of mating and parenting are free to vary in response to social learning and multiple aspects of the contemporaneous environment. Nonetheless, some decision rules for mate choice would have been sufficiently general-purpose that they may well have become encoded genetically. In agreement with G&S, these inherited programs may include a tendency to seek strong and healthy mates and avoid weak and diseased mates.

A reinterpretation of the evidence that G&S offer follows from minimalist assumptions that humans are genetically endowed with a general motive to mate, which operates in conjunction with the tendency to seek strong and healthy mates and avoid weak and unhealthy mates. From this perspective, women's tendency to engage in short-term mating with men marked by low fluctuating asymmetry (FA) does not require the assumption of trade-offs between child-rearing and mating or of an inherited contingent decision rule. Instead, a plausible alternative theory follows from first assuming that women find men high in FA relatively unappealing, because women follow the rule about avoiding mates who are weak and potentially diseased. To the extent that high FA men manifest abnormalities and weaknesses, women generally avoid them for both short-term and long-term mating.

The second assumption required for this alternative theory is that, with respect to sexual behavior, there are two types of men who are low in FA; these types reflect, not differences in genetic quality, but different conditions of rearing in their families of origin. Consistent with evidence provided by Draper and Harpending (1988) and Miller and Fishkin (1997), men's sexual behavior echoes the security of their bonding with caretakers in their families of origin. Men who were insecurely attached to their own parents have difficulty forming enduring relationships with women and instead are vulnerable to becoming promiscuous, philandering men who invest minimally in their partners and offspring. Men who experienced more favorable parenting are more likely to form stable, monogamous marriages and to invest in their children.

For short-term mating, women seeking sexy, healthy, attractive partners would have little option but to pair with promiscuous, philandering men, because such men are readily available for sexual encounters, whereas securely attached men are typically unavailable. Therefore, the reason that FA is correlated with indicators of mating success is, in part, that high FA men have difficulty attracting women under any arrangements. The promiscuous subtype of low FA men also help produce the negative association between FA and mating success, because these men have multiple relationships. In contrast, the securely attached subtype of low FA men dampen this association somewhat, because they have relatively few partners, although probably more than the high FA men, who are unappealing to women for short-term and long-term mating. The rather weak correlations that G&S cite between FA and variables such as number of sexual partners and investment in relationships are fully consistent with this reasoning. Other types of empirical evidence would be required to distinguish between G&S's theory and the alternative that I propose.

According to this alternative theory, promiscuous men do not offer better genes than men who are securely bonded to their mates. Also, the aggregate reproductive success of men in the two groups may be comparable because promiscuous men's casual

matings with many women are balanced by bonded men's enhancement of the health and welfare of a single mate and her offspring, who are then more likely to survive. Moreover, a contingent genetic program driven by good genes selection does not underlie women's tendency to form short-term relationships with promiscuous men. Rather, women are interested in sexual affairs when their primary mateship is damaged, ordinarily because it is sexually or emotionally unsatisfying. Sometimes this damage follows from a woman's bad luck in attempting her primary relationship with a low FA man who has difficulty with long-term attachments. The cost-benefit analysis that then guides the sexual decision-making of women with damaged mateships would incorporate various considerations, including sexual desirability (low FA men tend to be sexually appealing) and ease of establishing short-term relationships (men from the promiscuous subgroup of low FA men tend to be available).

Other utilities guiding women's sexual decision-making would take into account the likely consequences of a sexual affair. These consequences may include being stigmatized in their community and alienating a long-term mate who contributes fathering and other valued resources to the family. These perceived utilities are constrained by social norms that govern family life and sexuality, which may differ for women and men. As Eagly and Wood (1999) argued, in societies in which men and women occupy distinctively different social roles, the sexes perceive different utilities and have somewhat different mating preferences. The mating preferences and behaviors of women and men are more similar when they occupy more similar positions in the social structure. More generally, the context for human sexuality is a community that establishes family roles, defines allowable sexual behavior, and specifies appropriate mate choices.

Human mating models can benefit from comparative primatology and careful methodology

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Abstract: Conditional mating strategies and within-sex variation in mating patterns occur across a wide range of primate taxa. Attempts to model the evolution of human mating strategies should incorporate current primatological data sets and phylogenetic perspectives. However, comparisons between interview and questionnaire-based human behavioral data and observationally and experimentally generated nonhuman behavioral data should be conducted with prudence.

Conditional mating strategies and within-sex variation in mating patterns are not unique to humans but are prevalent across a broad range of primate taxa, and the examination of these patterns is critical to modeling of the evolution of social organization. When searching for the set of behaviors apparent in any period of human evolution (such as the Environment of Evolutionary Adaptiveness, EEA, for example) a phylogenetic perspective across primate taxa will facilitate a robust set of hypotheses regarding the evolutionary sequences of current behavior (Rendall & DiFiore 1995). I applaud Gangestad & Simpson's (G&S's) attempt to model the variation and trade-offs that have molded human mating strategies over the course of our evolutionary history and to posit actual mechanisms for these strategies. This interest in variation in mating patterns and strategies is well in line with current reanalyses of mating systems across a number of taxa (Black 1996; Fuentes 1999b; Henson & Warner 1997). However, their primary reliance on human interview data and extrapolations from the avian literature ignores the diversity of primatological data relative to their inquiry and weakens their ability to effectively design

evolutionary models. If we are to "understand the psychological architecture that guides social interactions" (Introduction) it is critical that the investigation include the available data from those organisms which are phylogenetically, physiologically, and behaviorally closest to our species.

In the target article, G&S suggest that good genes sexual selection (GGSS) and good parenting sexual selection are the main factors in the evolution of variation in human mating patterns. They rely heavily on basic behavioral ecological concepts of male and female sexual strategies (Buss & Schmitt 1993; Trivers 1972) and studies of fluctuating asymmetry (FA) in humans and birds to convey their hypotheses.

Data from recent primatological studies suggest that the traditional examination of male mating and parental investment has overlooked the wide and costly array of physiological and social mechanisms. Physiological studies on a wide range of primate species (see Berkovitch 1991; 1999, for a review) have demonstrated greater pre-mating investment on the part of males than previously considered (i.e., based on Trivers 1972). An examination of the physiological and social pre-mating investment mechanisms in primate males (including humans) would add to, and broaden G&S's model and could affect their assessments of male and female choice as it relates to parental investment (a major component of their conclusions).

Relying on fluctuating asymmetry as "the best available measure" (sect. 3.3) to test the Good Genes Sexual Selection model is overlooking data from primate studies. For example, Fox et al. (1999) reported lack of support for "good genes" hypothesis in mating patterns in a long-term study of orangutans in Sumatra. Extra-pair copulations (epc) in pair-bonded species are frequently examined in discussions of "good genes" models, yet G&S do not refer to the wide range of recent work on epc's in pair-bonded primates (Brockleman et al. 1998; Palombit 1996, 1999; Reichard & Sommer 1997). Interesting to note, the correlation between men's FA and extra-pair sex partners reported by G&S ($r = -.17$, sect. 4.2) is rather low.

G&S utilize examples from studies on Zebra Finches and Barn Swallows to support their discussion of FA in humans. The meta-analysis (Moller & Thornhill 1998a) of FA on which G&S rely for their support of GGSS is heavily biased by avian and insect studies with only five mammalian species, and no primates aside from humans, represented in the data set. Given the wide differences in morphological adaptation across taxonomic classes, the usefulness of this comparative tool is debatable without the inclusion of additional mammalian studies.

A brief review of the primatological literature is of particular relevance to section 4.5 (Evidence for women preferring symmetrical men for their gametes). For example, the target article cites one study in which female macaques orgasm more frequently with dominant males (Troisi & Carosi 1998) for primatological evidence in support of the assertion that female orgasm favors more symmetrical males in humans. However, van Noordwijk (1985) demonstrated there was no consistent relationship between female orgasm and macaque male dominance, and recent work by G. Goldstein and myself also reveals a lack of correlation between female orgasm and male rank in macaques (unpublished data). Additionally, G&S rely on Bellis and Baker's (1990) reports of human epc's during peak fertility (based on interviews and questionnaires), but do not include data from field observations of other primates' epc patterns (i.e., Brockleman et al. 1998; Palombit 1996; 1999; Reichard & Sommer 1997).

There is a diverse and growing body of literature specifically regarding pair bonds, monogamy, and mating patterns in primates (see Fuentes 1999a; 1999b for reviews). There has also been a diversification in the literature concerning the evolution of human social organization, especially in regard to child rearing investment by nonparents and other aspects of social organization (see Bird 1999; O'Connell et al. 1999). The inclusion of primatological and human evolutionary literature would enhance G&S's attempts to model the causal factors behind human mating patterns and po-

tentially alter their conclusions. Their current focus on avian studies and human psychological research limits their applicability in a comparative evolutionary context.

Finally, I would add a word of caution from the perspective of anthropological methodology. G&S (and many others investigating human psychological evolution) rely heavily on interviews and questionnaires for their data on human behavior. However, they make direct comparisons to field and laboratory observations of nonhuman behavior as if the two data types were essentially equivalent. Care must be taken when conducting such comparisons. While expanding our data sets is beneficial, the confounding variables in the methodology of many human studies can make direct comparisons difficult (unless similar methodologies are used for human and nonhuman subjects, see Cords & Killen 1998; McDowell et al. 1999). Additionally, human focused studies need to consistently gather a wide range of information from across the human social and cultural continuum to assess accurately human mating preferences and strategies (see Yu & Shepard 1998).

While investigations, such as the target article, into current human mating patterns are important for modeling human evolution, successful models for mating strategies will need to incorporate a wider range of phylogenetically relevant data.

Sexual strategic pluralism through a Brunswikian lens

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Abstract: Genes controlling the choice of sexual strategy must be sensitive to critical environmental contingencies, including the presence of other strategically relevant genetic traits. To determine which strategy works best for each individual, one must assess both its environment and itself within that environment. Psychosexual development involves an assessment of sociosexual affordances, strategically calibrating optimal utilization of physical and psychosocial assets.

Many years ago, Sheffield et al. (1951) examined Mower (1938) and Hull's (1943; 1951) drive-reduction theory of reinforcement, reporting that male rats acquire an instrumental response when the sole consequent of the response is copulation with a receptive female. The rats were not permitted to ejaculate. Later work in this area reported that (1) mounting itself provided no reinforcement; (2) mounting and intromission somewhat better reinforcement; and (3) mounting, intromission, and ejaculation the best reinforcement in an instrumental situation (e.g., Kagan 1955). Upon reading the present article, we find ourselves, like Sheffield's rats, rewarded but not completely satisfied. To help produce a more fully rewarding state of affairs, we attempt to articulate the theory as we construe it and then try to flesh it out. We then invite the authors to correct any misrepresentations that we might have introduced.

Any given autosomal gene spends an average of half its history in a male and half its history in a female body. The fact that its expression is constrained by its environment, including other genes, suggests that an autosomal gene may be expressed in one way in a female body and another way in a male body. Assuming that there exists a gene or set of genes we might term Sexual Strategy Regulator Genes (SSRGs), identical SSRGs could have unique expressions when contained in male and female bodies. Furthermore, many other characteristics of that body may also be relevant.

We highlight these genetic interactions because some of the documented correlates of the alternative sexual strategies described by Gangestad & Simpson (G&S) are troubling. For example, of the mediators listed for the effect of Fluctuating Asymmetry (FA) on sexual attractiveness, and indirectly on optimal selection of sexual strategy, only Social Dominance is a plausible

behavioral reaction contingent on FA. Body Mass and Physicality are biological traits that, although influenced by FA, are not exclusively attributable to FA. Some of the documented correlates of the proposed conditional sexual strategy are therefore traits that could be independently inherited and are not necessarily produced by FA. We therefore suspect that behind the current discussion, focusing primarily on direct and indirect effects of FA, lurks a more inclusive theory. Any hypothetical SSRG that controls the choice of sexual strategy must be sensitive to critical environmental contingencies, including the presence of other strategically relevant genetic traits, such as FA.

The genetic basis for the strategic pluralism proposed in G&S may therefore represent a conditional adaptive strategy involving elements of reactive heritability. Although behavioral ecologists have specified the functional requirements of conditional strategies, the proximate mediation of such an adaptation is not well specified. One common metaphor is the "developmental switch," an ethological mechanism, analogous to imprinting, in which a specific environmental contingency directly triggers an innate releasing mechanism for the conditional strategy. This kind of "push-pull, click-click" mechanism was historically favored by ethologists and behavioral ecologists to avoid conjecture about mental faculties (cf. Tinbergen 1950). Although such simple mechanisms might exist in less complex species (e.g., insects; cf. Thornhill & Alcock 1983), there also exist well-established mechanisms of behavioral development in complex vertebrate animals (e.g., humans) that can plausibly produce the functional equivalent of a conditional developmental strategy.

Unlike classical learning theories (Hull 1943; Spence 1956), wherein conditioning unconsciously reinforces associations between stimuli and responses, cognitive learning theories (e.g., Brunswik 1952, 1955; Tolman 1925) suggest that an organism learns the relative efficacy of various responses, representing alternative means to a desired end. Through interactions with the environment, an organism establishes a hierarchy of alternative ("vicarious and intersubstitutable") responses based on experience with the relative ecological validities of alternative means for producing a given distal achievement (cf., Petrinovich 1979), which assess the relative efficacies of various biologically prepared adaptive strategies. Learning need not be totally *de novo*, but is instead based on evolved behavioral programs (e.g., human language acquisition; see Pinker 1994; see also, Garcia & Ervin 1968; Garcia et al. 1974; Mayr 1974; Seligman 1970; Seligman & Hager 1972; Waddington 1957).

Because interaction with the environment determines which behavioral strategy works best for each individual, other individual differences also matter. An individual not only assesses its external environment, but also assesses itself within that environment. Gibson (1979) refers to similar transactional contingencies as *affordances*. Psychosexual development involves a self-assessment of sociosexual capabilities and opportunities, calibrating optimal utilization of physical assets such as size, strength, health, and attractiveness, as well as psychosocial assets such as intelligence, self-efficacy, social skills, personality, and socioeconomic status and/or prospects (cf., Hunter & Figueredo 2000). Individual differences in self-assessment also play a major role in which of the available strategies is implemented.

Figueredo et al. (2000) recently applied this framework to address the ultimate causes of adolescent sex offending behavior by proposing a Brunswikian Evolutionary Developmental (BED) Theory, wherein an inability to use mainstream sexual strategies lead an individual to develop deviant sexual strategies. Because some adolescents suffer psychosocial problems and consequent competitive disadvantages in the sexual marketplace, sex offending behavior may represent the culmination of a tragic series of failing sexual and social strategies, leading from psychosocial deficiencies to sexual deviance, thence to antisocial deviance, and finally to sexual criminality. When indirect means of sexual competition fail, more direct means are selected (Thornhill & Thornhill 1992).

By analogy, the proximate mechanism implied in G&S is that

noncoercive mate diversification strategies are developmentally selected by individuals who are supernormally endowed with certain sexually attractive attributes, such as men low in FA (reflecting high pathogen resistance) and women low in WHR (reflecting high fecundity). Such sex-specific factors alter the relative cost-benefit ratios of mating effort with respect to parental effort in these individuals, thus biasing their Gibsonian affordances. Buss (1994b) and G&S might therefore both be right. Buss writes about desire; G&S write about behavioral strategies. Although appearing in conflict, the models hold for their different domains.

We have presented many complex ideas in very few words. If the authors disagree with our representation, we invite them to show us where we have gone wrong.

Sweet savage love: FA, BO, and SES in the EEA

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Abstract: Proxies of mate value must be evolutionarily salient. Gangestad & Simpson (G&S) have made a good case that fluctuating asymmetry is an important proxy of male mate value that correlates well with genetic and developmental quality. The use of financial variables as proxies for male investment ability by Gangestad, Simpson, and virtually every other investigator of human mating in evolutionary perspective, is, however, more problematic.

Complex, cognitive adaptations evolved to solve problems encountered in the small, kin-based groups that characterized the human environment of evolutionary adaptedness (EEA). The EEA concept is not only logically necessary when studying adaptation, but also provides a badly needed guide to both the probable domains of human decision-making as well as – importantly – the cues that are likely to inform these decisions. Gangestad & Simpson make skillful use of this powerful tool to achieve striking results. Faces and bodies were indisputable features of the EEA, and could potentially have yielded a richly informative dossier on an individual's past and present health, status, fighting ability, economic productivity, parenting ability, and genetic quality. The challenge is to discover those cues that natural selection could plausibly have relied on to “read” this dossier.

One metric, fluctuating asymmetry (FA), is computationally tractable and is reliably associated with both health and genetic quality in a number of species. It is therefore possible that adaptations have evolved to assess FA as a proxy for health and genetic quality – both significant aspects of mate value, among other things. Importantly, consistent with this hypothesis, FA has been found to be a component of human male facial attractiveness. We are particularly impressed with the finding that women in the fertile phase of their reproductive cycle are able to detect olfactory correlates of male FA. If women are indeed detecting cues of genetic quality, this would suggest that *all* women are monitoring their environment for the highest quality genes during the fertile phase of their cycle, an even stronger endorsement of good genes sexual selection than the conditional mating strategies posited by G&S. Alternatively, because bacteria contribute significantly to human scents (e.g., Gower et al. 1994), and because low FA males may have fewer or different bacteria than high FA males, it is possible that women in the fertile phase of their cycle may prefer the scent of low FA males for reasons other than harvesting good genes. If women were more vulnerable to bacterial infections and toxins at this time (perhaps owing to the increased rates of copulation that might be associated with the increased probability of conception; see, e.g., Wood 1994, p. 310), then they could have evolved to modulate their vigilance across the menstrual cycle. This and other alternative hypotheses need to be ruled out.

The conditional mating strategy hypothesis proposed by G&S relies heavily on a comparison between good genes versus male investment; it is therefore critical that proxies for the latter be as evolutionarily plausible as proxies for the former. Unfortunately, this is not the case. Future earning potential and family SES are, at best, weak proxies for male investment ability. Money in its present form is a distinctly modern invention that did not exist in the EEA.² In addition, animals have generally evolved to heavily discount the future, and family resources are often unequally distributed among offspring (e.g., Daly & Wilson 1980; Hagen et al., submitted). Important to notice, economic resources are only one of many forms of male investment that also include protection of the mother and children, territorial defense, childcare, child education, and social resources (see, e.g., Hewlett 1991; 1992). We recognize that the use of financial proxies for male investment ability is utterly standard in the human mating psychology literature, so our criticism is not aimed at G&S in particular. However, when significant correlations with a genetic quality proxy are contrasted with nonsignificant correlations with male investment proxies (e.g., in sects. 4.2, 4.5.1, and 5.1), and these within-sex contrasts are critical for the hypothesis, it is especially important that all proxies be convincing as reliable indicators of their respective mate value components *in the EEA*.³

One source of evolutionarily salient cues of male mate quality is women's mating fantasy literature, that is, romance novels (Symons et al. 1997), a genre that accounts for nearly half of all paperbacks sold in the USA (Gorry 1999). In a recent survey of 45 popular romance novels, Gorry (1999) found that traditional proxies for male investment ranked fairly low. Only 19 heroes in the 45 novels were wealthy, and 10 were actually poor! Although 25 heroes held a high status rank or occupation, 5 had a low status occupation, and 16 were social outcasts. Very few were described as industrious (12) or ambitious (6), and three did not even work.

However, male willingness to invest is clearly central to *all* romance novels surveyed. The hero is unfailingly described as obsessed with the heroine, and the plot inevitably revolves around the heroine's ultimately successful attempt to establish an exclusive, long-term romantic relationship with the hero. What qualities, then, do heroines (in novels) uniformly seek in heroes? G&S found that physical and social dominance mediate much of the relationship between FA and men's sexual history.⁴ Gorry found that similar qualities, physical and social *mastery*, were universal characteristics of romance heroes. If these qualities merely indicate good genes, then why are heroines so keen to marry men that possess them?

It is interesting that low FA men are more willing to offer physical protection to their mates. We believe ethnographic accounts of conflict and violence in small scale, kin-based societies indicate that this form of investment is both valuable to females and children and potentially more costly to males than G&S allow (e.g., Asch & Chagnon 1975; Chagnon & Bugos 1979; Gardner 1964). More generally, we predict that cues of physical and social mastery will prove to be more evolutionarily (and thus psychologically) relevant indicators of male investment ability than are the usual financial variables, and their use would facilitate the parceling of male mate value into its genetic and investment components.

Finally, with the exception of some ad hoc speculation on associated personality traits, G&S fail to provide evidence that female variation in sociosexual orientation reflects adaptive decision-making on the part of women. Despite a brief qualifying footnote, they also appear to favor the view that women engage in short-term mating primarily to obtain good genes, a view they support theoretically by citing the animal behavior literature on mating patterns and markers of heritable fitness. However, there is also a sizable animal behavior literature on nuptial gifts – tit-for-tat exchanges of resources for mating opportunities (see, e.g., Stanford 1998, p. 202; Vahed 1998) – and abundant behavioral evidence that human females also engage in short-term mating in exchange for resources. Prostitution is widespread cross-culturally (e.g., Bullough & Bullough 1993; Burley & Symanski 1981) and ethno-

graphic evidence suggests that exchanges of meat for sex also occur (e.g., Kaplan & Hill 1985).

These reservations aside, G&S have made a solid case that FA, and by implication good genes, are a component of male mate value and that, as a consequence, men and women predictably modify their mating behavior in response to both within population male variation in this trait, and to between population variation in parasite loads. This is a significant contribution to the nascent literature on conditional mating strategies in humans (e.g., Bereczkei et al. 1997; Hewlett 1991; Waynforth & Dunbar 1995).

NOTES

1. Address correspondence to the first author.

2. Although many small scale societies involved in nonmarket economies employed some form of money, many did not. Where money was used, it often had attributes that modern money does not (e.g., personal or spiritual qualities). None of these forms of money possessed all the features of currencies used in modern, state-level societies (e.g., liquidity; see, e.g., Dalton 1965).

3. It is also important that if failure to find correlations is evidence in favor of the hypothesis, then the probability that a type II error has been avoided must be determined.

4. Gangestad & Simpson also appear to assume that the total number of lifetime partners for low FA men is purely the result of female choice rather than male coercion.

Conditional mating strategies are contingent on return from investment

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Abstract: Gangestad & Simpson present an evolutionary functional analysis of mating strategies. This commentary interprets their argument using a central concept from life history theory, return from investment. Incorporating return from investment allows further specification of costs and benefits from short-term mating in women as well as men and in ecological settings of high environmental variation in mortality and resource availability.

Gangestad & Simpson (G&S) present an evolutionary analysis of conditional mating strategies in men and women, using a cost/benefit approach. Maintaining that the most advantageous strategy for humans in most situations is devoting effort to long-term mating and parental investment, they clarify the conditions where the benefits of short-term mating might exceed the costs. This extension is an important contribution to the area. They assert that our key adaptation (sect. 2.4, para. 4) is a “set of decision rules about when and how to allocate reproductive effort wisely and contingently.”

I will interpret their proposal in a broader framework of life history theory, in order to elaborate on the role of effort allocation as a basis for gender differences and environmental effects on strategy. Gangestad & Simpson employ the general concept of tradeoffs in effort expenditure. Tradeoffs apply to choices between somatic effort (own growth and maintenance), mating effort (attracting mates), or parental/nepotistic effort (caring for offspring or kin) (Roff 1992; Stearns 1992). One central concept in life history theory, *return* from investment, could be incorporated more thoroughly here. The shape of the relationship between investments and return in fitness (the return curve) is not known for humans. For most animals, we assume that the curve for return from parental investment (PI) is logarithmic, with an initial increase, then a point of diminishing returns (Clutton-Brock 1991; Horn & Rubenstein 1984; Trivers 1972). Hill and Low (1992) used return curves to illustrate conflicts of interest between men and women on termination of parental investment in a specific off-

spring, under various conditions. The same common denominator can be used to address gender differences and the effect of differing environmental conditions. This optimality approach provides insight into selective pressures on behavioral and mental mechanisms that comprise adaptive strategies, but it does not imply that mechanisms would operate optimally under current conditions in industrial societies.

Three environmental factors (value of parental investment, female independent access to resources, and parasite load) are mentioned by Gangestad & Simpson. There is extensive previous work on the role of ecological factors in human mating systems and reproductive decisions (Borgerhoff Mulder 1992; Chisholm 1993; Draper & Harpending 1982; Lancaster & Lancaster 1987; Low 1993; Wilson & Daly 1997). Mating systems (e.g., monogamy, polygyny, extended familism with short-term mating) vary across societies according to ecological factors such as mortality rate and causes, and resource distribution and defensibility (uniform, unequal, or unpredictable). In some settings for some individuals, the return is greater for investment in kin than would accrue from investing in one's own mating. A comprehensive model of reproductive strategies must account for all of these possibilities.

Considering return from PI would simplify the discussion (sect. 5.5) of mortality rates and pathogens. If the major sources of mortality are not preventable by PI, such as infectious epidemics, then there may be less return from PI. Similarly, if future resources are highly unpredictable, investment in self (and thus future mating) is less beneficial than current PI, on average (cf. Hill et al. 1997). Also, return from PI is synonymous with the “value of parenting” (sect. 5.7.1). Researchers have interpreted short-term mating strategy in terms of the lower return from PI in an unpredictable environment (Chisholm 1993; 1996; Hill et al. 1994; Weinrich 1977).

G&S conclude that ecological factors shape the behavior and distribution of females, whereas male behavior results from adaptation to the task of monopolizing females (sect. 6), which is the case for various animals (Emlen & Oring 1977). Their analysis of the costs and benefits of strategies for men and women is thus not parallel. The analysis for men is much more complete. An analysis for women as rich as that for men would involve first examining how women's personal characteristics (age, health, physical attractiveness, socioeconomic resources) affect the costs and benefits of various strategies. Second, given individual differences among women in optimal strategy, the criteria for optimal choice of male mates could be analyzed. The authors delineate developmental factors in choice of strategy for men. However, they appear to assume that all women face fairly equivalent constraints. Of course, variation in human female reproductive success is much lower than for men, but it is not zero. One's own personal characteristics and environment affect the probable return from a strategy.

In section 4.1, the authors report their finding that women's asymmetry measure was not correlated with their number of sex partners (nor to body mass, physicality, or social dominance, sect. 4.4), but number of partners is not the most relevant currency. Clearly, women will not “convert intrasexual competitive advantages into increased number of mates” (sect. 4.1), but women should convert these advantages into increased reproductive success (e.g., offspring survival or quality of mate). The factors that affect women's standing in intrasexual competition (such as age, which affects women's probability of marriage and remarriage; see Hill & Low 1992) should enter into optimal decision making on short and long-term strategies.

When either sex is choosing mates for long-term partnership with high parental effort, important mate criteria include reliability, longevity, trustworthiness, and cooperation (see Buss 1989). When men are choosing women for short-term mating, they would be optimally designed to prefer women who would successfully invest effort in a potential offspring, that is, women who are healthy enough to invest in a pregnancy now (vigor, vitality, and sufficient body fat), who also have adequate resource support for rearing a new child, either from family or from their own resources (young

women still living with parents, women with stable marriages to less valuable mates, or older independent women).

The kind of complex analysis that is necessary is exemplified when G&S compare mate choice for women stratified by degree of sociosexuality; examining preference for male symmetry when choosing short-term partners (sect. 4.5.3). Here they break down characteristics of the chooser and then analyze mate choice with female strategy in mind. This procedure illustrates their thoughtful approach, but the comparisons could benefit from grounding in a broader theory that extends to both genders and myriad environmental settings.

Are rigorous evolutionary histories of human mating possible?

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Abstract: Critics of evolutionary psychology object that it is not rigorous science compared to other evolutionary science. Advocates reply that it is rigorous science, and that the critics are uninformed. Still, informed people having opposing preconceptions of what counts as rigor may reach opposing evaluative conclusions. I shall clarify the very idea of rigorous evolutionary histories in relation to the basic objection that “evolution without history” is not rigorous.

Laudan’s (1998) model of knowledge development helps clarify the justificatory relationships between the aims, methods, and theories of a science as its research tradition changes. In a rigorous science, aims A will justify methods M and harmonize with theories T, methods M will justify theories T and exhibit the realizability of aims A, and theories T will constrain methods M and exemplify aims A. This model yields a broader conception of rigor that characterizes scientific success than “employs rigorous methods” or “meets high standards” or “strictly follows the rules.” Another virtue is that it focuses on piecemeal scientific change in which, given points 1 and 2 in time, the components can change gradually piece by piece rather than holistically, that is, in Kuhn’s terms “either you are converted to evolutionary psychology by Gangestad and Simpson or you are not.” Instead of paradigm debate as wholesale, unintelligible changes in world-view, we focus on rationally argued changes from A1 to A2, M1 to M2, and T1 to T2. Most philosophers of science find Laudan’s model superior to Kuhn’s holistic model.

Laudan’s model readily applies to the Gangestad & Simpson (G&S’s) target article. Let A1, M1, and T1 designate the research tradition in the field at time t_1 prior to their own research. At the present time t_2 , their research advances the tradition to consist in A1, T2, and M2. They endorse the original aim A1: “In the evolutionary approach one tries to understand psychological design . . . by identifying plausible constraints from selection pressures during evolutionary history.” They modify theories T1 of human mating to encompass theories T2: sexual selection theory incorporates trade-offs between good-provider and good-genes selection to explain within-sex variation in mating tactics; selection produced mixed strategies conditional on environmental circumstances and cues; and so on. They also seek to modify methods M1 to expand to M2, using three basic methods already in M1. They used the behavioral genetics and population genetics method to measure heritability, genetic variance, and the forces of mutation and selection. They used the comparative method to test good-genes selection via meta-analyses of measured fluctuating asymmetry in nonhumans and humans. They used the reverse engineering method, based on inferences to “designing” selection pressures from apparent psychological design, to predict psychological preferences. They tested these predictions about the relative roles of good-genes and good-provider selec-

tion and about between and within population differences in mating tactics.

The well-known critique from phylogeny is best expressed using Laudan’s model. The central aim of evolutionary psychology A1 explicitly commits the field to providing evolutionary histories, but because phylogenetic information is omitted we are given “evolution without history.” Let us grant that G&S carried out methods M2 in a rigorous manner as compared to other researchers in the field, that M2 improves on M1, and T2 improves on T1. Still, in the absence of phylogenetic information, M1 and M2 are insufficient to justify T1 and T2, and neither M1 nor M2 can realize the aim A1. We currently lack the right kind of evidence to justify evolutionary psychology’s theories, to make its explanations worthy of belief, and to realize its central aims. Because such evidence is not likely to be forthcoming, especially since behavior leaves no fossils and the phylogenetic record on humans is silent on key research topics, rigorous evolutionary histories in human psychology are neither actual nor possible.

This general critique can be expressed in ways that make contact with specific details in the target article. First, the findings based on population genetics methods M2 do give evidence that selection occurred. But to demonstrate something about the character and strength of good-provider and good-genes selection that can pry apart their relative roles in past selection, we need phylogenetic information about the character and extent of variation in ancestral forms. In order to assess whether the postulated mating strategies and tactics are adaptations, we must know which mating traits are primitive or derived, whether a trait is ancestral within a clade, whether it evolved in single lineage, or whether its presence is the result of convergence among lineages.

Second, findings based on the comparative methods M2 are conjectural even if we grant that the mind evolved by selection. Unless a trait is derived within a lineage, it cannot be an adaptation; yet cladistic methods were not used to reconstruct primitive and derived traits. Claims to have identified an adaptation are strongest if there is more than one independent evolutionary origin associated with comparable selective regimes. Historical variables for rates of evolution, ancestral environments, and branching of lineages are needed to construct the course of evolution. Natural selection is a mechanism governing the course of evolution, not the cumulative results of evolution directly. It follows that an “evolution without history” approach, which examines cumulative results only, cannot succeed in showing that specific strategies were selected for which explain the specificity of apparent psychological design.

Third, findings based on reverse engineering methods M2 cannot rule out a host of rival selectionist hypotheses. A trait perpetuated by one form of sexual selection is potentially subject to all forms: male preferences for females, female preferences for males, male-male competition for mates, and female-female competition for mates. Females should prefer the scent of males who win male-male contests based on phenotypic outcomes of good genes, but lower ranking females might prefer the scent of males who avoided male-male competitions to minimize risks of injury and lowered social status. Given that men’s evolutionary role as hunters and warriors against other groups gave them the power to persuade, coerce, and rape females in their own group, variation in female tactics of short-term mating and extra-pair copulations should depend on how often ancestral males could force females to have sex regardless of female preferences, and female preferences could then be constrained by male power to take for granted that females will often have multiple mates. The fitness-enhancing value of these tactics could also be affected by their age (because reproductive value varies with age), number of previous partners, number of previous births, the female’s social status, and future reproductive prospects. We could use such points to construct a number of competing hypotheses.

Typically there are two or more historical routes from a past population composition to a present one. So, tracing current functions of current traits cannot tell us which is the correct route.

Instead of the vague EEA concept, which compares selective pressures in only two environments (modern and ancestral = Pleistocene), we need a detailed chronology that reaches deeper into our hominid and primate ancestry to know which sequences of ancestors, environments, and alternative phenotypes are the proper focus of inquiry for which traits.

Dynamical systems and mating decision rules

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Abstract: Dynamical simulations of male and female mating strategies illustrate how traits such as restrictedness constrain, and are constrained by, local ecology. Such traits cannot be defined solely by genotype or by phenotype, but are better considered as decision rules gauged to ecological inputs. Gangestad & Simpson's work draws attention to the need for additional bridges between evolutionary psychology and dynamical systems theory.

What would the world look like if women were as unrestricted as men? Attraction patterns in male homosexuals are in many ways similar to those of heterosexual men. Both, for example, emphasize attractiveness over status and both change preferences from relatively older to younger partners with age (Bailey et al. 1994; Kenrick et al. 1995). But homosexuals' partners are, on average, as unrestricted as they are. Gay men who contracted AIDS during the 1980s had an average of 1,100 partners, and those without AIDS had several hundred (Michael et al. 1994). In contrast, the mean lifetime total for heterosexual males is 12; most men having fewer than 5 (Michael et al. 1994; Smith 1994). But over 70% of men accepted a female stranger's invitation for sex in one field experiment, suggesting things might change if heterosexual men had more offers (Clark & Hatfield 1989). Such statistics support Gangestad & Simpson's (G&S's) conclusion that men gauge their levels of restrictedness to women's. The majority of men, free of temptations offered by female strangers, marry and remain faithful to their wives (Michael et al. 1994).

We have used computer simulations to study how decision-rules of one sex affect mating decisions made by the opposite sex. Figure 1 depicts an initial arrangement in one such community. We estimated initial numbers of restricted and unrestricted individuals from published data indicating 67% of college women and 42% of men desire only one sexual partner for the remainder of their lives (Miller & Fishkin 1997). We also surveyed students about thresholds required to change restricted individuals to unrestricted behavior, and the converse. Students estimated that individuals of both sexes would favor their original strategies, and that it would be more difficult to change women than men from restricted to unrestricted, and vice versa. Thus, a woman playing a restricted strategy would remain restricted unless 78% of local men were unrestricted, whereas a man would change from restricted to unrestricted if 63% of local females were unrestricted.

These communities are arranged so individuals' mating decisions are affected by decisions of contiguous individuals of the opposite sex (thus indirectly affecting same-sex neighbors). When those differential decision rules are applied, and interactions iterated over several rounds, the community depicted in Figure 1 moves toward the stable state in Figure 2. We ran this simulation 100 times, randomly changing initial locations of restricted and unrestricted individuals. In one instance, the whole community ended up restricted; in all others, the result was a mixed, but spatially organized, arrangement in which a minority pocket was segregated from a majority (as in Fig. 2). Such stable organized patterns, in which local majorities draw in neighboring cells, are ubiquitous in networks of all kinds, and mirror many natural systems.

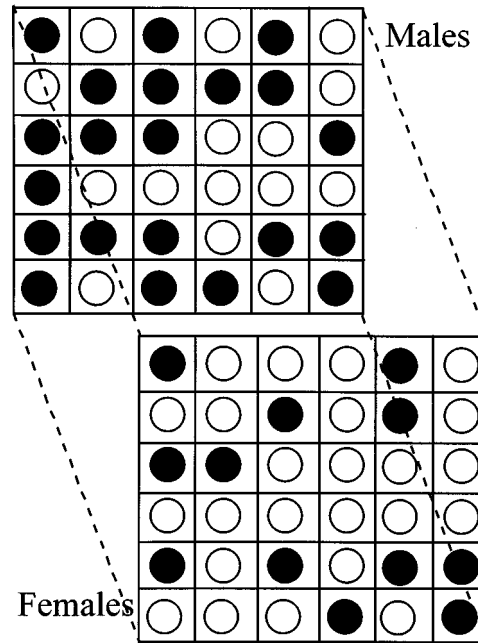


Figure 1 (Kenrick et al.). Initial distribution of restricted (open circles) and unrestricted (solid circles) males and females in a neighborhood. Males and females check with contiguous members of the opposite sex in deciding whether to change or remain with current strategy.

Thinking in dynamical terms draws attention to a point often made by evolutionary and/or personality psychologists – that a “trait” is not a rigid locked-in setting, but a variable decision-rule keyed to the environment. An individual predisposed towards unrestrictedness, for example, may act restricted in contexts where opportunities disallow unrestricted behavior, and vice versa. Consider what happens to the system depicted in Figure 1 if females used a male decision-rule for change (see Fig. 3). Note that, at the

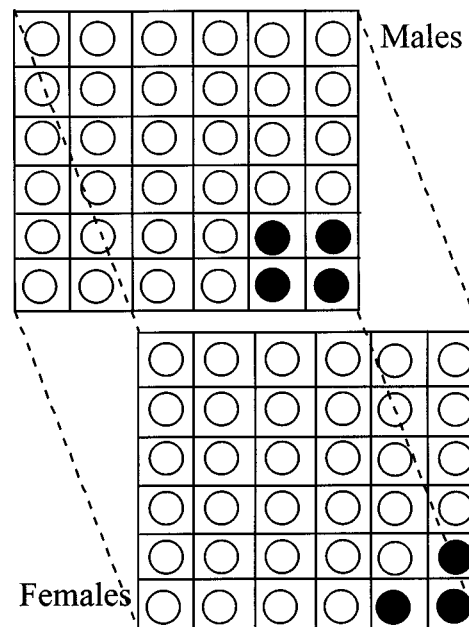


Figure 2 (Kenrick et al.). Stable equilibrium in neighborhood after five rounds of interaction.

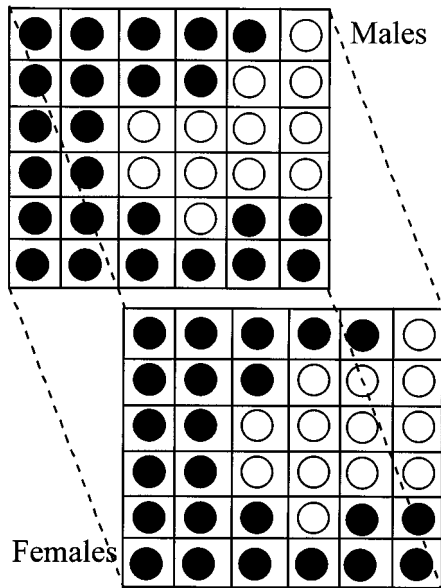


Figure 3 (Kenrick et al.). Stable equilibrium with same beginning strategies as in Figure 1, but with females using male decision rules.

“genotype” level, males did not change their “traits” in any way, but their behavior was phenotypically very different when local females adopted different decision rules.

A key point implied by a dynamical analysis is that “restrictedness” need not be locked in at birth, or by early experience, but could be a decision-rule shared by all individuals of a given sex, manifesting itself in different overt behaviors depending on local ecological circumstances. As G&S indicate, decisional possibilities will vary with chronic social characteristics of the individuals involved. However, once a local system stabilizes, individual differences have minimal impact. An unrestricted individual dropped into the majority pocket of restrictedness in Figure 2, for example, would adopt a restricted strategy, and the converse would be true for a restricted individual dropped into a stable unrestricted area.

We are not suggesting that individual differences are irrelevant in such dynamical systems, however. Indeed, just a few females adopting an unusually unrestricted strategy, or a few males adopting an especially restricted strategy, could result in very different outcomes at the neighborhood level.

Mating decisions inherently unfold in a dynamical context. Given that evolutionary psychologists and dynamical systems theorists both aspire towards a comprehensive paradigm for the social and life sciences, it is essential to develop more conceptual bridges between them.

Good genes, mating effort, and delinquency

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Abstract: High mating effort and antisocial and delinquent behaviors are closely linked. Some delinquent behaviors may honestly signal genetic quality. Men who exhibit high mating effort and who have high genetic quality would be expected to engage in more sexual coercion than other men because its costs to them are lowered by female preferences for them as sexual partners.

Gangestad & Simpson’s (G&S’s) theory of strategic pluralism exemplifies selectionist thinking leading to novel and testable hypotheses. One of G&S’s central ideas is that males who display high genetic quality spend more energy than other males attracting new sexual partners (mating effort or ME) and less investment in providing for mate and offspring (parenting effort). The variation in the ratio of mating to parenting effort expended by males as a function of genetic quality is the result, in part, of females’ preference for males with high genetic quality, especially in the context of short-term mating. Males with good genes may even have an overall advantage in most mating contexts, because displaying good genes may be harder to fake than the promise of future parental investment. One strong prediction from G&S’s theory is that individual differences in male genetic quality will lead to female extra-pair mating in any species with biparental care.

Landolt et al. (1995) found that men who scored high on a measure of “self-perceived mating success” more often selected short-term mating tactics in a hypothetical dating situation than men who perceived themselves as less successful, particularly when the prospective partner was very attractive. Thus, as predicted by G&S’s theory of strategic pluralism, variation in men’s self-perceived mating success was associated with variation in mating tactics.

Although G&S’s theory suggest that low quality males should be especially attentive and caring in heterosexual relationships, one can also suspect that the amount and degree of jealousy, mate guarding, overt threats, and abusive behaviors by male partners may be inversely related, *ceteris paribus*, to their genetic quality, especially in environments in which genetic quality is important and valued by women. Low quality men “know” that their genetic legacy is at risk from their partners’ EPCs.

One intriguing and novel aspect of G&S’s theory is that high male ME is seen as the result of high genetic quality and female choice rather than the result of competitive disadvantage in inter-male competition. This is of particular interest because high ME is one of the most important correlates of both delinquency and sexual coercion among young men (e.g., Bogaert 1993; Elliott & Morse 1989; Flannery et al. 1993). In fact, Rowe’s construct *deviance proneness* includes behaviors associated with early onset of promiscuous sexual activities (e.g., Rowe et al. 1989). With regard to sexual coercion, men who report having been sexually coercive report more extensive sexual histories, including having more casual sex partners and earlier age of first intercourse, together with a greater preference for partner variety (reviewed in Quinsey & Lalumière 1995; Lalumière & Quinsey 1999). In one study, Simpson and Gangestad’s (1991) measure of unrestricted sexuality was one of the best measures distinguishing sexually coercive from nonsexually coercive young men (Lalumière & Quinsey 1996).

Evolutionists usually consider both delinquency and sexual coercion to be alternative strategies used when competition for resources and status is unlikely to be successful (e.g., Rowe 1996; Thornhill & Thornhill 1983). As first sight then, G&S’s link between ME and good genes is paradoxical. But, of course, G&S do not attempt to explain all sources of variation in ME: their assertion is that increased ME may be expected of males with high genetic quality. Even so, is there a way to integrate the fact that delinquents engage in high ME into G&S’s theory of strategic pluralism?

We offer a few suggestions. First, ME and antisociality are intimately linked (Lalumière & Quinsey 1999; Rowe 1996). Antisociality represents behaviors, attitudes, beliefs, personality features, and interpersonal styles that are self-serving and generally harmful to others. Antisocial tendencies may be necessary to pursue a high ME strategy because this strategy involves not compromising with women’s preferences and often results in harm to their reproductive interests. Thus, high quality males who engage in a great deal of ME may develop an antisocial impersonal style that facilitates the successful pursuit of multiple sex partners. In this view, both ME and antisociality would sometimes result from high genetic quality.

Second, many delinquent acts could be viewed as signals of good genes because they display qualities that are very hard to fake. Willingness to fight, robbery, and rule breaking display qualities such as physical strength, bravery, and willingness to incur risks. Being a gang leader displays social dominance. If these and other delinquent behaviours act as honest displays of good genes, and if good genes lead to greater ME, then the association between delinquency and ME is not so puzzling.

Third, males who have adopted a high ME sexual strategy may use sexually coercive tactics more often than other males when prospective sexual partners offer resistance because those with good genes have less to lose, being more attractive to females. Sexually coercive tactics may not be preferred but may be part of a panoply of short-term mating tactics – along with charm, display of prowess, and false promises – used to increase the number of sexual partners (Lalumière et al. 1996). Female resistance to sexual advances may even serve as a “test” of some of the qualities of males with good genes, especially sexually dimorphic traits associated with low FA such as high body mass, muscularity/robustness, and dominance (G&S, sect. 4.4).

The point here is not that antisociality, delinquency, and sexual coercion by young males are always the results of high genetic quality. There is evidence that some delinquents have early disturbances in neurodevelopment (e.g., Raine 1993) and that some sexual coercion is the result of paraphilic interests (Lalumière & Quinsey 1994). Our point is that the adoption of a high ME strategy may be accompanied by an interpersonal style characterised by antisociality, the use of sexually coercive tactics, and the use of behavioural displays that are hard to fake. If this is the case, then the association between delinquency and ME does not contradict G&S's thesis.

Variation in mating dispositions

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Abstract: This commentary focuses on the omission of genetic and environmental variation in several competing evolved motive dispositions that not only react to different environmental contexts but also result in people structuring contexts to obtain psychological rewards. Cross-cultural research is poor evidence for alternate strategies because natural selection may operate to produce geographical variation in dispositional tendencies. Finally, I defend a traditional concept of plasticity in opposition to the alternate strategies concept of flexibility.

Gangestad & Simpson's (G&S's) research on fluctuating asymmetry (FA) is a fascinating addition to the study of human mating, but they omit an important source of variation – genetic and environmental variation in motivational systems. They show that FA is heritable, but the idea that the conditional strategies they propose are genetically monomorphic is a priori and unlikely, given that virtually all phenotypes of interest to evolutionists show genetic variation. One would expect far more powerful effects of FA than those reported in the target article if conditional strategies were monomorphic.

Genetic and environmental variation influence personality systems important for human mating. Human personality systems embedded in the Five-Factor or Model are conceptualized as universal mechanisms with an affective, motivational core (MacDonald 1995; 1998). For example, behavioral approach mechanisms (Factor I) are linked with reward sensitivity (including sexual pleasure and attraction to sexual variety), sensation seeking and social dominance, while Factor II (Nurturance/Love) is conceptualized as an evolved reward system underlying close relationships of intimacy and mutual support. Individual differences in these universal dispositional systems resulting from genetic and (mainly

unshared) environmental variation represents a continuous distribution of phenotypes matching a continuous distribution of viable strategies – that is, niche diversification (MacDonald 1991; Wilson 1994); this variation is a resource landscape in which people evaluate others in terms of their utility for meeting their own interests (Lusk et al. 1998). Variation also results from different evolved dispositions pulling in different directions in response to different environmental contingencies (e.g., environmentally triggered conflicts between a disposition to seek sexual variety [associated with being high on Factor I] and a disposition to seek close, intimate relationships [associated with being high on Factor II]; MacDonald 1995; 1998). This perspective is compatible with theoretically expected mean group differences, such as theoretically predicted sex differences in behavioral approach (males > females) and Nurturance/Love (females > males).

Rather than only reacting to environmental context with different strategies (the perspective of the target article), these motivational systems are also appetitive; people structure their environments in order to obtain psychological rewards. The dispositional perspective predicts that there will be considerable inertia in many people's preferences because for genetic and environmental reasons they are, for example, highly motivated to achieve close intimate relationships (high on Factor II). FA correlates only -0.20 with men's willingness to engage in sex without closeness and commitment, leaving the vast majority of the variance to be explained at least partly by variation in other dispositions. Low FA men are chosen as extra-pair and short-term sexual partners only by “sexually unrestricted” women, suggesting that sexually restricted women have a dispositional tendency toward high-investment parenting, presumably including a disposition to obtain the psychological rewards of intimate relationships fairly independent of their ability to support children without paternal investment. There is also inertia in women seeking economically successful, high status mates even when they have education and income (Buss 1989; Wiederman & Allgeier 1992). The target article discounts these findings because of the possibility that women learn the value of men's resources within a particular culture, but it is not clear how this can be analyzed within the domain-specific framework adopted by the target article: It would appear that women's conditional strategies are altered by domain-general learning peculiar to a certain culture.

Cross-cultural research is poor evidence for alternate strategies because natural selection may operate to produce variation in dispositional tendencies between different areas. The target article proposes that female preference for attractive males should be least where paternal investment is needed to produce viable offspring. However, geographical variation may well have resulted in natural selection for dispositional tendencies toward high- or low-investment parenting. Several theorists have proposed that the adverse, ecologically marginal environments created by the Ice Age shaped the high-investment reproductive behavior of northern populations – a tendency that shows considerable inertia in contemporary environments (Lenz 1931; Lynn 1987; MacDonald 1994; Miller 1994a; Rushton 1995). If low-investment parenting was not typically a viable option, psychological mechanisms would evolve resulting in people seeking psychological rewards associated with high-investment parenting independent of current context. This perspective is compatible with evidence that life history variables (including variables related to sexual restrictedness-unrestrictedness) are substantially heritable (see MacDonald 1997).

All of the data cited in support of strategic pluralism can be accounted for within the dispositional perspective outlined here. One need only assume that the tendency to prefer low-FA mates is one among several evolved motive dispositions related to mating. The key difference is whether variation is conceptualized as resulting from strategic pluralism deriving from a universal set of conditional strategies centered around variation in FA or whether variation results mainly from genetic and environmental variation in a variety of evolved motive dispositions, interactions between

motivational systems, and interactions with environmental contextual variation (MacDonald 1998).

The emphasis on female choice and pathogen prevalence in polygyny ignores the role of intrasexual competition among males. At the state level, polygyny results from wealthy males being able to commandeer the production of lower ranking males (Betzig 1986; Dickemann 1979), while in mid-level societies polygyny is enabled by women being able to produce enough to rear their own children thereby freeing males for increased mating effort (Draper 1989). The male winners in sexual competition may have lower FA, but my reading of the anthropological literature indicates that female choice is far less important than male intrasexual competition, the main mechanism being purchase of females by wealthy, powerful males (bridewealth).

Finally, I reject the notion of flexibility underlying the target article. Citing Tooby and Cosmides (1992), they claim that “plasticity” can only be retained if it guides behavior into an infinitesimally small adaptive space, with “plasticity” in quotes because it is only apparent – the result of large numbers of conditional “if-then” mechanisms responsive to recurrent contingencies in our evolutionary past. This is an a priori claim that ignores a great deal of data supporting continuous, quantitative models of developmental plasticity, as in behavior genetic models (MacDonald 1991). The target article notes that modern environments where contraception is available do “not imply that evolved psychological mechanisms no longer influence human mating.” I agree, but the claim that plasticity is only apparent requires a much stronger thesis – that the availability of safe contraception and abortion has no influence at all because women could not have evolved conditional strategies responsive to the dramatically lower cost of sexual intercourse. There is a great deal of evidence that sexual behavior has changed dramatically since the advent of safe and reliable contraception and abortion (e.g., Furstenberg 1991). There is plasticity in the sense of being able to modify behavior and pursue evolved goal states in response to complex, novel, and nonrecurrent environments with relatively domain-general processes like the *g*-factor of IQ testing and social learning (MacDonald 1991). Geary (1998) has detailed how domain-specific and domain-general mechanisms (general intelligence) are integrated in order to solve adaptive problems. Stanovich and West (2000) describe a set of depersonalized and decontextualized domain-general cognitive mechanisms able to flexibly abstract general rules and principles, which function to maximize personal utility (e.g., achieve evolved motive dispositions).

Low fluctuating asymmetry (FA) and short-term benefits in fertility?

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Abstract: Preference for partners with low fluctuating asymmetry (FA) may produce “good gene” benefits. However, Gangestad & Simpson’s analysis does not exclude immediate benefits of fertility. Low FA is related to fertility in men and women. Short-term changes in FA are correlated with fertility in women. It is not known whether temporal fluctuations in the FA of men are related to short-term fertility status.

Gangestad & Simpson (G&S) have made an elegant and convincing case for conditional mating strategies in humans. However, we must proceed cautiously in considering the proposed relationships between short-term mating, low fluctuating asymmetry, and good genes. Of course a component of FA is related to developmental instability but a preference for low FA may also correlate with an immediate benefit to women, that is, high male fertility.

There is evidence in both women and men that low FA is related

Table 1 (Manning & Gage). *Analyses of change across 24 hours in total FA of 10 subjects*

| Subject | F Ratio | p value |
|---------|---------|---------|
| 1. | 0.35 | 0.99 |
| 2. | 2.02 | 0.008 |
| 3. | 2.72 | 0.0004 |
| 4. | 0.97 | 0.54 |
| 5. | 7.45 | 0.0001 |
| 6. | 4.48 | 0.0001 |
| 7. | 2.79 | 0.0003 |
| 8. | 5.89 | 0.0001 |
| 9. | 2.86 | 0.0002 |
| 10. | 1.37 | 0.14 |

Subjects were measured twice per trait (six traits) every 30 minutes, that is, 48 measurement occasions. The F ratio gives the ratio between FA changes across measurement occasions divided by measurement error as represented by differences in the repeated measurements. High F values indicate real changes in FA across measurement occasions. Similar results were obtained for relative FA scores. Repeatability (r_1) was high for the first pair of measurements of the 10 subjects ($r_1 = 0.90$, $F = 18.29$, $p = 0.0001$).

to fertility. In women, breast FA has been found to be negatively correlated with lifetime reproductive success in samples from Spain, the USA, and England (Manning et al. 1997; Møller et al. 1995). In men, digit FA has been reported to be negatively correlated with sperm number per ejaculate, sperm speed, and sperm migration in the masturbatory ejaculates of 53 men attending an infertility clinic (Manning et al. 1998). A sample of 34 young Englishmen also showed a negative relationship between FA (2nd digit, ears, wrist, and ankle) and sperm number per copulatory ejaculate (Baker 1997). Biljan et al. (1994) have found that the fertilisation rate of eggs from IVF couples is significantly related to sperm migration indices ($r = 0.62$) and to sperm numbers ($r = 0.28$). Low male FA may therefore indicate immediate fertility benefits.

Soft tissue is not fixed. It is high in children (Wilson & Manning 1996) and old adults (Livshits & Kobylianski 1991). More important, it shows short-term changes. In women, FA varies across the menstrual cycle, reaching its lowest point on the day of ovulation (FA of breasts, digits, ears, Manning et al. 1996; Scutt & Manning 1996). In men there is also evidence of short-term change. We

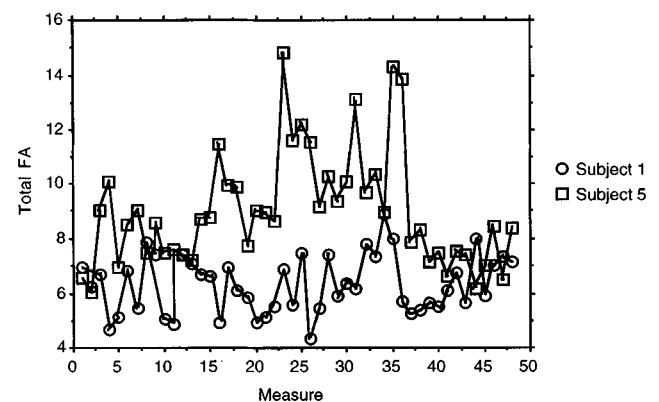


Figure 1 (Manning & Gage). Change in total FA in two subjects (1 and 5) with low and high F ratios, respectively. A similar pattern of change was obtained for relative FA scores.

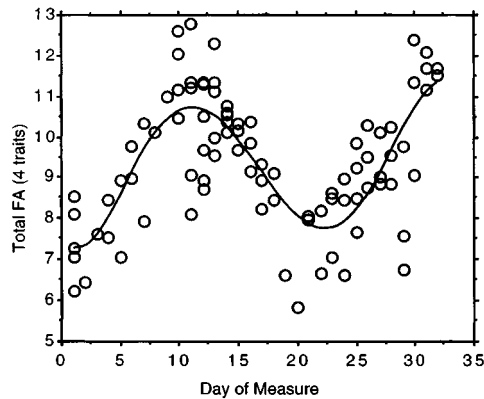


Figure 2 (Manning & Gage). Changes in Total FA (four traits, digits 2–5, each trait was measured twice and mean FA calculated) across 32 days in one male subject (90 measurement occasions). A fifth order polynomial analysis suggests a cyclical pattern of change ($n = 90$, $r = 0.76$, $F = 23.16$, $p = 0.0001$). Relative FA showed a similar pattern of change.

measured the FA (ears, wrists, 2–5th digits) of 10 young men ($x = 27.30 \pm 1.31SE$ years) over a period of 24 hours. Measurements (two per trait) were made every 30 minutes (= 48 measurement occasions per subject). Total FA (the sum of absolute FAs) showed significant changes across measurement occasions in seven subjects (see Table 1 and Fig. 1). In addition, a single subject (age 54 years) was measured 90 times (two measurements per trait, four digit traits) over a period of 32 days. There was evidence of significant changes in total FA (Fig. 2).

We do not know what drives change in soft tissue FA. Changes in concentrations of such hormones as oestrogen and PTH may result in fluctuations in the ionic content and osmotic pressure of the blood (Hyttén & Leitch 1976). Small alterations in absolute trait size could result in very large changes in FAs. In women, low FA may signal periods of high fertility (i.e., ovulation). In men, ejaculate sizes and sperm activity scores are not constant. They vary significantly from day to day and are depressed by febrile and many other illnesses (Hargreave & Nillson 1983). Is short-term change in FA related to illness? Do day to day changes in male FA vary in relation to ejaculate size or sperm motility? More work is needed.

We conclude that short-term mating preferences for low FA in women and men may result in the selection of partners with high fertility. It could also lead to mating with men with good genes. Before we can be sure of the latter, we must understand the mechanisms and the correlates of short-term change in soft tissue FA.

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Good genes and parental care in human evolution

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Abstract: Prior to agriculture, human societies were small, with little variation for good genes sexual selection (GGSS) to work on. Across cultures, variation in paternal care makes the benefits of GGSS highly variable. Despite these caveats, female preferences for traits like male body symmetry suggest one reason for female short-term mating is gene shopping.

Gangestad and Simpson (G&S) deserve praise for amassing so much data in support of good genes sexual selection (GGSS) in

humans, though much more is needed. When females obtain nothing from males but sperm, they should mate with males of superior viability, but when male care is important, they will often face a trade-off between having a lower-quality, long-term mate to provide care, or a higher-quality, short-term mate to pass on good genes. Concealed ovulation may have evolved to enable women to have both (Benshoof & Thornhill 1979). Just how important GGSS was in our past depends on how much variation in male care versus genetic quality contributed to offspring fitness.

Across foraging societies, male contribution to diet varies from 20–90% (Kelly 1995) and time spent holding infants from 2–22% (Hewlett 1992). Increasingly, the importance of male care in pair-bonding is being challenged (Blurton Jones et al. 2000; Gowaty 1996; Hawkes 1991), but I would agree with G&S's claim that, among humans, males provide "substantial parental care" (sect. 1.1, para. 4), at least by mammalian standards. Even though male care varies greatly, marriage is a universal and presumably ancient trait. The question then is, how much and how often it would have paid females to seek short-term, "good genes" mates, and risk either losing this care, or being injured and perhaps killed.

G&S cite estimates of the relevant genetic variation (CV_a) of morphological and fitness traits as evidence of the opportunity for GGSS (sect. 3.1). However, genetic variation (and its effect on preferences) may have been less in the small foraging societies of the past with no racial/ethnic variation and considerable inbreeding. Such inbreeding, however, might have selected for heterogeneity and thus, low fluctuating asymmetry (FA). As with contemporary foragers, there would also have been no variation in language, cultural values, or wealth. Contemporary foragers live in camps with an average population of 25 (Lee & DeVore 1968). Frequent moves and visiting between camps allows for mate shopping, though mating is usually endogamous within ethnic group, which typically has a population of 500–1,000 (Kelly 1995). Not only would there have been limited variation but one would have known a great deal about all potential mates, everything from character to disease history to foraging success, thus there may have been less reason to focus on good genes indicators.

Among Hadza hunter-gatherers with whom I work, most men have a chance at marriage, perhaps partly because they are willing to marry women who already have children. I found, however, that Hadza men provided more care to their biological children than to stepchildren, which would not be expected if male care were only mating effort (Marlowe 1999). I also found Hadza men provided less care in camps where they had more potential mates, suggesting they trade off parenting for mating effort in relation to operational sex ratio. I did not, however, find men trading off direct for indirect care (provisioning). One might expect foraging ability to vary positively with athleticism and negatively with FA. Therefore, if low FA men were more attractive, we might expect the best foragers to spend less time providing direct care to children, but they did not. If females valued male parenting ability above all else, then human ancestral males, unlike zebra finches (Burley 1986), may not necessarily have provided less care when more attractive because attractiveness and parenting ability may have been one and the same.

Because serial monogamy is common among the Hadza, females often have the opportunity (or face the necessity) of shopping for a new mate. Australian foragers, on the other hand, were highly polygynous, with old men sometimes having up to 10 wives. Perhaps this intense polygyny was the result of GGSS if males proved their viability with longevity, but female mating strategies were constrained by arranged marriages. For females betrothed at birth, the only chance to choose a mate was through extra-pair mating, and the only chance for most young males to mate at all was with other men's wives. Such affairs did sometimes occur and offenders were severely punished (Hiatt 1996). One might think females foraging in the bush would have ample opportunity to cuckold mates, but Hadza females have surprisingly little opportunity, even when their husbands are gone for days. When a female is in camp, other people are usually around, and when she is

out foraging, she is with a group of females. A married female leaving camp by herself would make others suspicious. Language means secrets are difficult to keep and adds a dynamic to human mating which is missing in the well-studied extra-pair copulations of socially monogamous birds. Certainly, it is much easier for females to cuckold their mates here in large cities where one can move freely and anonymously.

Much of the variation in male provisioning in the past may have been smoothed out by extensive food sharing, as it is among contemporary foragers. Still, with some variation in provisioning, there should be an overlapping interest in monogamy by high-quality females (who hope to garner all of their high-quality mates' resources) and low-quality males (who hope to get any mate at all). High-quality males and low-quality females should favor polygyny (or short-term and extra-pair mating), their males hoping to increase the quantity, and the females the genetic quality of their offspring. However, human male quality, as G&S acknowledge, is not easily assessed: females may prefer males who signal superior viability, provisioning, protection, status, or all of the above, some of which may, or may not be mutually exclusive. Nonetheless, some female preferences (e.g., the preference for the smell of low FA men during ovulation, sect. 4.5.2) imply females can assess male genetic quality and that GGSS might explain some short-term mating by females. We still know little about female preferences for short-term mates but G&S have shown much of what is known.

I doubt evolutionary explanations

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Abstract: No doubt all our behavior is the result of evolution, but I express skepticism about the validity of detailed arguments that purport to explain in detail how or why this occurred historically.

Since Trivers's (1972) seminal remark that reproduction among mammals places less demand on male than female resources, his evolutionary perspective has become increasingly popular to explain the stereotypes that men promiscuously sow their wild oats, while women want stable sexual relationships with reliable breadwinners. If this explanation works for mammals as a class, it is less successful among our hominoid relatives, the apes. Male gorillas and orangutans do indeed seek multiple mates, while females are usually limited to a single male. But gibbons and siamangs are monogamous. Among chimpanzees, both sexes mate with multiple partners (Goodall 1986). Among bonobos (pygmy chimpanzees), females freely seek sexual relations with males and other females (de Waal 1995). Thus, the hypothetical difference in mating strategies is not apparent in most apes nor in those most closely related to humans, the chimpanzees.

Recognizing that men's and women's mating strategies are not so sharply different as stereotypes presume, Gangestad & Simpson propose a contingent model: Men will sow their wild oats when they can, but often they cannot and therefore resort to marriage; women seek marriage to secure its attendant resources but may dally when they are unconstrained and can afford to. This is essentially a traditional (pre-Darwinian) view of how men and women behave. I wonder why it now needs an elaborate evolutionary argument because it follows from the simple assumption that both men and women want sex and will get it in those ways most opportune and affordable.

Perhaps the import of the evolutionary argument lies in its claim that asymmetrical men, with bad genes, suffer poorer access to casual sex than do more handsome, symmetrical men. As a result, asymmetrical men are more willing than symmetrical men to make long-term commitments. No doubt this explains extreme

cases, like Quasimodo's persistent attachment to Esmerelda; but if ordinary variations from symmetry noticeably detracted from male sex appeal, men would part their hair down the midline. I was surprised and impressed to learn that women prefer the smell of T-shirts worn by symmetrical men to those worn by asymmetrical men. While awaiting independent confirmation of this finding, I ponder the evolutionary reason why sexual attractiveness of a woman is judged so severely by her looks, using criteria that sometimes change rapidly over time (Mazur 1986), when one ordinarily healthy young female is about as good as another for the purpose of having babies.

Unrestricted women's sexuality or opportunism? Quasi-mathematical asides on Gangestad and Simpson's strategic female pluralism

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Abstract: Women's mating strategies have typically been characterised as restrictive or coy. However, recent research on sociosexual behaviour suggests that the frequency of women's extra-pair copulations is a function of an unrestricted personality. While agreeing with the general thrust of Gangestad & Simpson's strategic pluralism theory we suggest that it is more likely a matter of finely calculated reproductive opportunism.

Gangestad & Simpson's (G&S's) target article is a valuable contribution showing how our species' sexual relations are really more pragmatic than most gender theorists would have us believe. As we find G&S's contribution persuasive in its entirety, we would simply wish to extend their analysis as it relates to "unrestricted" women's mating strategies.

Perhaps the most interesting part of G&S's strategic pluralism is their challenge to the widespread belief that only men routinely seek extra-pair couplings. This is highly unlikely. There is far too great an emphasis in the literature on women's modesty ranging from Wilson's coyness (Wilson 1978) to Buss and Schmitt's Sexual Selection Theory (1993). Revealed wisdom is that women risk too much in such encounters for sexual liaisons to be entirely casual affairs but as G&S have ably demonstrated the same logic that makes men decide to commit or run, applies to women, if with less reproductive degrees of freedom. It is entirely likely that women have been engaging in "good genes" extra-pair couplings for as long as cheating has paid dividends and that this has become an evolved strategy, but not one pursued by all women.

The important point is that what looks like seemingly indiscriminate sexual availability of an unrestricted sociosexual orientation is probably not simply a female form of R strategy, but rather a finely calculated estimation of what degree of sexual availability (promiscuousness) it takes for a less favoured woman to get an injection of superior genes into an otherwise ordinary set of offspring. We suggest that reproductive cheating is a far more routine female strategy than the literature on sociosexuality might suggest.

How might we know? As Dorothy Eimon (1994) notes, major surveys of the numbers of lifetime sexual partners each sex claims to have had, routinely finds women acknowledging far fewer sexual encounters (Johnson et al. 1992; Walsh 1993). This poses a problem for evolutionary theorists which only seems to have interested Eimon up to this point. If women claim far fewer sexual partners than men, whom is serving whom? Eimon's research suggests that female reticence and modesty notwithstanding, alternatives such as a few heroic hypersexual women, or a lot of hard-working prostitutes, are unlikely explanations to account for this large discrepancy. It seems the only way out of this dilemma is that men are inflating their conquests and women not (highly unlikely).

Another way to address the question is to resurrect an interest in paternity certainty studies. Unfortunately in an increasingly litigious time, ethics committees actively discourage researchers asking fathers if they knew that their putative offspring was not really their own. From what research we do have (fairly dated) it seems there are a lot of fathers out there who are unaware of their cuckoldry (Baker & Bellis 1995).

It would be wonderful if someone were able to correlate women's attractiveness (and all the other decisional factors involved in G&S's strategic pluralism) with paternity certainty correlates. Such a study would be revealing and shed new light on "unrestricted" sociosexuality.

Although it is always risky to engage in quasi-maths we would hypothesize that female strategic pluralism would go something like this: a woman's decision to engage in a potentially reproductive extra-pair coupling is a finely balanced calculation that involves her decisions about her attractiveness (physical or otherwise); her estimation of what she is likely to attract by way of a casual sexual partner; and that once calculated, this decision would become a function of her estimation of what degree of "unrestricted" sexuality she would have to engage in to attract a sufficiently high calibre mate. It would also be a function of her differential ability to detect and attract "good genes." This calculation would then necessarily involve a cost/benefit analysis of the degree of cryptic promiscuity one could get away with in attracting a high quality mate before disqualifying oneself. Obviously this calculation is a function of the prevailing mores and gender relations but in general terms it would be a finely calculated, close run race between attracting the best possible extra-pair mate before one's reputation started sliding, or even worse arousing paternity uncertainty in her mate of record.

We would agree with G&S that men have evolved a set of contingent decisional rules which reflect female calculations. While the literature is replete with suggestions that men will have casual sex with anything that moves (Kenrick & Trost 1989) the same studies show that men are far more discriminating when matrimony or paternity is at stake. What often seems like unrestricted sociosexuality is probably less a matter of personality, than of what life or nature has provided by way of opportunities. In support of this, we would also agree with G&S that the crucial difference between the sexes is differences in what women prefer in long and short-term mates. Rather than short-term mating simply being a test drive of future potential, it reflects quite different mating strategies. We would also note from our own research in natural mating groups (McKnight & Hills, in press) that women have a far better idea of what is attractive to men, than men have, suggesting that women have a more evolved interest in the question.

Mating strategies as game theory: Changing rules?

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Abstract: Human behavior can be analyzed using game theory models. Complex games may involve different rules for different players and may allow players to change identity (and therefore, rules) according to complex contingencies. From this perspective, mating behaviors can be viewed as strategic "plays" in a complex "mating game," with players varying tactics in response to changes in the game's payoff matrix.

Gangestad & Simpson (G&S) have done two things in their target article: (1) they have summarized the last decade of research findings as related to the evolutionary psychology of human mating, and (2) they have tried to place these findings within a framework

based on life history theory. In order to integrate the diverse empirical findings, G&S have called upon the explanatory concepts of: (a) species-wide, conditional (environmentally contingent) strategies; (b) sex-specific strategies; (c) heritable (stable) individual differences; and (d) intra-individual, socially-facultative changes in tactics. Traditionally these explanations of behavioral variability have been considered to be alternative rather than complementary, and critics might argue that G&S are trying to "eat their cake and have it, too." "If you are going to argue for the existence of genetic algorithms for behavioral decision-making" they might ask, "how do you think you can get away with constantly changing the rules?" In anticipation of this criticism, I would like to argue that G&S's approach is the only realistic one: simple models do not work because the world is not simple.

Life history theory is, essentially, a version of mathematical game theory; indeed it is from game theory that the target article's terminology of "strategies" is derived. Games do not have to be simple: different kinds of players might play in the same contest and yet have different sets of moves available or allowable (as do the various pieces in chess). Thus, in complex games it is not the case that the best strategy for one player is necessarily the best strategy – or even a possible strategy – for another. Furthermore, games are dynamic: status may change, alliances may be forged or broken, and promises and threats may be proffered or retracted; a pawn, under certain circumstances, may turn into a bishop or a rook.

The mathematical algorithms of a game (its payoff matrix) can get enormously complex – involving many "do if" and "do iff" statements, each of which may have its own complex arguments, loops, and contingencies. In the case of the "mating game," game, rules (play options, payoff contingencies, available resources, etc.) will differ across individuals of differing age, sex, and status. Further, they will change within individual lifetimes as an individual's age, sex, and status change. Because the availability and value of a particular strategy is always dependent upon the unique circumstances of the particular player, and because the values taken by relevant game variables change for players over time, it may seem (from the perspective of each player) that the rules of the game are constantly changing. From a higher perspective, however, the player has merely entered into a new (previously unencountered) loop or sub-routine of the game's complexly contingent rule system.

While the mathematics of a complex game may be too complex for us to follow consciously, our brain is a massive computing system, and our genetic "blueprint" is the end product of an enormously long run of evolutionary simulations with real contingencies and real payoffs. It is quite reasonable to postulate that the contingencies in the complex rulebook of the mating game will lead to sex differences, to age differences, and to heritable strategies within some loops and contingent strategies within other loops.

Life history and game theory models have been applied to the analysis of variation in human biology, personality and social interactions (e.g., Belsky, in press; Low 1998; Mealey 1990; 1995; 1999; 2000; Moffit et al. 1992; Morbeck et al. 1997). They can also be applied to analysis of other, perhaps more conscious strategic social decisions such as educational and occupational choice, crime, emigration, marriage, divorce, contraception, and abortion (e.g., Chisholm 1993; Miller & Pasta, in press; Vila & Cohen 1993), as well as to higher level systems in which players are businesses, political actions groups or nation-states (e.g., Hardin 1968; Hirschleifer & Rasmusen 1989). What all of these domains (playing fields) have in common is that in each, the costs and benefits (payoffs) of various behaviors (play options), depend, in complex relation, on the behavior of other players. Unlike some types of models, models of these systems will not profit from the "parsimonious" use of Occam's razor. Rather, we need to build complexity into the models if we want them to reflect reality (rather than wishful thinking or traditional disciplinary boundaries).

Geographical variability, pheromones

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Abstract: The worldwide variation in mating strategies can be explained by differential paternal investment theory, which traces the differences back to the climates where the various peoples (races) evolved. Male provisioning is necessary for women and children to survive cold winters, which is less essential for tropical women. Androstenone may be the substance that makes symmetrical men smell better to fertile females.

The two aspects the target article that I will comment on are (1) geographic variability in mating strategies, and (2) a possible pheromone that may play a role in female mate choice. Although both are relevant, they are different points.

Gangestad & Simpson (G&S) present evidence that mating strategies differ around the world, with strategies in the tropics being less restrictive, with more polygyny. The worldwide variation in mating strategies can better be explained by differential paternal investment theory, which traces the differences back to the climates where people evolved (Miller 1994a).

In the warm tropics, females could gather enough to support both themselves and their children. In contrast, in the cold areas, winter gathering yields little. Fruit, berries, and eggs are out of season, snow cover and frozen ground prevents digging for tubers. Hunting large ungulates (deer, etc.) provides the major winter food sources. Females, especially if pregnant or nursing, are poor hunters. Male provisioning is essential. Offspring of non-provisioning males have difficulty surviving. Females evaluate mates by ability and willingness to provision. Thus, in colder climates the optimal male strategy is to devote more effort to parenting, and less to mating. In the tropics the optimal male strategy involves devoting more effort to parenting and less to seeking mating opportunities. Polygyny (a marker for mating strategy) correlates with latitude (Miller 1994a).

Male mating is assisted by a strong sex drive, aggression, dominance, sociability, extraversion, impulsiveness, sensation seeking, and high testosterone. Provisioning (male parental investment) is assisted by anxiety, altruism, empathy, behavioral restraint, gratification delay, and a long life span. Thus, this theory can explain racial differences in many traits related to mating strategies including age at first sexual activity, illegitimacy, divorce, marriage, AIDS, and polygyny rates, as well as a long list of other traits (hormone levels, monamine oxidase levels, testosterone levels, lactase dehydrogenase metabolic paths, life spans, prostate cancer rates, hypertension, genital sizes, vocal frequencies, liver size, muscle structure, mesomorphy, bone density, sports performance, crime rates, rape, child abuse, earnings). The theory was later shown to be able to explain racial differences in intelligence also (Miller 1995).

Admittedly, polygyny also correlates with the presence of disease as Low (1990a; 1990b) has argued. Females should prefer the more disease resistant males. However, a male strategy of "love them and leave them" requires that females be able to provision themselves and their children. Because lack of food severely lowers disease resistance, females can afford to sacrifice male parental investment to obtain genetic disease resistance only in areas where male provisioning is not critical.

Conceptually, the adaptation of human mating strategies to environmental conditions requires only that the frequencies of certain personality determining genes differ with the environment of evolution. Several writers (Belsky et al. 1991; Chisholm 1996; Simpson 1999) apparently trying to avoid recognizing genetic differences between the world's peoples, have proposed that that humans have evolved a mechanism which detects parental stress, and causes children when grown to change mating strategies.

However, the theory has many difficulties, such as whether conditions in adulthood are predicted from current childhood stress, which have been discussed elsewhere (see Miller 1994b). Even if

stress when young reliably predicts difficult conditions when an adult (doubtful), having many offspring in adverse time forces parents to divide their total resources among many children, which could decrease fitness. Most of the effects are more parsimoniously explained by simple genetic inheritance. For instance, divorce rates are a marker for mating strategies. The traits that lead to divorce appear to be highly heritable as shown by the fact that the co-twins of divorced monozygotic twins are nearly three times as likely to be divorced themselves than are the co-twins of still-married twins (Lykken et al. 1990). Thus, the finding that children who experienced the stress of marital separation when growing up are more likely to divorce themselves is explained by a simple genetic theory without recourse to elaborate developmental switches.

Now to the entirely separate question of odors and symmetry. G&S describe studies in which female opinions of the odors of freshly worn tee-shirts depends on the symmetry of the males that had worn them, but only during the most fertile period of the women's cycles (Thornhill & Gangestad 1999b). This naturally inspires speculation about what the male emitted substance might be that females respond to this way. A possible candidate is androstenone (the ketone produced by oxidation of androstenol emitted by the apocrine glands). Grammer (1993) has reported that the odor of androstenone varies during the menstrual cycle, with its normally unattractive odor being neutral at the optimal conception time.

Certain of the results reported for androstenol (the alcohol version of androstenone) would be consistent with it acting as a pheromone. For instance, Cowley et al. (1977) found that women rate men more positively when exposed to androstenol. Benton (1982) found that women exposed to androstenol on the upper lip rated themselves as more submissive around mid-cycle, a feeling that encourages impregnation. However, women in the fertile period of their cycle prefer symmetrical men's scent, which is interpreted as an evolved preference for sires with good genes (Thornhill & Gangestad 1999b).

Androstenol is a steroid closely related to testosterone. It is possible that high testosterone individuals also emitted large amounts of androstenol from their apocrine glands. The asymmetry related traits of facial attractiveness, body mass, physicality, social dominance, willingness to fight, and tendency to directly compare with other male competitors are all traits that could reflect testosterone levels. Testosterone is believed to be an immune suppressor, so that it is possible that males whose non-testosterone related genes produce strong immune systems could have high testosterone levels. Androstenol could then be a marker of a strong immune system.

However, if androstenol is a pheromone, it could serve other purposes such as informing females when they have a mate (Miller 1998), or making them more social in the presence of that mate (Miller 1999).

For the short-term: Are women just looking for a few pair of genes?

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Abstract: Although we find Gangestad & Simpson's argument intriguing, we question some of its underlying assumptions, including: (1) that fluctuating asymmetry (FA) is consistently heritable; (2) that symmetry is driving the effects; (3) that use of parametric tests with FA is appropriate; and (4) that a short-term mating strategy produces more offspring than a long-term strategy.

Gangestad & Simpson (G&S) address an important issue: If “men” and “women” differ in their mating strategies because of differences in underlying biology (Buss & Schmitt 1993), why is there such overlap between genders in mating strategies? In contrast to Buss (1998a), who implies “that evolution would not have favored a male strategy entailing little desire for multiple mates”, G&S argue that “most men may have benefited reproductively by having little interest in pursuing multiple mates.”

On the other hand, they argue that men may have evolved the “capacity” for “a desire for sexual access to a large number of women” (Buss & Schmitt 1993, p. 208) but that this “desire for short-term mating should be expressed conditionally, and it should be observed infrequently under conditions when only a few men are able to attract short-term mates.” Who might these few men be? They are those with “good genes” and “researchers should show that direct indicators of individuals’ genetic fitness are associated with their attractiveness as a mate (particularly as a short-term mate).” The best available measure of genetic fitness, they argue, may be fluctuating asymmetry (FA). Essential to their argument would seem to be the following:

1. That fluctuating asymmetry is consistently heritable. (Møller & Thornhill 1997). But, serious methodological questions about this meta-analysis and its interpretation have been raised. Whitlock and Fowler (1997) point to

major flaws in the [Møller & Thornhill 1997] analysis and meta-analysis of these data. We suggest that most of the studies in question were inappropriately done . . . with confounding factors, such as maternal effects or common environments. . . [While the six] selection experiments give low ($0 < h^2 < .1$) but significant heritability for FA . . . and the valid correlations among relatives also gives results consistent with these values . . . this effect is almost entirely due to one character in one species: bristle counts in fruit flies. A combined probability test of the data on other characters shows no significant deviation from zero ($p = .7$). (p. 66)

Palmer and Strobeck (1997) point to the confounding effects of (1) measurement error, (2) directional asymmetry and antisymmetry, (3) overall size variation and to studies overlooked in the analysis, and conclude that Møller and Thornhill’s (1997) “use of meta-analysis to buttress claims for a robust *quantitative* estimate [of heritability of FA] seems misleading at best or deceptive at worst” (p. 48).

2. What’s driving the effects for asymmetry? Are the relationships between asymmetry and other variables (e.g., number of sexual partners) fairly linear? Or, is there a small group of highly symmetrical men who differ from most other men? Or, are highly asymmetric men repelling potential short-term partners? Correlations are highly sensitive to outliers, yet their role is unspecified. A related point involves concerns about the acknowledged positive skew of the data (Gangestad & Thornhill 1998). We concur with the concerns raised by others elsewhere (Swaddle et al. 1994) regarding severe violations of the assumptions of parametric tests. Although Gangestad and Thornhill (1998) argue that parametric tests are sufficiently robust given adequate sample size, in fact, parametric tests are sensitive to even moderate violations of the assumptions (e.g., normality and homogeneity of variance) of these tests (Cliff 1993; Wilcox 1992; 1994; 1996).

As hundreds of articles in statistical journals have pointed out and for reasons summarized in several books . . . , standard methods are not robust when differences exist or when there is an association between random variables. . . . Unfortunately, violations of the assumptions of these tests not only inflate Type II error, they can also inflate Type I error . . . [and] “the actual probability of a Type I error can be substantially higher or lower than the nominal α level” (Wilcox 1997, p. 70).

Similarly, Tabachnick and Fidell (1996) note that “especially worrisome is that an outlier can produce either a Type I or a Type II error, with no clue in the analysis as to which is occurring” (p. 381). Furthermore, non-robustness and statistical inferences are apt to become more problematic as “skewness or kurtosis of the sampled

population departs increasingly from its normal-distribution value” (Bradley 1982, p. 87).

3. Fluctuating asymmetry is important as a cue to men’s (but not women’s) “good genes.” Do the correlations reported on relevant variables for males and females differ? Are there mean differences for men and women on the same variables? The authors do not always provide the needed comparisons. For example, “in fact, a man’s attractiveness in short-term mating contexts is just as important to women as a woman’s attractiveness is to men when men evaluate long-term mates” (G&S citing Buss & Schmitt 1993). But, actually, there was a main effect there – attractiveness for both men and women is more important in short than in long-term relationships.

4. For human males, having many short-term partners actually produces more offspring who survive to reproduce than a more long-term strategy. The evidence regarding this point is far from clear. For example, G&S’s Bateman (1948) citation refers to fruitflies. The best data we could find relevant to this point is from one of the few national sex surveys (Laumann et al. 1994) that used probability sampling over numerous cohorts in the lifespan. Men who have been married had six times more conceptions and averaged far more offspring with far fewer partners (with over 75% of them faithful during the course of their marriages). It is clearly essential for G&S’s theory to document how these different strategies, for humans, translate into differentials in number of surviving offspring.

In short, although we find the theory intriguing, we believe the evidence presented warrants caution.

Evolution of mating strategies: Evidence from the fossil and archaeological records

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Abstract: Gangestad & Simpson provide a persuasive argument that both men and women have evolved conditional mating strategies. Their references to “ancestral” males and females are rather vague, which is unfortunate, as they seek to justify their arguments by invoking human evolutionary history. When one actually examines the evidence for human evolution further, more support for their arguments can be found, as predominant types of mating strategies are likely to have shifted in light of environmental and anatomical developments. We can also see in the archaeological record evidence for a further dimension of strategic pluralism – the use of material culture to advertise good genes in some species of ancestral males.

Gangestad & Simpson’s (G&S’s) target article provides a persuasive argument that both men and women have evolved conditional mating strategies – a behavioural flexibility to maximise returns from particular circumstances. The concern with our evolutionary past is to be applauded but the article is too vague as to what specific period is being referred to when “ancestral” males and females are being invoked. It is important to be more specific. When the fossil and archaeological records are examined one can reconstruct how, when, and why the sexual strategies of males are likely to have evolved from predominately seeking short-term mating opportunities to one in which long-term relationships involving energetic investment in both females and young are likely to have become more common. A key task in this is reconstructing the evolutionary history of human life-history and reproductive costs from the fossil record – an area of considerable current research with which evolutionary psychologists should engage (e.g., Key 2000; Key & Aiello 1999; O’Connell et al. 1999; Power & Aiello 1997). If we consider human ancestors and close relatives between 4.5 and 2 million years ago, for instance, these being the australopithecines and earliest *Homo*, it is apparent that there is considerable sexual dimorphism suggesting that males were competing

for short term mating opportunities, using their body size to advertise “good genes” in the manner that G&S describe in section 3.1. These hominins had brain sizes similar to chimpanzees today and most likely also had an ape-like life history pattern. In contrast, the males of species such as archaic *Homo sapiens* and *H. neanderthalensis* living after 250,000 years ago and with brain sizes equivalent to those of modern humans, are likely to have more frequently made substantial investment in securing long term relationships with specific females partly through provisioning to both females and the young. The switch in emphasis is simply owing to female needs – as the energetic costs of reproduction soared due to increased brain and body size they were concerned with not simply securing good genes for their offspring but also substantial energetic support.

A particular interesting phase of human evolution lies between these two extremes, with hominins such as *Homo ergaster*, as represented by the 1.6-million-year-old specimen, the Nariokotome boy (Walker & Leakey 1993). At this time brain size was at around 900–1,000 cc and there was limited sexual dimorphism due to an increase in female body size. Reconstructed life history patterns suggests something midway between an ape and human pattern (Key 2000). It would appear that the costs of reproduction were not such that females required substantial male investment, any support for pregnant/lactating females and offspring being provided by female kin alliances. Hence, male mating strategies would have predominately been concerned with short term mating opportunities. But with the loss of sexual dimorphism how were males able to advertise their good genes? There appears to have been a physiological constraint against further increase in male body size, perhaps the energetic costs of this were simply too substantial (as described by Gangestad & Simpson in sect. 3.2). The solution proposed by myself and Kohn is that males adopted items of material culture to advertise their “good genes” and that this explains some very curious features about Acheulian handaxes (Kohn & Mithen 1999).

These are tools that first appear in the archaeological record at c. 1.5 million years ago and remain as a key artefact for more than one million years (for review of the evidence see Schick & Toth 1993; Mithen 1996). They are found in all continents of the old world, often in abundant numbers and were made by the bifacial flaking of stone nodules to produce pear or ovate shaped artefacts. Such tools were effective butchery instruments, but many examples display degrees of symmetry and workmanship going far beyond utilitarian needs. Others are too large to have been of much practical use. Such artefacts are difficult to make, requiring strength, hand-eye co-ordination, access to good raw materials, and intelligence. We have suggested that some ancestral males of this period used such handaxes to display their good genes – by making such handaxes they were able to demonstrate physical fitness, intelligence, and knowledge of raw material (and hence resources in general) to females. These are features that would have been desirable in any offspring.

A key element of our argument relates directly to the use of fluctuating asymmetry as discussed by G&S. Perhaps the most striking feature of many handaxes is their degree of symmetry. Many have flake scars which show that tiny flakes were removed for no reason other than to impose a high degree of symmetry on the finished artefact, a degree of symmetry that has no utilitarian function. We argue that the hominins making such artefacts are simply exploiting the perceptual bias of females towards symmetrical entities – whether those entities are faces, bodies or artefacts. Symmetrical artefacts were more likely to have attracted the attention of females and cued evolved psychological mechanisms of sexual interest.

If handaxes were partly products of sexual selection – means by which males could advertise their good genes when competing for short term mating opportunities – then another very curious feature about the Acheulian is explained. This is that so many handaxes are found discarded without any evidence of having been used; many sites, such as Olorgesailie in Africa or Boxgrove in En-

gland, both of which date to 500,000 years ago, have a great number of handaxes scattered around occupation surfaces indicating that further handaxes were made while many pristine handaxes were already readily available. Why should ancestral humans of this time period have behaved in such a fashion? It appears quite wasteful of time, energy and raw materials and hence, quite counter to our usual measures of an effective adaptation to challenging Pleistocene environments.

The answer that Kohn and I suggest relates to the problem of cheating. When sexual displays involve objects, one male could easily cheat by having a large, symmetrical and skilfully made handaxe which had in fact been made by another individual. This might have simply been collected from another site or acquired by aggression or stealth. The only means females had to counter such cheating was by actually watching the handaxe being manufactured. Only by that means could they ensure that the “good genes” they desired would actually come with the hominin male who possessed the handaxe. Once such manufacture had been observed the handaxe had effectively done its job and consequently, many are found discarded in a pristine condition.

Handaxes effectively disappear from the archaeological record around the time of substantial encephalisation when biparental care of offspring and the provisioning of female needs would have become essential, c. 250,000 years ago. At that time it is likely that females began to select males on the basis of their provisioning abilities rather than simply “good genes.” Hence, we see a technological shift to the production of more effective hunting weapons, such as stone points made with the Levallois technique, and the loss of artefacts in the archaeological record that appear to have been largely about sexual display.

This theory about handaxes enables us to explain several features of the archaeological record that have long remained confusing to archaeologists, notably the high degrees of symmetry of many handaxes, their great number, and their discard in pristine condition. Handaxes were no doubt also very effective functional tools especially for butchering carcasses and some may have only played this role. But as products of sexual selection they show a further dimension of the strategic pluralism of ancestral males, in this case exploiting material culture to advertise their good genes.

The human mind today is a product of a long evolutionary history during which there were substantial changes in environment, anatomy, and brain size (Mithen 1996). As these varied so too did the relative value of seeking short term mating opportunities and developing long term relationships, with a substantial shift towards the latter in the final stages of human evolution. Gangestad & Simpson provide a very valuable reminder that at any one time, however, different males are likely to have adopted different strategies in light of their particular circumstances. And in light of such a varied evolutionary history it is not at all surprising that humans today are able to adopt such immense flexibility in their mating behaviour.

Sweet FA: The trouble with fluctuating asymmetry

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Abstract: Studies of fluctuating asymmetry (FA) in relation to sexual strategies in humans provide the empirical basis for many arguments in support of good genes sexual selection theory. Many FA studies, however, are flawed by bias in experimental design, inconsistent statistical analysis, and the sloppy handling of data.

Every so often in the field of evolutionary biology, an idea emerges that generates both heat and light – nature/nurture, neutral the-

ory, cladism, group selection, punctuated equilibrium, sociobiology – though it is sometimes the controversy itself that generates enlightenment. The latest addition to this distinguished list is fluctuating asymmetry (FA). Ever since Anders Møller (1990) introduced the measurement of FA as an index of genetic quality in studies of sexual selection, there has been much ado about noting its widespread applicability. Thus, FA seems to provide a magic bullet to solve the vexing problem of testing good genes theory in nature, a problem that had rendered a good idea (Zahavi 1975) largely untested. A reliable index of genetic quality that could easily be measured would indeed be sweet and could potentially shed light on a contentious area of sexual selection theory. The purpose of this review, however, is to turn up the heat.

Though FA is curiously missing from the title and abstract of the target article, Gangestad & Simpson (G&S) use studies of FA almost exclusively to support their core argument that good genes sexual selection (GGSS) theory can help us to understand human mating patterns. Indeed, in G&S, those studies form an essential logical link between some good ideas about trade-offs and conditional mating strategies and some fuzzy thinking about “strategic pluralism.” Unfortunately, the empirical data and attendant conclusions about the importance of FA are much more controversial than G&S would have us believe.

The reasons for controversy about FA as a test of GGSS theory are manifold and have been variously documented in empirical research (Hunt & Simmons 1997), commentaries (e.g., Palmer 1999; Whitlock & Fowler 1997), review papers (Palmer 1996), and book reviews (Houle 1998). *The Journal of Evolutionary Biology*, for example, devoted most of an issue to a target article on FA (Møller & Thornhill 1997) and seven largely negative commentaries. Since G&S chose to completely ignore this controversy, they give the erroneous impression that their arguments are supported by well-accepted research. FA studies of GGSS have proliferated exponentially over the past decade, largely due to the immensely productive output of three research groups – in Paris (Møller and colleagues), in Albuquerque (Gangestad, Thornhill, and colleagues), and in Liverpool (Manning and colleagues), the latter two focussing particularly on humans. All three of these groups (hereafter PAL), consistently find support for a negative relation between FA and some aspect of quality related to sexual selection and steadfastly use each others’ work to bolster arguments in favour of GGSS. For example, 25 of G&S’s 33 citations explicitly about FA are from PAL and only one critical paper (Clarke 1998) is mentioned, vaguely (G&S sect. 3.3, para. 2). In fairness the high productivity of the PAL researchers has resulted in their domination of the FA literature, but the published work of all three groups is open to comparable criticism. In particular, many published studies of FA in humans, lack the sort of rigour we should expect in evolutionary biology in general, but especially in the study of humans. To illustrate all of my criticisms I focus on their first paragraph (sect. 4.1) about FA research but these problems apply to much of the work on FA that G&S cite.

Few published studies on FA provide evidence that data were collected using standard methods to minimize bias. This is especially surprising because psychologists, who are involved in much of this research, have pioneered the methods to collect unbiased data in the study of humans. This problem is particularly critical in studies of human FA because measurement error is often high, differences between left and right sides often small, and a few of the individuals sampled frequently have high leverage in the subsequent data analysis. Moreover, though statistical analyses in FA research are often complex and reasonably sophisticated, too frequently too little attention is paid to testing assumptions and assessing the influence of outliers. As a result, interesting significant correlations abound in the study of human FA but are harder to find in animal studies that, by contrast, have clearly been carefully executed with large sample sizes (e.g., Dufour & Weatherhead 1996).

Even when quoting published work, many papers on human FA fail to present or use previously-published results correctly (see also Palmer 1999). In their discussion of the relation between the

lifetime number of sexual partners and FA, for example, G&S correctly quote that Thornhill and Gangestad (1994) found a correlation of -0.32 . (While I believe that the analysis in that paper was also flawed, that is another, longer story.) G&S then incorrectly list the partial r as -0.38 (when it was really -0.47 ; beta was $-0.38!$). Although this is not an egregious error, it is one of many; the sloppiness does call into question the care taken in the collection of field data, whose validity we cannot evaluate (see also Palmer 1999; Whitlock & Fowler 1997). G&S also claim that “Waynforth (1998) has found a similar correlation ($-.23$)” There was, however, no such correlation presented in Waynforth (1998, Table 2), though the P-value for this relation is listed as 0.23. Only by arbitrarily analyzing the data for men under 41, did Waynforth (1998, p. 1499) find that “high FA was marginally associated with a lower number of lifetime sex partners ($\chi = 2.82$, d.f. = 1, $p = 0.093 \dots$), a result that he oddly calls significant in his Discussion. G&S also claim that Waynforth (1998) “documented that more symmetrical males have higher fertility” but it was really fecundity – a very different measure – that he estimated; even that was based on self-report without consideration of the potential confound of cuckoldry. Because of such inconsistencies in information that I can check, I am more than a little skeptical about the quality of data presented in these papers.

Why should we care if there are a few mistakes in papers about FA? Cynics will say that some papers in all fields of science are a bit sloppy and that this is a necessary consequence of doing science in a climate where time is short, careers and grants depend increasingly on the quantity rather than the quality of publications, and there is a media frenzy over interesting science about human sex. It is my impression, however, that studies of FA, in general, and human FA in particular, are more problematic than those in most sub-fields of evolution and behaviour (see also Whitlock & Fowler 1997). Indeed sociologists may learn much about the scientific process by studying the development of this field (e.g., Simmons et al. 1999). Most important, though, I believe that students of human behaviour have a special obligation to be extra careful in their work. Early critics of sociobiology worried about the misuse of human data in directing social policy (see Wilson 1976).

While I believe that fear was somewhat unfounded, the publication of papers that are less than sound can only fuel the fires of such criticism. Evolutionary psychology, the young child of sociobiology, has made tremendous progress in the study of human behaviour as witnessed by the carefully articulated ideas in GS sections 1 and 2. We need to ensure that published data and analyses on FA are as rigorous.

Is fluctuating asymmetry a signal or a marker of genetic fitness?

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Abstract: Fluctuating asymmetry is more a signal of genetic fitness than a marker observable only to the researcher. Hence, it has to be demonstrated that low FA is an honest signal of genetic quality; this has not been demonstrated in Gangestad & Simpson’s otherwise useful review.

The main part of Gangestad & Simpson’s (G&S’s) target article is their review of research in fluctuating asymmetry. They present very rich material in a well organized and lucid manner – not to mention that much of the original research in this fascinating subject has been done by themselves. The theoretical framework outlined in sections 3.1.–3.3 of their target article, however, is incomplete, if not flawed. Fortunately, the flaws need not be fatal, but we cannot know that beforehand. Strangely, the paper shows

some signs that the authors might be aware of the deficiencies, but they do not suggest how to overcome them.

Fluctuating asymmetry (FA) is a marker of genetic fitness, not only for the eyes of the researcher but also for the eyes of women looking for a mate. If so, FA is also, as the target article demonstrates, an important, signal of genetic quality; hence males have a strong incentive to fake this signal. It is difficult to see why accordingly, G&S do not apply the first twelve sentences in section 3.2. which are on honest signaling, to the body of observations regarding FA.

One of the strongest evidence that Fa is more a signal than a marker, is its exclusive relevance for males. FA may be a weaker marker of genetic fitness in females, because the variance in male's reproductive success (RS) is greater, but it cannot be no marker at all. Should pathogen resistance and developmental precision not be a good predictor of female RS as well, likewise because FA is heritable? Do all the genes responsible for FA sit on the Y chromosome? Or, if we hypothesize genomic imprinting, why should evolution select the inactivation of genes favoring pathogen resistance and developmental precision?

It is also difficult to see how the factors leading to low FA should be direct causal factors for a body odor which pre-ovulatory women like (sect. 4.5.2). Moreover, of the three sexually dimorphic traits – body mass, physicality, and social dominance – which together account for 70% of the total FA effect of lifetime number of partners, neither body mass nor physicality can be direct effects of FA (sect. 4.4).

Still, given all the observations collected in G&S's target article, FA might prove one of the most important signals of a male's genetic quality for females making their choice. But then it has to be shown that it is an honest signal, and, if so, its precision as the signal has to be determined. For that, some internal male quality Q has to be identified which is (1) not directly (or only after long acquaintance) observable to a mate; (2) costly to fake; (3) heritable; (4) causal for FA. Then, it has to be established that Q is a determinant of RS. Next, it has to be demonstrated that a low degree of FA is more costly to produce the lower a male's Q. Since women do not need low FA for a high RS, evolution may also concede males some freedom about which level of FA to choose. These are the conditions for a signal's honesty to be evolutionarily stable, as Zahavi (1977) and Grafen (1990) have shown theoretically, and as Moeller (1987) has empirically demonstrated for the size of the chest spot being an honest signal of male sparrow's dominance, or as Mueller and Mazur (1997) have demonstrated for facial dominance being an honest signal of a man's dominance – the first such demonstration in humans.

I am sure that G&S know best what the good candidates would be for Q. They consequently owe us a rigorous demonstration that FA is an honest signal Q. That would greatly increase the value of all the valuable material on FA presented in their target article.

The limits imposed by culture: Are symmetry preferences evidence of a recent reproductive strategy or a common primate inheritance?

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Abstract: Women's preference for symmetrical men need not have evolved as part of a good gene sexual selection (GGSS) reproductive strategy employed during recent human evolutionary history. It may be a remnant of the reproductive strategy of a perhaps promiscuous species which existed prior to the divergence of the human line from that of the bonobo and chimp.

When do Gangestad & Simpson (G&S) believe that the evolution of good genes versus good provider reproductive strategies oc-

curred? Is it likely that a good gene sexual selection (GGSS) reproductive strategy was important in our recent evolutionary past or should we be looking elsewhere? Not every evolved human characteristic is the result of selective pressures operating during the environment of evolutionary adaptedness (EEA).

For modern humans, the ability to acquire culture, the desire to enculturate children, the compulsion to behave according to cultural norms, and the tendency to reject individuals who behave "abnormally" are among the strongest and most important structural elements in what G&S refer to as "the psychological architecture that guides social interactions." Human psychological architecture undoubtedly has other design features but they must operate in conjunction with the powerful instinct to be cultured. Culture has a particularly profound influence on reproductive behaviour. The reproductive strategies used by its members are of great interest to everyone who belongs to a culture and the only strategies available to members are those which the culture recognises. This means that any hypothesis about the selective advantage of a particular strategy has to be plausible within the context of the particular culture likely to have been in force when selection was taking place.

The influence of culture does not mean that human behaviour remains the same when environments suddenly change. Humans do not slavishly continue to follow cultural norms when it is unnecessary or disadvantageous to do so. But neither do individuals respond to environmental change by consulting their evolved psychological mechanisms, inventing novel behaviours, and pursuing them on their own. Humans change their behavioural options at the population level by making adjustments to the cultural norms which already exist. This places limits on the kinds of new behaviours that become available when environments change. For example, men in the modern western "global" culture have the option of behaving polygamously by having a series of sex partners or having several sex partners at once, but their potential for polygamous behaviour is held within strict limits by cultural norms. They cannot, for example, purchase a harem of young teenage girls from the Philippines, even though the market price might well be within the reach of many of them.

Human behaviour strategies can be partly explained by looking at how they allow individuals to respond to variations in the physical and biological environment. To gain a fuller understanding, it is necessary to look at the cultural environment. The observations of female reproductive behaviour cited by G&S were mostly of women living in the United States in the 1980s and 1990s. What if ancestors of G&S had measured the Sociosexual Orientation Inventory (SOI) scores for the grandmothers of these women, living in the United States of the 1930s and 1940s? If they had managed to avoid being arrested for indecency, they would undoubtedly have found these women far less willing than their granddaughters to engage in sex without closeness or commitment. These women may well have preferred the look and smell of symmetrical men but their culture did not allow them to act on these preferences.

The changes that have taken place in women's behaviour over the last two generations have not been a response to changes in the physical or biological environment. They are owing to changes in the cultural environment. Modern women are surrounded by an essentially infinite number of available men. Having short-term sexual partners is condoned, even encouraged. We possess the technology for avoiding pregnancy and sexually transmitted diseases. In America today, a single woman can thrive and bring up her children alone. In all of human history, when have women had such an ideal environment for exercising a preference for symmetrical men? And only if a preference is exercised can it confer an advantage and be selected.

But this conclusion poses the question when in human prehistory could a preference for symmetrical men have conferred a selective advantage? Humans are social animals and, like other patrilocal social primates, they tend to associate in male kin bonded groups, though with the important difference that each man's clos-

est companion is a woman (Bailey & Aunger 1990). The sparseness of food resources kept population densities quite low prior to the development of agriculture. A group of about 500 might be recognised by its members as sharing a language or culture, but individuals would have spent most of their time in groups of between 10 and 30 or even smaller single family groups (Foley 1996). Such a small group would provide women with few opportunities for the kind of sexual shopping-around necessary to take advantage of GGSS and, since the men available are likely to be brothers, the genetic choice would be even more limited.

The existence of a weak preference for symmetrical men in modern women does not necessarily indicate that the use of short-term and extra-pair mating tactics has been a routine occurrence in recent evolutionary history. This preference could be a very old adaptation, the remnant of the GGSS reproductive strategy of a perhaps promiscuous species which existed prior to the divergence of the human line from that of the bonobo and chimp. As the hominid line evolved, infants became harder to raise and offspring were more likely to survive if their father made a contribution to their care. The more reproductively successful females would have been those who could ignore their preference for symmetry and mate enthusiastically with men willing and able to provide them and their offspring with resources. In this way, natural selection would have weakened the preference for symmetrical men but, as long as it was not strong enough to inhibit females from mating with slightly asymmetric good providers, there would be no selective pressure to eliminate it completely.

Idealized human mating strategies versus social complexity

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Abstract: Gangestad & Simpson present an idealized model of human mate strategies based on rational economics and genetics that elides most social constraints on human sexuality. They do not deal with observable complexities of courtship nor with ambiguities in short- and long-term mating. The model successfully explicates a narrow set of premises, but cannot yet explain complex sexual behavior.

The greatest strength of Gangestad & Simpson's (G&S's) target article is its analysis of connections between long- and short-term mating strategies and sexual selection for good genes and/or for resources. Furthermore, they make the excellent point that choosing between the two strategies depends on complex contingencies of genetics and economics. However, on closer study, their argument becomes less persuasive.

G&S present a highly abstract, strongly idealized model of mate choice strategies that strips away a great many details. Indeed, the organisms that make mate choices in the model are so abstract and so idealized that they barely seem human. G&S discuss mating strategies as if enacted by completely rational economic and genetic monads devoid of all society and history, and who lack all religion, institutions, traditions, and laws concerning mate choice and its social consequences. No kinship systems, symbols, or customs influence or control mating. Instead, mate choices are analyzed as if isolated individuals made purely rational individual decisions. We doubt if such monadic purity of purpose has ever existed during human history or evolution.

This lack of social context for mate choice creates a serious definitional problem concerning the widely-used notions of short- and long-term mating. In actuality, the two concepts depend on a complex and modern moral and symbolic framework for assigning social value and meaning to sexual encounters after the fact. For example, Joe and Sally are each drawn to the other on a first date for reasons they themselves may label as "short-term" sexual in-

terest: he is symmetric, sexually available, and willing to wine and dine her; she is young, clear-skinned, lustrous-haired, and pretty. They have great sex – and decide to do it again. A year later, they are still together. Were then enacting short- or long-term strategies? Had they stopped seeing each other after one date, they themselves would post facto speak of a "short-term" relationship, but that label becomes inappropriate if they remain together.

If one studies human courtship using ethnographic and ethological field observations (see Givens 1978; 1983; Moore 1985; 1995; 1998; Moore & Butler 1989; Perper 1985; 1989; 1994; Perper & Weis 1987), one sees why the couple cannot themselves determine if a relationship will prove to be short- or long-term. Initially, neither person fully knows what they themselves want or what the other person might offer – such knowledge emerges only as their interaction itself creates their feelings for each other. Such floating emotionality is characteristic of courtship, so that uncertainties are intrinsic, and one cannot predict the future of a love affair (Perper 1999). Accordingly, most relationships begin with "strategic ambiguity," where it is not clear what either person wants or expects. It is therefore not obvious what strategy each is actually enacting except in 20-20 hindsight.

The expressions "short-term" and "long-term" are also deeply problematic as evolutionary concepts. Consider a band of some 100 proto-humans 300,000 ybp, where we use an imaginary time machine to observe one female for a month or so. She mates nine times with one male, five times with another, and twice with yet another. Which strategy is she using for which male? We might say that the two matings with the last male represent the short-term strategy, but a year later, we still find her mating twice a month or so with that male. Infrequent, yes; short-term, no. The labels "short-term" and "long-term" do not unequivocally characterize her sexual behavior.

Even if, in modern times, we symbolically identify two polar types of sexual encounter – conveniently, if opaquely, labeled short- and long-term – their evolutionary origin is not elucidated solely by good genes and resources. For example, a married woman might obtain resources from her husband and yet maintain a lengthy secondary sexual relationship with a man who does not give her money but provides much appreciated love and emotional support. Are Gangestad & Simpson arguing that the "strategies" underlying her life-choices are only matters of resources versus good genes? The actual complexity of mate choices and sexual behavior does not easily fit into G&S's idealized analysis of dichotomized mating strategies. Nor do the complex spiritual/sexual lifestyles recently compiled by Francoeur et al. (1999). Probably few social scientists would accept the view that women choose men solely as providers of resources or solely for their genes.

The natural and social sciences have produced two general answers for how to study complex phenomena. One, illustrated by this paper, is to build theory from a few – and only a few – explicit principles that justify narrow but extensively analyzed conclusions. This approach is validly reductionist, first in seeing strength in theory developed from a few premises, and second in depending on biological and genetic principles deemed logically and causally prior to the complex phenomena themselves. The other approach can be called "grounded," because it starts with the phenomena and tries to identify generalities and principles whether or not these match the premises of reductionist theory. One of us (Perper) has used this approach for studying courtship. Grounded theory necessarily makes simplifications as it develops, whereas reductionist theory tends towards more complexity. Ideally, they will meet in the middle, but in the meantime it is worth pondering what is lost through the reductionist hope of identifying a few sovereign principles that regulate human sexual behavior.

Yet we cannot really fault Gangestad & Simpson for their narrow focus. Their paper is a serious effort to explore the implications of a small set of ideas, rather than to prepare a synoptic view of the evolution of human mating. If G&S's presentation seems abstract and idealized, or lacks the rich substance of human real-

ity, it is because they examine one lode of thought in great depth. The exercise proves valuable partly because its extremely clear focus shows how much has been perforce omitted and how much we still have to learn.

Functional significance of human female orgasm still hypothetical

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Abstract: Human males are more polygamously inclined than females. However, there is substantial within-sex variation in polygamous inclinations and practices. This is acknowledged by Gangestad & Simpson but we pose the question: Is the target article's "strategic pluralism" pluralistic enough? In addition, we argue that the hypothesis that the female orgasm is an adaptation for post-copulatory female choice between rival ejaculates demands more research.

It has long been evident that in people, as in most other mammals, males are more polygamously inclined than females, while the latter are choosier in evaluating possible copulatory partners. These sex differences are readily understood in the light of the Bateman-Williams-Trivers theory of sexual selection and parental investment (e.g., Daly & Wilson 1978; Symons 1979).

Many people, including some evolutionists, dislike these truisms, but no one has mustered an evidence-based case against them. Nor are they called into question by Gangestad & Simpson (G&S), who are concerned with subtler issues: Why are these sex differences true only on average, with much overlap between women and men, and why is there so much variation in polygamous inclinations and practices within each sex? The target article reviews some relevant hypotheses and recent empirical evidence, including the authors' own contributions, and it should stimulate additional discoveries. We wish to draw attention to two issues in need of further research.

First, we wish to pose the question: Is the target article's "strategic pluralism" pluralistic enough? The authors have demonstrated large individual differences in "sociosexuality," a dimension which they characterize here as being primarily a matter of variable willingness "to have sex without commitment" and "to engage in short-term mating" (sects. 4.5.3 and 5.4). A central hypothesis is that "restricted" women who demand commitment from long-term partners are opting for paternal investment in a biparental partnership, whereas "unrestricted" willingness to forego such commitment entails trading off the material benefits that an investing partner would provide, in exchange for a "good genes" payoff. Without denying the plausibility of such trade-offs, we would suggest that this scheme is not pluralistic enough, especially with respect to relatively "unrestricted" female strategies. Cuckolding a long-term partner in order to recruit better genes through adultery is surely quite different from the polyandrous strategies of women who consider men too unreliable to bother seeking commitment. To suggest that an unrestricted female strategy of short-term mating entails giving up material compensation is curiously forgetful of the world's "oldest profession": the trade-off for women choosing whether to adopt a short-term mating strategy is in large measure a trade-off between material compensation now versus (promised) material compensation in the future, and a big determinant must be one's assessment of the trustworthiness of promises. Moreover, insofar as good genes sexual selection has been an important force in the evolution of the female psyche, we might expect that women would adjust "prices" for both short-term and long-term mates as a function of genetic quality cues.

The second issue demanding more research concerns the hypothesis that the female orgasm is an adaptation for post-copulatory female choice between rival ejaculates, and hence between

potential sires (Baker & Bellis 1995). G&S invoke this intuitively appealing notion in the context of arguing that women bias the chance of conception towards more symmetrical partners (sect. 4.5.1), but although their evidence that men's fluctuating asymmetry (FA) is negatively correlated with their sex appeal is persuasive, the evidence that women can and do bias the outcome of sperm competition by orgasmic timing is still very weak. At best, all that Baker and Bellis have shown is that women retain more sperm in their reproductive tracts if they experience orgasm between about 1 minute before and 45 minutes after their partner ejaculates than if they have an orgasm earlier or not at all. Even this ostensible fact requires not just replication but confirmation using other techniques, for as it stands, the inference is premised on the assumption that the number of sperm ejaculated is identical regardless of whether or when female orgasm occurs, so that sperm retention can be computed from an estimate of that ejaculate minus "flowback." This may not be true, since the duration of pre-ejaculatory male sexual arousal is most likely confounded with the criterion used to categorise female orgasms as either low or high sperm retention (i.e., whether they occur before or after male ejaculation). This is important since the number of sperm ejaculated by human males is positively correlated with the duration of pre-ejaculatory sexual arousal for specimens collected during copulation (Zavos 1988) and via masturbation (Pound et al. 1999). Consequently, Baker and Bellis's estimates of the number of sperm retained for copulatory episodes during which the female has an orgasm after the male are likely to be based on overestimates of the number of sperm ejaculated. The "high sperm retention" (HSR) orgasm may thus be simply an artifact of a method that fails to take into account an important determinant of ejaculate composition.

In any event, even if female orgasms can affect the number of sperm retained, the impact of biased retention on the outcome of sperm competition needs to be assessed; it could be substantial or negligible. At present there is no evidence that female orgasms, copulatory or otherwise, have any effect on conception rates, as one might expect if "HSR" orgasms really improve the retained sperm's chances of encountering the ovum, and more crucially, it remains to be shown that a woman who copulates with two men during a single fertile period is more likely to conceive a child sired by the one with whom she experiences a copulatory orgasm.

This may seem like quibbling, since it is the conceptually integrated story of contingent female orgasmic response that makes the hypothesis of post-copulatory female choice so plausible. But the story of contingent female response is itself still just an hypothesis, too, albeit a strong one. Thornhill et al. (1995) found that women with low-FA partners reported more frequent HSR orgasms (by the above timing criteria) than women with high-FA partners. But although Thornhill et al. found no evidence that women with low-FA partners are simply more orgasmic than other women, their main finding is nevertheless a between-subjects result. They did not establish that individual women vary their orgasmic behavior in relation to partner's FA, and it remains possible that those women who are most likely to have copulatory orgasms are those most likely to have low-FA partners. Moreover, even a demonstration of Thornhill et al.'s effect within individual female respondents would not close the question. The women were merely asked how often they attained orgasm before, after, or at the same time as their partners during sexual intercourse, a question that cannot show that it is the women who are responding differentially to men varying in FA; an alternative hypothesis is that low-FA men ejaculate sooner. Finally, Thornhill et al. (1995) define HSR orgasms as those that occurred during sexual intercourse after (or at the same time as) male ejaculation, but this definition may not be ideal; it excludes, for example, cases in which the penis is withdrawn after ejaculation, but sexual stimulation is continued and the woman reaches orgasm soon after, even though these would seem likely to also be HSR orgasms according to the Baker and Bellis scenario.

There is variability in the frequency with which women have or-

gams, in their timing relative to partner orgasm, and in the sexual activities during which they occur, but we do not yet know how much of this variability can be attributed to relatively stable differences among females, and how much to attributes of their partners. These two sources of variability will undoubtedly prove to be confounded, and yet they must be separated before we can be confident that female orgasm really functions to bias the outcome of sperm competition.

Analyses of mating differences within-sex and between-sex are complementary, not competing

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Abstract: Analyses of between-sex differences have provided a powerful starting point for evolutionarily informed work on human sexuality. This early work set the stage for an evolutionary analysis of within-sex differences in human sexuality. A comprehensive theory of human sexual strategies must address *both* between-sex differences and within-sex differences in evolved psychology and manifest behavior.

Gangestad & Simpson (G&S) present a clear and convincing theoretical case for the evolution of conditional mating strategies in human males and females. In addition, the authors present an organized and impressive array of empirical data corroborating their theoretical claims. G&S's analysis of the conditional mating strategies of humans relies on several cornerstones of modern evolutionary psychological science. These cornerstones include an appreciation that adaptations are not optimally designed; that adaptations have both costs and benefits in reproductive currencies; that organisms face "trade-offs" in how a limited quantity of time and energy can be allocated to solving different adaptive problems; and that adaptations do not operate in a vacuum, but instead require input for their operation (Dawkins 1976; Williams 1966).

G&S have significantly advanced the field of human sexuality by providing a cogent analysis of within-sex differences in male and female sexual strategies. The authors take as a starting point that previous work on human sexuality informed by an evolutionary perspective (e.g., Buss 1989; Buss & Schmitt 1993) over-emphasized between-sex differences. They contend that previous work paints a picture of human males as exclusively interested in short-term sexual relationships and of human females as exclusively interested in long-term, committed relationships. Early work in human sexuality informed by an evolutionary psychological perspective addressed sex differences in mating psychology and behavior, in part because these differences are so cleanly and clearly predicted from straightforward evolutionary logic (Symons 1979; Trivers 1972; for review, see Buss 1994b). None of this early work, however, discounted the reality of within-sex differences in sexual behavior and psychology. Instead, much of this early work noted that a weakness of evolutionarily-informed analyses of human sexuality is that within-sex differences were not fully explicable based on then-current theoretical accounts (see, e.g., Buss 1994b; Buss & Schmitt 1993; DeKay & Buss 1992).

The early focus on differences between the sexes in sexuality was a reasonable and powerful starting point for evolutionary psychological work on human sexuality. G&S correctly note that this early work failed to successfully explain within-sex differences in mating. But this was not the intent of this early work on human sexuality informed by an evolutionary perspective. The intent of this early work was to document predictable and on-average differences between men and women in their mating desires and behaviors. This focus on sex differences soon brought to the fore-

front the presence of substantial within-sex differences. A comprehensive and empirically supported analysis of within-sex differences in human sexuality awaited the insight of researchers such as G&S.

G&S provide a missing piece to the puzzle of human mating psychology and behavior. Men and women, on average, clearly differ in several key features of sexual psychology and behavior. All men are not alike, however, and neither are all women alike. We now have a comprehensive theory and supportive empirical work to explain these within-sex differences. Between-sex differences and within-sex differences are different and complementary, not competing, levels of analysis. One need not argue that there are either between-sex differences or within-sex differences. There are both.

The thrust of the target article is that within-sex differences are substantial and worthy of focused theoretical and empirical work. We agree, and we expect that researchers who have produced the work on sex differences in human sexuality also agree. We are concerned, however, that some readers might misunderstand G&S as arguing that within-sex differences are more important than between-sex differences in human sexuality. This sort of misunderstanding is akin to arguing that the neurobiological level of analysis is more important than the psychological level of analysis in understanding human cognition. Neither level of analysis is more important; instead, they are equally important but definitively different levels of analysis. And so is it the case with analyses of between-sex differences and within-sex differences in human sexual psychology and behavior. Previous work by researchers such as Buss and Schmitt (1993) advanced the field of between-sex differences. G&S provide a valuable contribution to the emerging field of within-sex differences. A comprehensive theory of human sexuality must address *both* levels of analysis.

Sexual attractiveness: Sex differences and overlap in criteria

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Abstract: Women with high sociosexual orientation inventory (SOI) scores may trade signs of willingness to invest for signs of ability to invest, instead of, or in addition to, genetic benefits. The target person's status traits affect women's judgments of sexual/physical attractiveness more than men's. An objective measure of a physical trait such as FA is therefore crucial in untangling the factors affecting women's judgments of attractiveness.

Gangestad & Simpson (G&S) propose an interesting thesis and provide a thorough analysis of pertinent literature to support it. Their argument has important implications for research on sexual attractiveness and mate selection and deserves to be explored from a variety of angles. I wish to clarify only a few points.

In real life, both sexes' judgments of attractiveness are typically affected by both physical and social traits (Townsend 1989; 1993; 1998). In some conditions, however, one sex may be unaffected by traits that significantly affect the other. Male law students, but not females, were affected by models' physical attractiveness when models were portrayed as having high status (Townsend & Roberts 1993). Women's judgments, but not men's, of physical, dating, or sexual attractiveness were affected by peer opinion (Graziano et al. 1993), target persons' costume (Townsend & Levy 1990), dominance (Sadalla et al. 1987), and apparent socioeconomic status (Townsend & Wasserman 1998). Consequently, when studies indicate that some women (e.g., women with high SOI scores) place more emphasis on physical attractiveness (e.g., Townsend 1993), it is not certain whether the traits assessed as "physical attractiveness" are physical, social, or both. An objective

measure of a physical trait such as fluctuating asymmetry (FA) is thus crucial in untangling the factors affecting women's judgments of attractiveness. In this respect, G&S current research represents a major advance.

In Townsend (1993), college women with high sociosexual orientation inventory (SOI) scores wanted to marry as soon as women with low scores, and women who believed that they might marry someone they met in college had lower SOI scores. In contrast, more sexually active men wanted to delay marriage, and believing they might marry someone they met in college was not associated with their sexual activity. These correlations between SOI scores and marital prospects suggest that the proceptive behavior of high SOI females in college may represent a mating stage rather than a lifetime tactic, and they may shift to higher-investment relationships when it is "time to settle down" – a possibility that G&S acknowledge (1991a). This possibility is important to bear in mind when evaluating studies of attractiveness and sexual behavior because most samples involve college students.

The Abstract of the target article states that women make "tradeoffs between a mate's genetic fitness and his willingness to help in child-rearing." Elsewhere (sect. 6, Summary and Conclusions), G&S propose that women "trade-off evidence of a man's genetic fitness for evidence of his ability and willingness to invest in offspring." Presumably, willingness to help in child-rearing reflects willingness to invest in offspring, but men with higher *ability* to invest (e.g., men with high socioeconomic status [SES]) are often less willing to assist in domestic chores and child care (Townsend 1989; 1998). It is therefore crucial to distinguish between evidence of male ability and willingness to invest. My own research suggests that physical traits definitely affect women's judgments of male attractiveness, but they appear to have their greatest effects on choices *within a pool* of men who have acceptable status and social characteristics (i.e., evidence of ability to invest). Regression analyses (Townsend 1993) revealed that college men who had higher SOI scores had higher anticipated incomes, were less concerned with their partners' SES, and placed more emphasis on their future wives' physical attractiveness. Females' SOI scores also correlated with their emphasis on future husbands' physical attractiveness, but these women were equally insistent that their husbands' SES be equivalent or superior to theirs.

In Townsend and Wasserman (1998, Study 1), women with higher SOI scores expressed more willingness to have sexual relations with attractive models, but they were just as influenced by models' status cues as women with low scores. In Study 2 women with higher SOI scores expressed more interest in target persons' popularity and less interest in target person's willingness to commit in a relationship, but they did not place less emphasis on target person's SES, nor were they more likely than women with lower scores to determine coital acceptability on the basis of a visual scan of physical traits. In contrast, men with higher SOI scores placed less emphasis than men with lower scores on target person's SES, and were more likely to determine coital acceptability on the basis of a visual scan (Townsend & Wasserman 1998). Hence, high SOI women's greater expressed willingness to have sexual relations does not seem to be the result of a greater tendency to determine coital acceptability on the basis of a visual scan of physical traits. Compared to low SOI women, high SOI women are more likely to say they would have sex with attractive strangers and to forgo preliminary evidence of willingness to invest, like sexual exclusivity and emotional attachment, but they do not seem to be any more willing to forgo signs of *ability* to invest, like status, dominance, and resources.

Symons (1985) suggested that although men tend to agree on what is attractive, men with lesser competitive abilities may actually perceive attractiveness differently and may find female physical attractiveness less important for sexual arousal than do males with greater competitive abilities. Waller (1994) found that men with higher incomes and Social Potency are especially likely to express a desire for younger women. Men with higher SES actually

do marry more physically attractive women (Udry & Eckland 1984). Buss (1994a) argues that, taken together, these findings suggest that people high in mate value shift their preferences so that they are more exacting on those dimensions that are typically preferred by their sex. Kenrick and Keefe (1994) note that the mechanisms mediating such shifts might be fixed early in development, or they might be triggered at any time during the life course by the appropriate environmental stimuli.

My findings are consistent with these prior studies and with G&S's proposition that men shift between short-term and long-term mating tactics. Men with high mate value apparently shift to a low-investment tactic in which they emphasize physical traits, deemphasize social traits, determine sexual desirability by means of a visual scan, and engage in casual relations with multiple partners. My surveys and ethnographic interviews suggest that the men with the greatest numbers of sex partners invariably enjoy high status in local hierarchies (e.g., star athletes, members of rock bands, upper-classmen in prominent fraternities) although these men might not have high SES as conventionally measured (Townsend 1998; Townsend et al. 1995).

Women also appear to shift mating tactics, but their emphasis on status traits and their negative emotional reactions to low-investment copulation appear to remain constant (Townsend 1995; 1998; Townsend & Wasserman 1995; 1998). The finding (sect. 4.5.2) that women find the smell of more symmetrical men more desirable primarily when they are ovulating is striking and deserves further study; however, it does not imply that these women deemphasize in their judgments of attractiveness men's status or ability to supply material advantages (G&S n. 6). Men's local status/dominance may correlate negatively with FA, particularly for successful athletes, and high-status men are probably more able to provide protection for their mates than low-status men. Disentangling the associations between males' FA, SOI, SES, dominance, physical attractiveness ratings, perceived ability to provide protection, and status in local hierarchies should prove to be a frustrating but fruitful area of research.

"What's love got to do with it?" Self-awareness and human mating strategies

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Abstract: Gangestad & Simpson make a convincing case for male and female psychological access to sexual strategies that dispose us towards both faithful long-term mating and promiscuity – according to socio-ecological conditions. However, their model fails to acknowledge how the human self-system's mediation of conduct can permit us to override voluntarily the pseudo-imperatives of optimizing inclusive fitness.

Crook's (1980) preliminary analysis of fraternal polyandry amongst Tibetan peasant farmers helped to pioneer socio-ecological understandings of sexual-strategic pluralism. Yet he stressed cultural tradition's part in sustaining this adaptation, and its heavy dependence upon the wife's skill at defusing inter-male jealousies which could yield maladaptive conflict. Following Humphrey's (1976) argument that self-conscious deployment of a theory of mind evolved to serve manipulative functions, Crook sees human social life as profoundly transformed by self-awareness. That "unique cognitive attribute of man: the self-process" permeates much of our information-processing (Crook 1980, p. 228).

This "functional-interactionist" paradigm for sociobiology represents its least reductionist variant (Vine 1992). It recognizes how "open" genetic programs, plus emergent properties of self-aware social intelligence, permit distinctively human kinds of personal development and normative culture. Even Dawkins (1976) ac-

knowledge that human genomes largely relegate control of adaptive strategies to the semi-autonomous, general-purpose brains they help to construct. Functional-interactionist assumptions about the causation of fitness-optimizing strategies imply possibilities of overriding some pseudo-imperatives embodied in inherited genetic programs.

Gangestad & Simpson's (G&S's) account of reproductive strategic pluralism does not reveal their level of commitment to the contentious paradigmatic assumptions within fashionable, tightly adaptationist formulations of evolutionary psychology (EP). In conceding its incompleteness, they beg major questions about the behavioural import of their sexual strategies theory (SST). I cannot present here the fundamental critique of EP's reductionism which informs the present commentary. But EP's defensible case for postulating a mind/brain built upon genetically specified modular units with specific functions is too glibly dismissive of general-purpose mental systems as incapable of their alleged tasks (Pinker 1997). This sidelines the evolved but cognitively and motivationally flexible self-system, which arguably mediates moment-to-moment and long-term intentional social conduct, and permits novel socio-cultural processes (Vine 1987; 1992).

The subjective self expands ego-serving motives, through social self-extensions which accommodate the fitness-related interests of individuals we identify with strongly (or of whole groups mentally embraced by our social identities). Conscious self-functioning remains subject to various cognitive-affective "ego-serving biases" – of the kinds which EP recognises within modules for theory-of-mind social prediction, for attributing social causation and responsibility, and so on. What the self-system perspective must contend against EP's reductionism is that we have scope for nurturing moral capacities which transcend fitness-optimising strategic goals and tactical impulses. It is dogma to assume that freely choosing to override our perceived ultimate reproductive interests necessarily involves ego-protective self-deceptions and false rationalisations.

G&S's argument for the sexual flexibility which SST does recognize is ably made at the level of natural preferences and temptations, plus broad behavioural trends within populations. I claim only that statistically significant generalizations will mask some cases where authentically self-aware individuals' deliberate moral choices and interpersonal commitments permit them to overcome fitness-oriented temptations to be unfaithful. However atypical these may be, they suffice to falsify the bio-reductionist EP paradigm.

Our admittedly fragile power to transcend genetic pseudo-imperatives has a clear foundation. Evolutionary sexologists like Perper (1985, p. 250) insist that "above all, human biology is a biology that creates meaning – signified by how we 'make love' rather than merely copulate." Subjective interpretations of deep emotional attachments, and self-identifications with partners, are processes missing from G&S's model. They will probably agree how extensively both affect and attribution biases mediated through self-process meanings impact on most aspects of our sexuality (Kelley & Harvan 1996) – such as how low self-esteem increases the probability of defecting from unsatisfying mating and bonding relationships. But do they accept one important inference from Perper's ethological and ethnographic studies of human courtship – that neither the external social environment nor internal templates for attraction suffice to determine whether particular sexually tinged encounters culminate in copulation? Those "symbols and traditions which function biosocially to provide meanings for the templated and preceptive behavior of both men and women" are inextricable features of mind that make all the difference (Perper 1985, p. 251). The delicate dynamic of mutual influences shaping sexual outcomes includes complex inter-subjective and cultural undersandings and misunderstandings – as when men often take female coyness strategies of "contingent reluctance with a possible Yes" to signify malevolent "teasing and goading" (p. 175).

Transient romantic states of overwhelming affect can turn into

monogamous commitments that represent companionate erotic love – realistic, lasting, responsible mutual attachment, identification, and loyal commitment. This ideal involves authentic respect for the other's autonomy, via ego-denying assimilation of their interests into one's personal self-standards (Fromm 1956). Even if we call it irrational for a childless but virile male to maintain fidelity long after his spouse's early death, such cases show that self-constructed meanings of relationships can counteract ego-serving fitness-optimisation.

The importance of reporting the distributional criteria of FA

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Abstract: Not all of the studies cited in the target article as evidence that fluctuating asymmetry (FA) predicts male mating success demonstrate that the observed asymmetry is, in fact, FA. FA is a population-level pattern of differences between sides. Unless the population-level distributional criteria of bilateral traits are reported, the meaning of asymmetry in individuals is unknown.

Gangestad & Simpson (G&S) review a number of studies showing that relatively symmetrical men enjoy reproductive advantages over asymmetrical men. The explanation is that asymmetry, or more specifically, fluctuating asymmetry (FA) is a marker of heritable fitness that reflects the true condition of men in terms of their "good genes." It is clearly in women's best interests to find the most symmetrical man possible (other things being equal) with whom to mate, as he should provide his offspring with the best genes. G&S also show that women may differ in preference for male symmetry depending on certain conditions; preference for good genes may be the over-riding consideration in short-term mating contexts whereas other male attributes may have greater salience in long term relationships.

My criticism of G&S's target article is that not all of the studies they cite as evidence that FA predicts male mating success demonstrate that the population-level asymmetry is, in fact, FA (e.g., Furlow et al. 1998; Gangestad & Thornhill 1997b; Thornhill & Gangestad 1994; Thornhill et al. 1995). While this criticism may seem minor in the face of an accumulating body of evidence that asymmetry (albeit not necessarily FA) is associated with reproductive disadvantages, it is critical because it addresses the fundamental meaning of symmetry in individuals. It is essential that the population-level distributional criteria for FA have been met in order to claim that individual symmetry reflects good genes. Otherwise, the meaning of asymmetry or symmetry in individuals is unknown. Traits that do not exhibit FA or whose distributional criteria are unknown should not be used as markers of good genes in individuals. This criticism applies to much of the mostly earlier FA work and is by no means new (see Palmer & Strobeck 1986; 1992).

The argument is as follows. FA is a pattern of population-level asymmetry with several distributional requirements: the population mean difference between right and left sides of a bilateral trait is zero and differences between sides are normally distributed (Van Valen 1962). In bilateral traits exhibiting FA, symmetry is assumed to be the normal developmental design because identical genes control development on both sides of the body (Clarke 1993). Gangestad and Thornhill (1999) argue that the distribution of differences between sides should be leptokurtic; this argument is not the issue here. If a bilateral trait that meets the distributional requirements of FA is found in a population, then it is legitimate to view individual asymmetry in that trait as evidence of developmental instability (Clarke 1993; Mitton 1993; Mitton & Grant 1984; Møller & Pomainkowski 1993; Møller & Swaddle 1997;

Palmer & Strobeck 1986; 1992; Van Valen 1962). Developmental stability refers to the presumably genetically-based ability to compensate for upsets in phenotypic development. In other words, developmental stability is a reflection of “good genes.” However, if population-level asymmetries demonstrate other distributional criteria, this conclusion cannot be made.

Directional asymmetry is a pattern of population-level asymmetry that occurs when the population mean difference between sides is significantly different from zero, and the differences between sides are normally distributed (Palmer & Strobeck 1986; but see Gangestad & Thornhill 1999 for a discussion of the shape of the distribution of asymmetries). There exist a number of naturally-occurring directional asymmetries such as number of lobes in the human lung, eye placement in flatfish, and ear placement in owls (Møller & Swaddle 1997). For example, the consistently larger left testis in birds is an adaptation that lowers the immunosuppressive costs of androgens produced in the testes; only the left testis produces sperm, while the right testis is compensatory, and therefore larger only if there is something wrong with the left (Møller 1994a). Møller found that male barn swallows and house sparrows of high phenotypic quality (and presumably high developmental stability, or “good genes”) as evidenced by large testes volume had greater *asymmetry* in testes size than other males. This suggests that individual symmetry, or right-larger asymmetry in a population showing left-larger directional asymmetry reflects *lower* developmental stability (i.e., poor genes). Clearly, it is important to understand the functional importance of asymmetry in a particular trait before assuming that symmetry in individuals reflects good genes. Other studies using some of the phenotypic traits reported in studies cited in the target article do show population-level directional asymmetry (e.g., Livshits & Kobylansky 1989; Manning et al. 1997) however, others do not (e.g., Manning 1995; Manning & Anderton 1998). These mixed results suggest that studies should not rely on previous demonstration of FA in particular traits; rather, it seems prudent to assess the distributional criteria separately for each sample.

Antisymmetry is another population-level pattern of asymmetry that occurs when the population mean difference between sides is zero, and the differences between sides are non-normally distributed (Palmer & Strobeck 1986). The shape of the latter is frequently bimodal or platykurtic. The signalling claw in male fiddler crabs is an example of a pattern of bimodal antisymmetry; whichever claw remains undamaged longer becomes the larger claw and apparently, since claw damage is random with respect to size, fifty percent of the population is right side larger and fifty percent is left side larger (Møller & Swaddle 1997). Antisymmetry presumably could occur when sub-populations with different patterns of asymmetry are mixed (e.g., two oppositely-oriented directionally asymmetric populations would appear as a bimodal frequency distribution of right-left differences).

Thus, the origin and meaning of individual asymmetry in population patterns of directional asymmetry and antisymmetry is different from traits showing FA; the former may represent genetic or developmental design for asymmetry (Palmer & Strobeck 1986). Unless the distributional context of the population trait under study is shown to evidence FA, conclusions about the relationship between symmetry and good genes in individuals, or about correlations between symmetry and indicators of fertility are premature. The meaning of individual symmetry or asymmetry is unknown until the population-level distributional criteria of the right-left differences are revealed.

Authors' Response

Trade-offs, the allocation of reproductive effort, and the evolutionary psychology of human mating

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Abstract: This response reinforces several major themes in our target article: (a) the importance of sex-specific, within-sex variation in mating tactics; (b) the relevance of optimality thinking to understanding that variation; (c) the significance of special design for reconstructing evolutionary history; (d) the replicated findings that women's mating preferences vary across their menstrual cycle in ways revealing special design; and (e) the importance of applying market phenomena to understand the complex dynamics of mating. We also elaborate on three points: (1) Men who have indicators of genetic fitness may provide more direct benefits when female demand for extra-pair and short-term sex is very low; (2) both men and women track ecological cues to make mating decisions; and (3) more research on female orgasm is needed.

We are delighted that our target article inspired 43 thoughtful commentaries. The commentaries critically evaluate the assumptions of our framework, raise several key research questions, and highlight many important issues for future debate within evolutionary psychology. Our response is divided into two major sections. In the first section, we elaborate on three central themes: the meaning of within-sex variation in mating tactics, the application of optimality thinking, and the criterion of special design. In the second section, we discuss several salient issues that merit further exploration. By necessity, some excellent points made by individual commentators go unaddressed.

Before proceeding, we address an important matter of terminology. **Perper & Cornog** note some problems with the expressions “short-term” and “long-term” (borrowed from Buss & Schmitt 1993). Individuals probably do not enter most relationships intending them to be long-term or short-term; these preferences and desires unfold over time. We agree that these terms may not fully convey our intended distinction. By long-term mating, we refer to relationships into which partners invest considerable time, resources, and effort over an extended period of time. Some potential long-term mateships may fail to become “long-term.” Other relationships, which we refer to as short-term, never have the potential for substantial investment. As **Perper & Cornog** imply, however, some low-investment relationships may actually be maintained over an extended period of time (e.g., an affair that persists for years). Low versus high-investment mating (see Kenrick et al. 1993) probably captures our intended distinction more accurately (particularly with regard to male investment; **Archer & Mehdikhani**). However, we retain the terms short-term and long-term for continuity.

R1. Addressing major themes

R1.1. The question of between-sex versus within-sex variation. Our target article focuses on within-sex variation in mating tactics. A few commentators accuse us of trying

to “minimize” (Bleske & Buss) or “downplay” (Archer & Mehdi khani) sex differences (also see Cornwell et al.). Bleske & Buss imply that we attempt to “play . . . to a politically correct crowd.” Claims of knowing our intent are odd, particularly in a field hampered by skeptical outsiders’ musings about the ideologies and motives of its practitioners. More important, they are irrelevant to evaluating our arguments.

We attempted to portray the size of sex differences in mating accurately. As we note in the target article, sex differences are well established and “fairly large by conventional standards” (see Pound & Daly, Shackelford et al.; see also Baum on how our notions fit with Trivers). Nonetheless, most of the variance in measures of short-term sex and mating resides within each sex, also requires explanation, but has received relatively little theoretical attention (e.g., Miller 1997). Our article focuses on the “subtler issues” (Pound & Daly) surrounding what might drive within-sex variation.

Bleske & Buss object that we did not report effect sizes for FA (fluctuating asymmetry) in the same metric as the sex differences. They claim that sex accounts for five times the variance that accounted for by FA in one effect that is central to our notions and, hence, we apply a “double standard.” This is simply not true. If researchers focused on FA to the neglect of other important factors, it would be appropriate to argue that most of the variation is unexplained. We never claim that FA accounts for more variation in mating strategies than does sex, never suggest that sex differences are unimportant, and thus never use a “double standard.” Rather than viewing the effects of FA as amounting to only 20% of those linked to sex differences, one can regard the total variance explained as 20% greater.

Ironically, however, Bleske & Buss’s own comparison of effect sizes is flawed (see also MacDonald, Eagly). The size of a correlation is affected by the strength of association between the two variables generating the correlation along with the validity with which they are measured. Sex is *perfectly* measured by a single questionnaire item; its measurement contains no error. In contrast, developmental imprecision (and underlying genetic variation in fitness) is measured *imperfectly* by FA. As we emphasize (see also Gangestad & Thornhill 1999), the measure of FA used in most studies we cite correlates about .5 with developmental imprecision. Correlations involving FA, therefore, underestimate those with developmental imprecision by about 50% (see Van Dongen 1998; Whitlock 1998). Gangestad and Thornhill (1999) have estimated correlations between men’s developmental imprecision and their number of lifetime sex partners, facial attractiveness, number of extra-pair partners, number of times having sex with extra-pair partners, frequency of partner orgasm, and psychometric intelligence ranging from $-.28$ to $-.60$, explaining 25% of the variance on average in these measures. In a recent sample of men from a small village on the island of Dominica, developmental imprecision explains about 50% of the variance in estimated number of partners (controlling for age; Gangestad et al. 1999b; this study partly addresses Fuentes’s request to study additional populations). These effects are as strong as or stronger than typical sex differences in this area.

Sex, of course, is a crucial factor in our ideas (Bleske & Buss), given the differences between women and men in obligate parental investment and parental certainty (Symons

1979; Trivers 1972). Contrary to Cornwell et al., we do not argue that “differential mating strategies within each sex would be greater than such strategies between sexes.” (Their inference that we seek to “overthrow” these earlier theories of mating leaves us baffled, especially since we quoted Trivers [1972] stating one of our main arguments [sect. 2.4].) The conditional strategies we describe are clearly *specific* to each sex so, in this sense, *all* of the variation in mating strategies exists between the sexes (even if distributions of specific mating tactics overlap; see Landolt et al. 1995; McKnight & Bond). Bleske & Buss claim that we gloss over the role of sex in our model to “make it more palatable for some”; once again, their attempts at mind-reading are curious but irrelevant. We never explicitly stated that the mating strategies we describe are sex-specific because we presumed this point was obvious.

R1.2. The use of optimality thinking. Apparently, we did not adequately convey one central point. Sex differences in short-term mating effort can and should be understood in terms of sex-specific returns on mating and parental effort. Similar thinking can be applied to infer differences in the optimal allocation of effort among same-sex individuals, which we attempted to do. As we highlighted in the target article, the concepts and theory we utilized – life history trade-offs, conditional strategies, “making the best of a bad job” – are all central to behavioral ecology and hardly novel, though our specific application of them to human mating may be novel (cf. Cornwell et al.). Bleske & Buss suggest that our ideas contribute little beyond Sexual Strategies Theory. According to their view, because SST offers a more extensive menu of strategic options for both sexes, our emphasis on genetic benefits generating within-sex variation focuses more narrowly on “strategic pluralism” than SST does. Though SST describes many tactics the sexes can employ, it does not directly address *trade-offs* and why so much variation in optimal tactic use exists within the sexes. Thus, our approach both differs from and extends SST.

Relatedly Bleske & Buss thought our portrayal of SST was “distorted,” saying that “most readers will come away from their article believing that SST is all about men pursuing short-term and women pursuing long-term mating strategies” (see also Shackelford et al.). This was not our intent. In fact, we explicitly state that “Sexual Strategies Theory acknowledges that both sexes do exhibit short-term and long-term mating tactics (i.e., that human mating strategies are mixed); indeed, this is one of SST’s defining features” (sect. 2.3). We do claim that SST implies that men have a near-universal desire for short-term mates. To our knowledge, we make no inaccurate statements about SST.

To derive specific predictions about the allocation of reproductive effort within each sex, we focused primarily on one factor that should affect returns from mating effort, male genetic fitness. While important, genetic fitness clearly is not the only relevant factor. Claims that the mating strategies we describe are insufficiently pluralistic (Pound & Daly, Bleske & Buss, Hagen & Hess, Alley, Beckerman) are points well-taken (see our n. 7). Future researchers might use optimality thinking to derive predictions about which women, for instance, might gain small investments through prostitution. As we stressed in the final paragraph of the target article, our framework is far from complete.

One implicit message of our article is that evolutionary psychology should incorporate optimality thinking more ex-

explicitly into its theories. **Shackelford et al.** state that we appreciate that “adaptations are not optimally designed.” As do Parker and Maynard Smith (1991), we actually believe that selection *does* tend to produce optimal outcomes (under constraints). Advances in adaptationist theory take into account certain constraints (even if some, such as genetic constraints, are often ignored). The resulting theories (which typically treat constraints as trade-offs) putatively describe selection pressures on organisms and can be used to predict evolved outcomes (e.g., clutch size, offspring sex-ratio, age at first reproduction).

Evolutionary psychologists tend to think about selection pressures as “adaptive problems” posed by a hypothetical EEA that our ancestors were selected to solve. Buss and Schmitt’s (1993) SST, for example, proposes that ancestral men faced the adaptive problem of “mate number,” leading men to have a powerful desire for multiple partners. While thinking about selection in terms of adaptive problems can be a useful heuristic, it has limitations. Buss and Schmitt’s notions about men’s desire for multiple partners imply that short-term mating effort provided reproductive payoffs for men. But would all men have benefited equally? Shouldn’t benefits have varied across individuals? If so, what are the implications? A complete understanding of how selection pressures might have operated on individuals requires a clear model of selection pressures, which requires more than merely “deriving” (in the absence of formal theory) a likely solution to an adaptive problem. Although one could, in principle, ponder how a given man should best allocate his total reproductive effort when short-term mating yields poor returns, this is not the type of question that evolutionary psychologists typically ask (and, if it were, explicit optimality thinking would be needed). The same can be said of most questions about trade-offs, including those dealing with honest signals. We, in fact, should have made fitness functions more explicit (**Cuthill & Houston**); see Robertson and Roitberg (1998) for a model of the trade-offs between male mating and parenting effort we imply (see also Waynforth 1999).

Evolutionary psychologists have criticized some human behavioral ecologists for applying optimality models to current behavior, and we agree with many of their points. We concur that “mechanisms” underlying behavioral decisions are what evolved, not behaviors themselves, and that adaptations may or may not be currently adaptive. But using optimality models to understand past selection pressures is a separate issue (**Mealey**). These models can be implemented within the framework of evolutionary psychology (e.g., Kaplan 1996; **Hill**).

Given that evolutionary psychologists have criticized some human behavioral ecologists for conflating models of selection pressures with models of how the mind operates (i.e., that it seeks to “maximize fitness”), it is ironic that reasoning about adaptive problems may yield a similar sort of error. As **Archer & Mehdi khani** point out, not all men pursue short-term matings because women simply will not allow it. Men should “prefer” to engage in short-term mating *if they could* because men who successfully did so were perhaps the most reproductively successful. But not all men should prefer to pursue the best line of action for men with maximal reproductive success. Psychological states motivate the enactment of some behaviors over others. The most successful ideal outcome is not necessarily the one that all individuals should be motivated to attain given *con-*

strained options. Despite suggestions by **Berry & Kuczaj** and **Figueredo & Jacobs**, we remain unconvinced that all men would benefit by desiring (i.e., showing strong interest in and pursuing) something that most women will not allow. As **Townsend** mentions, Symons (1985) has proposed that men who cannot attract the most desirable mates should adjust their perceptions of women’s attractiveness. (Parenthetically, Archer & Mehdi khani argue that our brain surgeon example is inappropriate because, whereas being a brain surgeon requires “talent and training,” adopting a successful short-term strategy requires only “opportunity.” This ignores the fact that the “opportunity” to engage in short-term mating is substantially affected by men’s phenotypes, based on both genetic and environmental inputs [colloquially, “talent” and “training”].)

To demonstrate that men lack a strong desire for multiple mates, **Cornwell et al.** call for evidence that some men are not aroused by the thought of sex with multiple women. Without a proper comparison group of women and an estimate of within-sex variation, it is unclear what this demonstration (or lack of it) would indicate. If **Cornwell et al.** believe that this is *the* criterion of a “powerful desire,” we disagree. We focus primarily on men’s allocation of effort to short-term mating. Many men should put little effort into short-term mating (**Baum**) and should not be motivated to perform costly behaviors toward (i.e., have a “powerful desire” to achieve) these ends. Whether these men would be aroused by the thought of sex with multiple women is an interesting question, but not one critical to our notions.

R1.3. The use of arguments based on special design.

Several commentators question whether the environments in which mating strategies evolved contained the features implied by our ideas. **Beckerman, Chisholm & Coall, MacDonald, and Hagen & Hess** speculate that ancestral women may have had little choice of mates. **Cornwell et al.** argue that women’s extra-pair sex would not have been beneficial given the costs of male retaliation. **Miller et al.** wonder whether short-term mating would have ever been favored. And **Mazur** apparently doubts all evolutionary explanations.

To reconstruct evolutionary histories, adaptationists draw on a variety of evidence. One major source is the organism itself. Because only natural selection can forge complex design features, complex design is a telltale sign that natural selection has occurred. Because such features are designed for something, they also yield insights into the specific functions that led to their evolution in the first place and, hence, the nature of selection pressures (Thornhill 1997; Williams 1966). Eyes, for example, represent strong evidence that seeing was selected for. Details of the immune system are evidence that pathogens were a selective force in evolutionary history. And female preferences that contain specialized design features are evidence that these preferences have been forged by selection. We assert that some of the female preferences we discuss exist because women *could* choose some of their mates in evolutionary history (even if their choices were constrained much of the time). Details of how these preferences operate contain clues about the selection pressures that shaped them.

R1.3.1. The design of preferences. Women’s olfactory preferences provide some of the most suggestive evidence that good genes sexual selection (GGSS) evolved in hu-

mans. Several studies now indicate that women prefer the scent of more symmetrical men but only near ovulation, precisely when they are most likely to have extra-pair sex. This result has been found in four studies, meeting **Mazur's** request for "independent confirmation": Gangestad and Thornhill (1998b), Thornhill and Gangestad (1999) and, in Austria, Rikowski and Grammer (1999). Three other studies (conducted in the UK and Japan) have documented that women's preferences for men's faces also vary across the menstrual cycle (Penton-Voak et al. 1999; Penton-Voak & Perrett 2000; see **Cunningham**), with women preferring less feminized faces near ovulation. Importantly, this shift is specific to men's attractiveness as short-term mates (Penton-Voak et al. 1999). Though links between symmetry and masculine features have not been fully established (but see Scheib et al. 1999), these findings suggest that women's preferences are designed to acquire good genes when they are most fertile, leading them to engage in extra-pair sex when its costs might be offset by potential genetic benefits to offspring.

Hagen & Hess pose an alternate explanation for changing preferences: Women may choose mates who pose less risk of infecting them near ovulation, a time when they may be more prone to infection. But even if women's infection risk peaks near ovulation, the design of these preferences is problematic. Women with in-pair partners can only increase their risk of infection by having sex with a second, extra-pair mate. **Manning & Gage** note that the sperm of more symmetrical men is more motile. Thus, women may prefer these men for their sperm and increased fertility, not genetic benefits to offspring. These findings are fascinating, but we are not convinced that women should seek symmetrical men's sperm mid-cycle for these benefits alone; the direct fertility benefits strike us as rather low compared to the indirect genetic benefits (though more work might show otherwise). **Cuthill & Houston** suggest that men's symmetry may be preferred owing to sensory exploitation. We do not see how this could account for various aspects of women's preferences, such as the changing preferences of olfactory cues associated with symmetry. Indeed, we did not propose that symmetry itself is a cue, as the sensory exploitation hypothesis requires. Naturally, however, all alternate explanations should be considered and tested.

The chemical that women detect in the scent of more symmetrical men remains unknown, but it should be an honest signal of condition. Gangestad and Thornhill (1998b; Thornhill & Gangestad 1999b) proposed one possibility: androgen-related substances, which may signal men's willingness to engage in costly mating effort (including male-male competition). **Miller** did as well. Consistent with this idea, Grammer (1993) has found that women respond more favorably to androstenol near ovulation. In a study by Ellison, O'Roarke, and colleagues (unpublished data), men's morning T levels did *not* predict female olfactory preferences or men's FA (Gangestad & Thornhill 1998d). Men's morning T levels, however, may not covary highly with T responses to social situations (e.g., Mazur & Booth 1998), which may better reflect men's allocation of effort to mating. This issue requires additional research.

R1.3.2. The risks of women's short-term mating. It is argued by **Cornwell et al.** that women would not have risked short-term mating in part because of the enormous benefits of paternal investment (see also **Campbell** and **Miller**

et al. on the doubled cost of parental investment for women who short-term mate). As **Beckerman** notes, however, most individuals in traditional societies are married (see also **Cornwell et al.**), short-term mating often occurs in conjunction with long-term mating (**Broude**), and women who engage in short-term mating do not always incur the full additional costs associated with losing paternal investment. Our claims are consistent with this view: "Most men would probably have profited from substantial investment in a primary mateship (or small set of mateships), investing fairly heavily in subsequent offspring. When men could obtain short-term, opportunistic matings with other women (often other men's primary mates), they could have profited by [doing so]" (sect. 2.4). (Hence, **Bleske & Buss** are wrong when they state that "men seeking long-term mating are portrayed as 'genetic losers'" in our article. Although some men may refrain from short-term mating effort due to their low success rates, we never say or imply that *only* those men who fail at short-term mating opt for long-term mates and invest heavily in offspring.)

We are not persuaded by **Cornwell et al.'s** hypothetical cost-benefit analysis of the risk of extra-pair sex to women, as they offer no compelling evidence for the supposedly tremendous costs. We state that women may have benefited from extra-pair mating "with males who had [good genes] indicators, even if it meant 'trading-off' or risking the loss of material benefits they could have garnered from a long-term mate" (sect. 5.3). The mean loss of paternal investment could be relatively small if the probability of being detected was low, contrary to what **Cornwell et al.** assume (which does not imply that the probability of detection was *generally* low). *Incremental* cost of investment in offspring from short-term, extra-pair mates would not have to be large if a women were to get pregnant by *some* mate in any case; through extra-pair mating, she chooses a sire and thereby incurs a potential cost, the mean size of which partly depends upon the probability that her in-pair partner detects her extra-pair mating; cf. **Archer & Mehdkhani**). The cost would also depend on the amount of lost paternal care if extra-pair sex is detected. **Beckerman** notes that, in the Barí of Venezuela, women regularly engage in extra-pair sex; ethnographies say the same of some other traditional cultures (e.g., Hart & Pilling 1960, on the Tiwi; Hill & Hurtado 1996, on the Ache; see also Hartung 1985). In cultures he has studied, Kim Hill (personal communication) observes that some lower status men tolerate their wives bearing other men's children early in marriage (and even care for those children), as such a strategy appears to offer their best chance to reproduce. Relatedly, **Marlowe** points out that some Hadza men of Tanzania are willing to invest in children sired by other men in order to mate with the mothers later on (see also Daly & Wilson 1998). In sum, it simply is not obvious that extra-pair sex is highly costly wherever it occurs.

Barí children with secondary fathers (men other than the mother's social partner who had sex with her and could potentially be the biological father) have higher childhood survivorship (80% to age 15) than those without one (64%; Beckerman et al. 1998); a similar pattern is observed in the Ache of Paraguay, a group in which over half of all children have secondary fathers (Hill & Hurtado 1996). Beckerman et al. anticipated that siblings of children with secondary fathers (who have no secondary father themselves) would also enjoy high survivorship because those fathers give conspic-

uous gifts of meat and fish to their potential children's mothers, who can distribute the food to all of their offspring. They found the opposite; relatively few of these siblings survived to age 15 (61%), even compared to children with no secondary father between themselves and their siblings (69%). Beckerman et al. speculated that children with secondary fathers are healthier because these fathers pass small amounts of food directly to their children during times of scarcity. However, another explanation should be considered: These children may have received genetic benefits (e.g., greater heritable resistance to pathogens) from a secondary father. Their siblings without secondary fathers (and thus fathered by their mothers' social partners) may die at relatively high rates because women are especially likely to choose extra-pair sires when their social partners are unlikely to impart genetic benefits (e.g., heritable disease-resistance) to offspring. Additional research may tease these alternative explanations apart.

In our view, the task of reconstructing the environments that shaped current human phenotypes need not be left to paleontologists alone (though their findings can inform and constrain evolutionary reconstructions in important ways; see **Mithen; Holcomb**). Once again, evidence demonstrating the special design of a phenotype is crucial. Evidence of female adaptations for selectively seeking extra-pair mates should address **Cornwell et al.**'s concerns. Ironically, the premise of **Cornwell et al.**'s argument that extra-pair sex could have benefited women – because men are vigilant to it and punish it severely – is itself evidence for female interest in extra-pair sex (Buss 2000). The costs men incur to control female sexuality can only be worthwhile if equally costly, legitimate threats of cuckoldry exist.

R1.3.3. Female orgasm. The evidence that female orgasm is designed to cryptically “choose” a sire in multiple mating circumstances is questioned by **Pound & Daly**. Although we wonder whether the hypothesized biasing effect on sire selection when there are multiple partners implies that orgasm should increase conception rates when there is just a single partner, their alternative explanation of Baker and Bellis's (1995) findings on sperm retention is insightful. **Brody & Breitenstein** claim that self-reports of female orgasm may be inflated. But the study in question (Thornhill et al. 1995) used partner reports as well. Recently, Montgomerie and Bullock (1999) failed to replicate the **Thornhill et al.** finding using an alternate method of measuring FA. We have concerns about the method they used. Nonetheless, more work on the replicability and interpretation of this effect is clearly needed.

R1.3.4. Can special design arguments be compelling? Commentator **Holcomb** asks whether special design arguments can ever convincingly support an evolutionary reconstruction because they are based on “evolution without history.” Adequate explanations of how features evolved, he suggests, require detailed evidence about ancestral environments (extending back through phylogeny) that simply is not available. Although we agree that facts about the past can be informative and in some cases crucial (**Mithen**), we question whether special design arguments are truly “without history.” **Holcomb** appears to demand of these arguments that they provide a precise timeline of when selection occurred. Special design arguments cannot do so. Nonetheless, they can address questions of what selection pressures

forged the phenotypic features that we can observe today. Answers to such questions inform our understanding of the psychological features that account for current behavior, irrespective of when the effective selection pressures first appeared in our ancestry. In some (perhaps many) instances, selection will not have forged design that is readily reverse-engineered due to genetic constraint or exaptation or, more generally, historical contingencies, a point that Gould has put forward in various guises for many years. But the fact that organisms *may* not exhibit special design because of historical contingencies is not evidence that they *do* not (e.g., Andrews et al. 1999). Adaptationists' functional approach – which effectively ignores phylogeny – would not successfully explain animal behavior were the design of organisms so highly contingent upon precise timing of evolutionary events so that ignoring phylogeny would spell failure. Yet this approach has enjoyed tremendous success.

R2. Outstanding issues and directions for future research

R2.1. Fluctuating asymmetry: What is it a marker of? Contrary to **Cunningham, Mazur, and Mueller**, we did not say that symmetry per se is a “cue” that perceivers use to infer condition. Indeed, symmetry in a single trait is a very weak cue of underlying condition (Gangestad & Thornhill 1999; Taylor & Thomas, in press). Facial symmetry is associated with greater facial attractiveness, but it may account for little variance in attractiveness (for a review, see Thornhill & Gangestad 1999a). The observation that most men do not part their hair down the midline (**Mazur**) is totally irrelevant to our claims.

We contend that developmental imprecision, which underlies FA, reflects important information about an individual's “phenotypic condition” (i.e., the ability to effectively garner and convert energy into fitness returns). Variation in phenotypic condition can be subtle. It is not merely overt health. For example, two disease-free individuals who differ in metabolic efficiency (and hence fitness returns on energy expenditure) differ in condition. Condition can be affected by many factors, including mutations, pathogens, toxins, and other stressors experienced during development. Because some of these factors are heritable, phenotypic condition is partly heritable (Rowe & Houle 1996). Because some disrupt development, they also affect developmental imprecision.

Individuals should possess evolved developmental programs that allocate resources to alternative fitness-enhancing activities and features in ways that optimize their fitness (at least in evolutionarily-relevant environments). Traits that become signals of phenotypic condition (and genetic variance underlying it) should be honest (**Mueller**). Honest signals must be either less costly or more beneficial for individuals in better phenotypic condition to produce or maintain (Getty 1999; Grafen 1990). We presume that many traits which are useful for male intrasexual competition, such as physical fitness, as well as psychosocial assets such as intelligence, social skills, the ability to attract effective social partners with whom to forge social networks, and so on, represent honest signals of men's phenotypic condition. Some are energetically costly (e.g., muscularity). Some have socially-mediated costs (e.g., behavioral status displays that signal one's willingness to engage in intrasexual competition,

which is costly if one cannot win). All of these traits may be more beneficial to individuals in good phenotypic condition because they are more likely to live and enjoy these benefits longer. In theory, FA is associated with a wide array of traits (such as intelligence, “physicality,” romantic attractiveness, and social status) because developmental precision correlates with phenotypic condition, which in turn correlates with these traits. In this sense, our focus on FA is much more inclusive than **Figueredo & Jacobs** suggest. We focused on FA because one can be fairly sure it has undergone directional selection. On an *a priori* basis, one cannot be sure other features (such as size and intelligence) have. Research devoted to identifying traits associated with developmental precision and phenotypic condition should continue.

Figueredo & Jacobs elegantly describe how men might assess their own sociosexual abilities and opportunities when deciding how to allocate effort to mating versus parenting. Because self-assessments are likely to depend on many traits that, through the processes just described, covary with developmental precision, men’s mating strategies covary with FA. We presume that the self-assessment process is nearly universal in that men of poorer condition would make the allocation decisions of men in better condition were they in better condition.

Cuthill & Houston and **Figueredo & Jacobs** encourage researchers to broaden measures of “quality” and “sociosexual abilities and opportunities” beyond FA. We fully agree. Again, however, given its connection with underlying condition, developmental precision may be a more inclusive measure than they recognize. Cuthill & Houston also claim that the evidence for FA being associated with condition is not well established (see also **Montgomerie**). They indicate that there has been much controversy over the strength and consistency of FA results in the animal literature (see Clarke 1998; Møller 1999). However, these studies often use single-trait asymmetry measures that tap developmental imprecision very weakly (Gangestad & Thornhill 1999). When the unreliability of these measures is taken into account, associations between FA and mating success are substantial (Thornhill et al. 1999). Disattenuated associations between FA and condition may yield similar conclusions. Still, the biological significance of FA should be evaluated on a species-by-species basis. Admittedly, some important aspects of our claims about human FA – such as its relation with pathogen resistance – have yet to be verified (**Cunningham**).

Cunningham hypothesizes that FA may be associated with testosterone. Because testosterone facilitates allocation of effort to intrasexual competition and mating, this expectation seems reasonable. As noted above, however, one study found no association between men’s FA and morning T levels. Men’s T responses to intrasexual competitive events, perhaps a more meaningful reflection of allocation of effort, has yet to be examined.

Eagly argues that men’s FA predicts their sexual history and investment in relationships because FA is a marker of health and strength. She claims that because women prefer healthy mates over weak ones, lower FA (i.e., more symmetrical) men are preferred as *both* long-term and short-term mates. According to this reasoning, these preferences are not about obtaining genetic benefits. Low FA men who are insecurely attached presumably “have difficulty forming enduring relationships with women” and are assumed to be a subtype of men who have more extra-pair sex and invest

less in their relationships (also **Cunningham**). This alternate explanation cannot explain a host of findings, including the facts that: (1) women’s preferences for men’s symmetry predictably shift across the menstrual cycle; (2) more symmetrical men are preferred by precisely those women who tend to engage in short-term sex (unrestricted women), *particularly* as short-term mates (Gangestad et al. 1999a); (3) in Dominica, symmetry strongly predicts men’s number of partners, but it more weakly predicts their attractiveness as investing, long-term mates (Gangestad et al. 1999b); (4) men’s symmetry significantly predicts their number of extra-pair partners and having been chosen as an extra-pair partner, while relevant measures of attachment style (Simpson 1990) do not consistently produce Eagly’s predicted pattern of effects (Gangestad & Thornhill 1997b). While the work on the relation between attachment styles and mating strategies is intriguing (see Belsky et al. 1991; Chisholm 1993; 1999b; see Simpson 1999, for a review), these perspectives are not incompatible with our notions. Nonetheless, more symmetrical men may be adaptively disposed to invest very heavily in relationships and offspring under certain conditions, as Eagly notes (see sect. R2.3 below).

Cunningham and **Perper & Cornog** emphasize that emotional support and communication are critical in mate choice (see also Buss 1989). **Perper & Cornog** argue that these vital factors are absent in our ideas, and that we focus only on genes and resources. According to our framework, however, any behavior that increases the well-being of a mate or offspring can count as a direct, material benefit to a mate, emotional support included (see Ellis 1998). We presume that feelings of intimacy and emotional connection are proximate psychological outcomes that promote concern for a mate’s well-being. Perrett et al. (1998), in fact, hypothesize that women prefer slightly feminized male faces precisely because men who bear them are perceived as more emotionally supportive. As discussed in the target article, more symmetrical men tend to be less willing to invest time and be sincere with their current romantic partners.

Lalumière & Quinsey propose that greater symmetry may be associated with greater risk-taking and delinquency, both of which predict greater short-term mating effort. A high risk strategy can pay off when large gains, even if improbable, offset probable losses. This situation may exist for males when many short-term matings are available in markets that, in turn, encourage high mating effort (see below). Whether more symmetrical men engage in greater risk-taking in these circumstances raises interesting theoretical and empirical questions.

R2.2. Controversies surrounding FA research. Several controversies currently surround research on FA. Given space limitations, we did not address these in the target article directly, but we cited a paper that does (Gangestad & Thornhill 1999a). Many of **Montgomerie’s** largely mistaken remarks and erroneous conclusions could have been averted if he had read that paper.

Montgomerie claims that many of the studies by Gangestad, Thornhill, and their colleagues on human FA “lack the sort of rigour we should expect in evolutionary biology.” He complains that “too frequently too little attention is paid to testing assumptions and assessing the influence of outliers.” **Miller et al.** note that FA is not normally distributed and parametric tests may be inappropriate. Several of the FA studies we cite in the target article, however, contain

randomization tests to control for nonnormality and outliers (e.g., Furlow et al. 1997; Thornhill & Gangestad 1994). Moreover, Monte Carlo simulations reveal that even with N s of 25, parametric tests on correlations with FA are robust (Gangestad & Thornhill 1998c). **Montgomerie** does not mention these analyses. Miller et al. do, but fail to see that they directly address their concerns about nonnormality.

Walters notes that not all asymmetries are fluctuating; some may be directional or antisymmetry. Antisymmetry yields platykurtic distributions, whereas actual asymmetry distributions tend to be leptokurtic, a pattern consistent with FA tapping individual differences (Gangestad & Thornhill 1999; Houle 1997; Leung & Forbes 1997). **Walters** suggests that directional asymmetry (DA) ought to be tested on a sample-by-sample basis. We disagree. Statistics on samples drawn from a population estimate the same parameters, and sample differences should be due to sampling error. Based on a sample of about 700 people, Furlow et al. (1997) estimated that DA on human traits is small, in samples drawn from the University of New Mexico college population. Samples drawn from other populations should be examined for DA. We are confident that FA (and not DA) accounts for the results we report. Indeed, Walters offers no alternative explanation why the results might be based on DA. **Montgomerie** fails to acknowledge efforts to deal with distributional assumptions.

But **Montgomerie** goes even further. After suggesting that research on human FA has paid insufficient attention to assumptions and the effects of outliers, he concludes that “As a result, interesting significant correlations abound in the study of human FA but are harder to find in animal studies that, by contrast, have clearly been carefully executed with large sample sizes (e.g., Dufour & Weatherhead 1996)” (our emphasis). Given that outliers and assumptions *have* been examined in human work, this remarkable conclusion is almost certainly wrong. The primary reason for differences in results between the animal and human studies may be that many studies of humans have used aggregated, more reliable measures of FA based on 7–10 traits, whereas animal researchers usually examine correlations involving single FA traits (e.g., Leung & Forbes 1997). If human studies used single trait measures, the mean correlation in most existing studies would be approximately $-.10$ (see Gangestad & Thornhill 1999). Single-trait observational studies of nonhuman mating success have yielded a slightly greater mean correlation, about $-.15$ (Thornhill et al. 1999). Ironically, then, a methodological *advance* in FA research on humans may partly account for its greater success. (Again, however, some differences in true effect sizes across species may exist and also account for some of the variation in study results.)

Montgomerie implies that positive findings on human FA come from a few labs – PAL (Paris-Albuquerque-Liverpool). On the contrary, evidence for the association between human symmetry and attractiveness has been found in studies from several other labs (including his own!): Hume and Montgomerie (1999), Mealey et al. (1999); Perrett et al. (1999), Rhodes et al. (1998), and Rikowski and Grammer (1999).

Montgomerie also claims that many papers on human FA fail to correctly report previously published results. He provides three instances in our target article. First, he claims that we underreport (as $-.38$ rather than $-.47$) the partial r between men’s FA and number of lifetime partners

found by Thornhill and Gangestad (1994). In fact, the partial r we report is correct. It was calculated from the original data, which we should have noted. Montgomerie miscites a partial r ($-.47$) from an analysis on the *full sample* of men and women (not even the one described in our article); because the results on women have not replicated, we did not report the results for women. Second, the partial correlation of $-.23$ found by Waynforth (1998) is also correctly reported in the target article, but it should have been cited as a personal communication (it did not appear in the published paper). We reconfirmed this figure. It applies to men 40 and under. The value for the full sample is $-.14$. (Human FA appears to increase through adulthood, perhaps differentially across individuals. The validity of FA in late adulthood as a measure of earlier developmental health is unknown.) Neither is statistically significant. Third, Montgomerie’s claim that we misused the term “fertility” is mistaken. Demographers and biologists use the term differently. Demographers use the term fertility to refer to actual reproduction (e.g., number of offspring; Hill & Hurtado 1996; Pressat 1972), which biologists call fecundity. Demographers use the term fecundity (or fecundability) to refer to ability to conceive (or probability of conceiving in a given time period), whereas biologists call ability to reproduce fertility. For a general *BBS* audience, we used the more familiar term, fertility, to refer to number of offspring. Ironically, we discovered more mistakes and incorrect information in **Montgomerie**’s brief commentary (including points on which he accused *us* of being wrong!) than he found in our entire target article. **Montgomerie** suggests that such “sloppiness does call into question the care taken in the collection of field data, whose validity we cannot evaluate” and, hence, he may be led by his own mistakes to question the care taken in his field studies. We seriously question the logic of his claim and therefore any implication of the mistakes in his commentary for the quality of his field work, which we admire. (Parenthetically, the Palmer [1999] and Whitlock and Fowler [1997] articles **Montgomerie** cites as additional examples of “errors” do not criticize any paper we have published. Their relevance to our paper is therefore unclear.)

Fuentes and **Montgomerie** point out that some studies of human FA rely exclusively on self-report data. While some studies do (e.g., those focusing on number of lifetime sex partners), many others do not (e.g., those dealing with partner-reported investment in a relationship, orgasm, scent attractiveness, and videotaped interactions). Selectively criticizing self-report studies when other studies using different methods corroborate the theoretical claims violates Carnap’s “total evidence rule” – that theory evaluation must be responsive to *all* relevant evidence.

We fully agree with **Montgomerie** that work on human FA must be rigorous and critically examined (as must criticism of this body of work). As Gangestad and Thornhill (1999) have emphasized, the statistical issues raised by Palmer and others are important and require thoughtful consideration. Moreover, in many instances, human researchers do not have the sort of control that nonhuman researchers have and, hence, human studies may have unique limitations. Our conclusions about FA, however, were not based on any one study; they were based on *several* convergent findings. Even so, we do not consider the existence of GGSS in humans as “proven”; more research is needed.

R2.3. The benefits associated with FA: Genetic or maternal? We argue that women prefer men who evidence developmental precision at least partly for good genes and that, as a result, these men allocate more effort to short-term mating than do other men. As a result, women tend to trade-off direct investment from these men for their good genes. Several commentators question whether these men provide fewer direct benefits (**Beckerman, Davis, Hagen & Hess, Manning & Gage, Marlowe, Townsend**). Men in better condition might, after all, possess greater status and access to more resources.

As we noted, informal status (e.g., unwillingness to back down from other men) and abilities to compete in intrasexual situations (e.g., greater intelligence and “physicality”) covary with FA in college men. In a recent study on the island of Dominica, more symmetrical men have higher status among their peers, which could explain much of the covariation between FA and peer-rated partner quantity found there (Gangestad et al. 1999b). **Townsend** has found that women who are interested in sex without commitment are not more willing to have sex based on men’s physical attractiveness alone. Rather, they particularly value men’s social status, and men with higher informal peer status tend to have more sex partners. **Hagen & Hess** cogently argue that social status is more likely to serve as an evolved cue of access to resources instead of income per se. If more symmetrical men not only advertise their “good genes” but also signal their greater ability to provide material benefits (in evolutionarily-relevant environments), how can we know whether they are favored for their genetic benefits? And how can we assert that women trade-off material for genetic benefits?

Our argument is based on market considerations. Assume an efficient mating market that allows polygyny. For the sake of simplicity, also assume that women are of equal mate value. Although some men may have greater ability to attract multiple mates, all men would be expected to “pay” the same amount for each mate. Men can pay in two broad currencies: material benefits and genetic benefits (as an analogy, call them “paper” and “coins”). Those who can offer more in one form of currency (e.g., coins) pay less in the other (paper). The fact that certain men can offer both more genetic benefits *and* more material benefits does not mean that they will; instead, they should increase partner number rather than pay more for a single partner (see **Townsend** on ability vs. willingness to invest; cf. **Hagen & Hess**). If female quality is allowed to vary, men should be willing to pay the same for a mate of a given quality.

This argument could be wrong for a number of reasons. For one, it assumes that “expenditures” are mutually exclusive; conferring material benefits on one mate is not assumed to have other fitness benefits. Some forms of investment, however, probably are not mutually exclusive. For example, men who elevate their intrasexual competitive status may *simultaneously* demonstrate their superior condition (signaling genetic benefits) along with their ability to provide protection or plentiful resources through their social networks. This is why we proposed that men who advertise good genes may also offer greater material benefits of particular forms (e.g., protection and social benefits through status). Nonetheless, for theoretical reasons discussed above, we still suspect that these men typically provide fewer material benefits of other sorts and, for a mate of a given quality, perhaps fewer material benefits

overall. In the Hadza, **Marlowe** has found no evidence that better hunters (a skill that might honestly advertise genetic quality) provide less direct parental care. More work examining this trade-off is needed. Ideally, female mate quality should be controlled for; if better hunters have better mates, variation in female mate value could attenuate inverse relations between hunting skill and direct care.

But our notions rely on more than this conceptual argument. We also offer evidence that women possess special design for obtaining genetic benefits. We do not know how women’s selective preferences *when they are ovulating* for the scents or facial features of certain men can be nicely explained as preferences for physical protection or material benefits associated with status. Contrary to **Davis’s** claim, then, we did consider alternative hypotheses.

Nevertheless, we probably overstated the conclusion that symmetrical men provide fewer material benefits. Men not only attempt to attract mates; they also invest in offspring. If the gains from paternal investment are high (so that the exchange rate of paternal investment for genetic benefits is low and the value of men’s paternal investment to their own fitness is high), women should be less inclined to seek extra-pair mates and men should benefit from investing heavily in offspring. If more symmetrical men have greater ability to invest in offspring, they might invest more under such conditions. In species of birds in which the extra-pair paternity (EPP) rate is very low, Møller and Thornhill (1998b) have found that attractive males do invest more in their offspring. When the EPP rate is high, however, attractive males tend to invest less. Covariation between indicators of good genes and the delivery of material benefits in humans may be similarly sensitive to female “demand” for extra-pair sex. Factors other than the value of men’s parental investment might also affect women’s demand for extra-pair partners. For instance, in some cultures men may be more motivated or better able to control women’s sexuality. Once again, a major challenge ahead is exploration of the adjustment of tactic choice that may have been selected by varying selection pressures.

Miller et al. question the strength of evidence for the heritability (h^2) of FA (see also **Montgomerie**). They note that Møller and Thornhill’s (1997) estimates of h^2 have been criticized (e.g., Houle 1997; Whitlock & Fowler 1997). These criticisms have been addressed by Gangestad and Thornhill (1999), who estimate that developmental imprecision has a h^2 of 35–55% based on Whitlock and Fowler’s (1997) reduced set of estimates for FA. In addition, the standardized additive genetic variance (CV_a) in developmental imprecision appears to be much greater than ordinary morphological traits such as height and weight.

Marlowe observes that genetic variation is smaller in small populations than in large ones and wonders whether genetic variation in fitness would have been large enough in traditional societies for GGSS to have operated. This is a reasonable question. A substantial portion of the genetic variance in fitness is due to deleterious mutations, which enter populations at a rate per genome independent of population size. The equilibrium amount of genetic variance in fitness attributable to mutations is the rate per genome times the mean percent effect on fitness per mutation (Burt 1995), which also is independent of population size. Thus, it is not a foregone conclusion that genetic variance *in fitness* would have been substantially less in traditional societies compared to larger modern populations. In fact, because people

in traditional societies most likely experienced greater nutritional and pathogen stress, which can increase genetic effects on fitness (e.g., the mean effect on fitness per mutation, the effect of variation in parasite resistance; Burt 1995), the opposite may be true. **Marlowe** also suggests that, with greater knowledge of potential mates, the effect of GGSS may have been weaker in traditional societies. His observation that the weighting of information should be affected by its reliability is insightful. The question of how much less individuals in modern societies know about the personal attributes of their eventual mates compared to individuals in traditional societies is an empirical one. We suspect that the differences may be smaller than assumed.

Chisholm & Coall argue that, because intensive biparental investment has been strongly selected for in humans, men with good genes should invest in offspring more, not less (see also **Cunningham**). Unfortunately, they confuse nearly universal fitness-enhancing genes in a population with genes associated with fitness variation. Alleles that increased paternal investment should have been selected into the human genome within the past 200,000 years, and these alleles should be nearly universal. Most of the genetic variance in fitness is probably due to deleterious mutations across the entire genome coupled with variation due to co-evolutionary processes (such as host-parasite coevolution). The question of whether men with greater genetic fitness would benefit more by engaging in greater parental effort (see Robertson & Roitberg 1998) is separate from the question of whether selection has led modern men to invest more in offspring than ancestral hominids did.

R2.4. Alternate versus conditional strategies. In the target article, we argue that mating strategies are conditional. Several commentators (**Belsky, Berry & Kuczaj, MacDonald, Miller**) suggest that they may actually reflect alternate strategies and, hence, be attributable to genetic differences across individuals. **MacDonald** argues that variation in motivational systems captured by the Five-Factor Model of personality may account for variation in mating strategies. He suggests that individuals differ in their desire for close, intimate relationships and, as a result, in their willingness to invest in offspring. He also suggests that genetic variation (and nonshared environmental variation) might be maintained by the advantages of niche diversification (Lalumière et al. 1996; MacDonald 1995).

We agree that genetic variation in motivational systems must be explained. Our article, however, does not ignore it. We propose that men who differ in their ability to appeal to women's mating preferences will, as a result, differ in their motivations to pursue multiple mates and close, intimate relationships (**Baum**). Because the ability to appeal to women's preferences should be partly heritable, the corresponding motives are also partly heritable. Genetic variation in phenotypic traits does not imply that genes code "for" traits themselves, as **MacDonald** suggests. Nor must the genetic variation be adaptive. In other species, male sexually selected characters have substantial genetic variation, on average 3–4 times more than ordinary morphological traits (Pomiankowski & Møller 1995). Males with poorly developed sexually selected characters, however, do not possess them because they have predisposing genes that are maintained by "niche diversification"; in many cases, they possess them because they are in poorer condition, which has genetic influences itself. Many sexually se-

lected characters capture genetic variance in condition because of their costs (Rowe & Houle 1996). The outcomes of intrasexual competitions in humans, which affect men's willingness to enter subsequent competitions, may similarly reflect genetic variance in condition. One need not assume that some men are genetically "predisposed" to avoid conflict with other men. (Genetic variation in life history variables, also mentioned by **MacDonald**, is probably also partly due to genetic variance in condition; Houle 1992.)

That being said, we suspect that large amounts of variance in motivational systems remain unexplained by these processes. **MacDonald** seriously underestimates the amount of variance in men's willingness to engage in unrestricted, short-term sex that is associated with developmental imprecision and, perhaps, genetic variance in condition (see sect. R1.1 above). But correlations between FA and personality traits (e.g., agreeableness, surgency, emotional stability) tend to be small, even though correlations between FA and theoretically meaningful behaviors are sizable (e.g., see Furlow et al. [1998] for data on FA and male fighting vs. general aggressivity, hostility, and anger; see Simpson et al. [1999] for data on FA and male intrasexual competitive behaviors).

Our reluctance to endorse **MacDonald's** suggestion that this variation has been maintained by niche diversification is not because the idea is implausible. Rather, there is little direct evidence for it. Heritable variation can be maintained by several processes, including mutation-selection balance, frequency-dependent selection, and sexual antagonism. Claims that a particular process has produced this variation require specific, testable hypotheses (including those that permit tests of special design). To date, niche diversification has not been directly tested. In earlier papers (Gangestad & Simpson 1990; Simpson & Gangestad 1991b), we proposed that genetic variance in women's sociosexual orientation could be maintained by frequency-dependent selection. Although this idea remains plausible, we focused on conditional strategies in the target article because they provide more testable hypotheses (see n. 9).

Belsky proposes that while some (perhaps most) people may utilize the conditional strategies we describe, others may be more inflexible. Wilson (1994) has described how selection can maintain a mixture of inflexible specialists and conditional strategists. The evolution of these alternate strategies is possible when: (1) the benefits of adjusting to immediate environmental conditions are not too great, and/or (2) the costs of remaining strategically flexible are high. Recent evidence indicating that children's development differs with respect to how sensitive it is to environmental variation is intriguing. Specific evidence that selection has maintained variation for the conjectured reasons, however, is lacking. On conceptual grounds, **Belsky** argues, "When average reproductive payoffs for flexibility were less, as they may have been for extremely symmetrical men or extremely healthy and beautiful women, fixed rather than flexible mating tactics should have evolved." The problem with this argument is that fixed strategies should be disfavored when practiced by individuals *not* in these extreme categories. Given the likely sources of genetic variation in men's condition (e.g., mutations, pathogen resistance), the genes responsible for an inflexible, short-term mating strategy could not remain strongly linked to those responsible for mating advantages in men. A similar argument could be made for women. The mean fitness of genes promoting flexibility could easily exceed those for inflexibility. Maintenance of

variation in flexibility requires special conditions (see Wilson 1994) and, at present, there is little hard evidence that evolutionary processes maintained such variation in human mating strategies. These ideas, however, like **MacDonald's**, may be explored in future work.

Miller argues that variation in mating preferences and tactics around the world may be predominately attributable to genetic differences rather than environmentally-sensitive conditional strategies (see also **MacDonald**). We cannot deny this possibility. However, some data militate against the view that this variation is along "racial" lines. Gangestad and Buss (1993) found that the association between pathogen prevalence and importance of physical attractiveness in a mate is enhanced, not diminished, when geographical region roughly indexing race (Europe, Asia, Africa, Middle East, and South America) is partialled out. While "race" does not account for variation in preference, the ecological variable (pathogen prevalence) does. Miller lists many attributes that might facilitate male mating effort (e.g., aggression, impulsivity) and male provisioning (e.g., anxiety, behavioral restraint, intelligence). Some of these links are questionable (e.g., anxiety-proneness actually predicts some of the heritable variance in divorce mentioned by Miller; see Jocklin et al. [1992]; the effects of intelligence on male mating success and provisioning are not established). While many of these traits have high h^2 , this does not imply that there are genes "for" these traits. Indeed, nearly half of the genetic variance in intelligence may be attributable to developmental instability (Furlow et al. 1997). The notion that differences between European- and African-Americans on these traits stem from differences in the frequency of genes "for" the traits in question remains very speculative.

R2.5. Frequency dependency. In previous articles (Gangestad & Simpson 1990; Simpson & Gangestad 1991b), we have conjectured that frequency-dependent selection could have maintained alternate female mating strategies. **Campbell** laments that it is "a pity that it [frequency dependency] has all but disappeared from the present model." As discussed above, we concentrated on conditional strategies in the target article because they generate clearer empirical hypotheses. There is a sense, however, in which frequency dependency retains an implicit presence in our current thinking.

We argue that market phenomena partly drive the choice of mating strategies. These choices can be partially understood in terms of frequency-dependent success. Given a certain level of female "demand" for male genetic quality (partly due to ecological factors), there should be a niche for men to pursue multiple matings by appealing to women's preferences for indicators of good genes (along with other factors that affect short-term mating; see above). Men's willingness to invest in mating effort (e.g., certain forms of intrasexual competition) should depend on their payoffs from this effort and the payoffs of alternative activities (e.g., direct parenting effort, mate guarding). But their success should not be based solely on their own abilities; it also should be sensitive to female "demand" as well as what proportion of other men are pursuing short-term mating. Men should therefore be responsive to the amount of short-term mating effort allocated by other men. Whether they learn this information through their own success rates or by observing other men is unknown (see **Alley**).

Campbell and **Marlowe** discuss the effects of opera-

tional sex ratios (as do **Bleske & Buss**). Our perspective highlights particular ways to understand these effects in the context of mating markets. All else being equal, when men outnumber women, women should be less interested in short-term and extra-pair matings because, given supply and demand, they can afford to expect greater investment from their mates. Hence, men should invest more in offspring and long-term mates. When there is a paucity of men, however, there is an increased supply of matings requiring low investment for men, and women's demand for extra-pair matings may also increase (though their poor bargaining position may increase the costs of pursuing them as well). All else equal, men should on average allocate more effort to compete for matings with relatively little paternal investment, and a large skew in the distribution of men's partner quantity may result. We believe that it makes more sense to view these outcomes through fine-grained analyses of markets than in terms of the which sex gets to impose its "preferred" mating strategy (see **Campbell**) which, we have argued, is not invariant. (The idea that one sex "gets its way" is misleading since men compete with men in mating markets and women compete with women. Some men [those who cannot attract short-term mates], in fact, may actually do *worse* when the "preferred" male strategy is imposed.) Moreover, contrary to **Campbell** but in agreement with **Marlowe**, we argue that the choice of mating tactics should depend on the operational sex-ratio *as well as* ecological factors. Even though the increase in single parenthood in the United States in past decades may be partly owing to changes in the operational sex-ratio, it also may be owing to decreases in the perceived marginal utility of paternal investment, given welfare subsidies or decreased parental division of labor (see Kaplan 1996; sect. 5.6.2).

This emphasis on market economics is consistent with **Kenrick et al.'s** call for the application of dynamical models. Their simulation data nicely demonstrate how individuals' choice of mating tactics can be contingent on which tactics others pursue. Such modeling may illuminate evolutionary processes best if tactic choice depends on utility (or fitness, as in game theoretic models) rather than on empirically estimated rules, for it would then simulate true markets (e.g., Grim 1995; Nowak & May 1992). (Models might also build in variation in individuals' "condition," which affect payoff functions.) But we strongly endorse **Kenrick et al.'s** melding of adaptationist thinking and dynamical modeling.

R2.6. The nature of life history trade-offs. Our discussion of trade-offs drew on life history theory. As **Hill** and **Chisholm & Coall** note, we could have incorporated certain concepts of that theory more fully. Parental investment (PI) return curves describe fitness payoffs as a function of parental investment in individual offspring. Optimal investment in an offspring depends on the PI return curve as well as return curves for alternate activities (e.g., investment in self, mating effort). Ecological variables should affect return curves (**Hill**). All else being equal, the greater the extrinsic mortality rate, the lower the return from PI owing to investments lost through offspring mortality. Increased mortality thus favors a shift from concentrated investment in individual offspring (i.e., increasing offspring quality) toward investment across multiple offspring (i.e., increasing offspring quantity; see **Chisholm & Coall**).

Hill suggests that the effects of parasite stress might

be understood in terms of PI returns. Parasite stress can increase extrinsic mortality rates, decreasing the value of men's PI. **Chisholm & Coall** go farther, arguing that the effects we predict boil down to the well-established quality-quantity trade-off. When men's PI is less valuable, individuals may increase offspring quantity by engaging in short-term mating.

In our view, applications of life history theory (e.g., Chisholm 1993; 1999b; Hill & Low 1992; Kaplan 1996) are among the most exciting recent developments in evolutionary psychology. We concur that a more direct treatment of fitness functions and life history concepts in our model would have been useful. But we disagree with **Chisholm & Coall** that the effects we predict simply reduce to quality versus quantity trade-offs. Shifts from investment in offspring quality to quantity do not have to entail shifts in total parental effort (Low 1978); total parenting effort may just be distributed over a larger number of offspring. We propose that one major avenue through which parasite stress affects mating dynamics is through the increased value of good genes and pathogen resistance. Parasite stress may increase the expression of individual differences in resistance (and, thereby, heritable variation in fitness), meaning increased fitness gains from female choice for disease-resistant mates. Men able to advertise the best condition become *particularly* preferred as sires, either as in-pair or extra-pair mates, and effective polygyny increases (Low 1990). The function of fitness returns from efforts to advertise resistance hence steepens, increasing male mating effort. Ultimately, women trade-off some amount of paternal investment for "good genes." We fail to see how this process can be reduced to the quality-quantity trade-off (although this trade-off also operates). **McKnight & Bond** observe that women's openness to sex without commitment is not simply "a female form of R strategy," but rather appears designed to pass on "good genes" to offspring.¹

We suspect that the returns from male PI are more complex than depicted in a single PI return curve. Intensive biparental care is relatively uncommon in the biological world. In humans, it may have evolved in response to the benefits of specialization and division of labor, and male and female investments may interact to affect return (Lancaster & Kaplan 1992; Kaplan et al., in press). The benefits of specialization and division of labor are likely to vary across environments, however, with women being able to handle the multiple tasks of childcare and food acquisition better in some environments than others (e.g., off the coast of North Australia, Tiwi women fish as well as gather; Lancaster & Kaplan 1992; see also Hurtado & Hill 1991). In these environments, the fitness gains from male investment should decrease and, *relatively* speaking, the fitness gains associated with choosing good genes may increase. Consequently, men should increase their mating effort and, ultimately, women should exchange some male investment for good genes (in the Tiwi, the extra-pair paternity rate is thought to be high; Hart & Pilling 1960). Again, we fail to see how this trade-off reduces to the quality-quantity trade-off.

Campbell suggests that parasite prevalence and environmental harshness covary positively and, hence, links between pathogen prevalence and mating preferences may simply be due to poverty. These factors correlate far from perfectly, however, and their unique effects can be examined through statistical partialing procedures. Gangestad and Buss (1993) found that parasite prevalence predicts mate preferences for

physical attractiveness across cultures even when mean income is controlled. They found no evidence that mean income independently predicts these preferences.

In the target article, we stated that women tend to track ecological factors, and men track women (**Chisholm & Coall; Hill**). We overstated this point. Men's allocation of effort to mating and parenting should be sensitive to their returns from both. Thus, men too should track ecological factors, particularly those that affect returns on parental investment.

We presented an argument outlining the effects of varying fitness functions on male mating effort, male parental effort, and female mate preferences. We concur with **Cuthill & Houston** that formal modeling is needed to explore these issues more fully (see also **Mealey**).

R2.7. Understanding female variation. **Hill** notes that we applied cost-benefit analyses more completely to men's mating tactics than to women's (also see **Bailey, Broode, Miller et al.**). Though we discussed how certain female characteristics (age, independent access to resources, family support as a function of residence) might affect the costs and benefits of various tactics, we endorse efforts to investigate these and other characteristics more fully. **Alley** suggests that female competence may affect strategy choice, and we agree. **Miller et al.** ask why women's developmental health (indexed by FA) would not affect their mating strategies. Although women cannot convert health advantages into more mates in the same way that men can (**Bailey**), women's costs and benefits could be affected by their genetic quality. For instance, if the effects of mutations are positively epistatic (so that mutation $n + 1$ has greater effects than the n th mutation; Charlesworth 1990), women with poorer developmental health could particularly benefit from mating with a male who has few mutations. But if marginal gains increase as a function of male developmental health (especially when variance in male reproductive success is high), more symmetrical women may especially benefit (indirectly, through their sons) by mating with males advertising good genes. The value of direct material benefits versus genetic benefits could also be influenced by the fitness functions of direct benefits. The direct benefits that highly attractive females can obtain in a market may reach diminishing returns, leading them to prefer indicators of good genes more than less attractive females do. Recent work with sticklebacks has found that females who are in better condition prefer attractive males more than females who are in poor condition (**Bakker et al.** 1999). **Little et al.** (in press) report that women who claim they are more attractive prefer masculine and symmetrical features in men's faces more than less attractive women. In sum, the effects of female attributes on the costs and benefits of different mating strategies may depend on various ecological or social factors.

Variation in women's sociosexual orientation has a heritability of about .5, similar to that of men's (**Bailey et al.**, in press). Although this finding does not necessarily imply that there are genes "for" sociosexual orientation per se, it needs to be explained (**Bailey, MacDonald**).

R2.8. Proximate mechanisms. **Berry & Kuczaj, Bailey, and Vine** correctly observe that we focus on cost-benefit analyses of tactic choices but say little about proximate mechanisms. Ultimately, both levels of analysis – the functional and the proximate – must be understood. Although

we said that selection should favor decision rules about tactic choice in response to recurrent evolutionary cues, we did not describe how relevant information might be processed (see Miller & Todd 1998).

Baum and **Brody & Breitenstein** propose some proximate mechanisms. Baum discusses the matching law. Given two response options, individuals' relative response rates tend to match the relative reinforcement of the responses. Hence, men should allocate effort to short-term or long-term mating contingent on their reinforcement rate. One potential problem with behaving in line with this law is that short-term mating effort may interfere with long-term mating prospects (because long-term mates may not tolerate it). Women should think about the costs of short-term mating partly in terms of how it might harm their long-term mate-ships (**Cornwell et al.**). Men may do so as well. **Brody & Breitenstein** suggest that differences in mating tactic choice may reflect differences in the relative value of sexual variety versus sex within stable, intimate relationships.

Bailey focuses on the flexibility of men's tactical decisions. As he notes, one possibility is that men's mating strategies are relatively fixed by the end of adolescence. Another is that men continuously monitor their mating opportunities and facultatively adjust their strategies. We agree with **Bailey** that the latter seems more plausible but that this issue warrants additional theoretical and empirical attention (see also **Buckhalt & Gannon**).

As do **McKnight & Bond**, we suspect that calculating a best set of mating tactics could be complex. They suggest a host of factors that might influence a woman's interest in extra-pair sex: her own attractiveness, her perceived ability to attract mates with "good genes," her estimation of the effort needed to attract such mates, the likely reputational damage her efforts could exact, the suspicion she could arouse in her long-term mate (plus the costs of her mate finding out versus the relative benefits of acquiring good genes). **Eagly** argues that women who engage in extra-pair sex do so because their primary relationship is either damaged or emotionally unsatisfying, a view compatible with Greiling and Buss's (2000) notion that extra-pair sex can be a first step in switching mates (see also Buss & Schmitt 1993). Although we sincerely doubt that only women whose relationships are damaged or unhappy have affairs, the costs of losing an established relationship should affect women's decisions about whether to have extra-pair sex for *any* reason. A man's calculations of how much effort to spend on short-term mating also should be governed by many factors, including: his estimated chances of success, his estimated marginal increase on success from additional effort (which should depend on how much other men invest in mating), the perceived utility of his parental effort (which could be affected by the mortality rate and "socioassays" [Chisholm 1993] thereof, observed returns on parental investment in his community, his own parental qualities [Kaplan 1996]), whether care of offspring he does not invest in will be subsidized by others (e.g., the maternal family or the mother's long-term mate), the dangers posed by an extra-pair mate's in-pair partner, and the impact of extra-pair mating on an in-pair mateship (see also **Figueredo & Jacobs**).

Because it is implausible that individuals could learn enough about fitness-relevant consequences through individual experience and general-purpose algorithms alone to make adaptive calculations, our view is that selection should

have favored certain special-purpose adaptations that lead individuals to attend to diagnostic information in their environments. Admittedly, we offer only women's shifts in mating preference across the menstrual cycle as strong evidence for this assumption.

MacDonald argues against an extreme view of domain-specificity, claiming that plasticity is merely "the result of large numbers of conditional 'if-then' mechanisms responsive to recurrent contingencies in our evolutionary past." The point that developmental plasticity and reaction norms may be continuously distributed is not convincing evidence for his argument. "Preloaded" mechanisms for decision-making can generate continuously distributed phenotypes in response to environmental variation, as in the case of growth in response to nutritional stress. In fact, however, we do not endorse the extreme view **MacDonald** criticizes (see also **Vine**). The term "plasticity" incorrectly suggests that individuals are "molded" by their environments and, for that reason, we put the term in quotes. Humans clearly possess broad capacities to learn, model, and copy, and they have general abilities to detect complex patterns in novel events (fluid intelligence). We do not doubt that some of the information affecting the choice of mating tactics is socially acquired (or cultural: **Newson & Lea**; Flinn 1997; see also **Buckhalt & Gannon**), including local norms that govern the reputational consequences of public acts important to an individual's well-being (**Eagly**; **Perper & Cornog**). However, social learning processes may be channeled by preloaded structures (see Flinn 1997). Moreover, inputs into general capacities (such as scenario-building) are often special-purpose in nature, affecting what we attend to, find interesting, or perceive as threatening. Hence, many of our daily actions are guided by input from cognitive structures that probably were specially designed by specific selection pressures (Tooby & Cosmides 1990b). We applaud efforts to clarify how special purpose and more general processes work in concert (e.g., Geary 1998; see **MacDonald**, **Vine**). In our opinion, however, the current state of the field is largely characterized by speculation, not firm knowledge (see Flinn 1997).

Vine argues that "authentically self-aware individuals' deliberate moral choices and interpersonal commitments permit them to overcome fitness-oriented temptations to be unfaithful" that "suffice to falsify the bio-reductionist EP [evolutionary psychology] paradigm." He further argues that "subjective interpretations of deep emotional attachments, and self-identifications with partners" are missing from our perspective (see also **Eagly**, **Perper & Cornog**). This reasoning is incorrect. Love and romantic attachment are implicitly woven into our notions. We suspect that these proximate mechanisms evolved from the same selection pressures that gave rise to intensive biparental care in humans and, therefore, we do not see them as *alternatives* to the views we espouse. We suspect that emotional attachments facilitate exclusive, long-term mating strategies (see Mellen 1981). At present, we do not know whether passionate love functions as a motivational system or as an honest signal to a partner of one's intent to remain faithful by leading individuals to take steps that would be sensible only if it were profitable to invest for the long-term.² If love does signal intent, this tactic makes sense *precisely because* individuals might benefit from seeking outside mates and need to signal they will not (cf. Miller & Fishkin 1997). In any event, we view these phenomena as evolved adaptations,

not as part of a system of meaning-ascription that counteracts ego-serving fitness-optimization (**Vine**). Because the fitness-enhancing effects of adaptations must be understood in terms of their aggregate effects, *not whether they promote fitness in every instance* (Flinn 1997), the example of the virile man who maintains fidelity long after his spouse's death in no way shows that emotional attachments did not evolve because they enhanced fitness (Vine).

R2.9. Phylogenetic considerations. We did not speculate about when conditional mating strategies may have evolved. **Mithen** offers evidence that intensive biparental care arose in the last 500,000 years. This evidence contrasts with **Newson & Lea's** speculations that these mating strategies arose much longer ago, perhaps in our chimp or bonobo ancestors. Given that mating behaviors vary tremendously between humans and apes, it seems highly unlikely that mating strategies that were adaptive in distant relatives, but not in hominids, would have survived selection.

Fuentes wishes we had considered evidence on primate mating, particularly with regard to GGSS. He claims that evidence for GGSS in our closest ancestors is lacking (see Fox et al. 1999). We view research on primates as interesting, but not critical to evaluating our arguments. GGSS in humans should be tested with research on humans, not on other species. Currently, there are relatively few studies on GGSS in other primates. If, however, researchers continue to find little evidence for GGSS in other primates, the question of why humans may differ in this regard becomes pertinent and interesting.

R3. Summary

The commentaries have led us to reinforce several major themes in our target article: (1) the importance of sex-specific, within-sex variation in mating tactics; (2) the relevance of optimality thinking to understanding that variation; (3) the significance of special design for reconstructing evolutionary history; (4) the replicated findings that women's mating preferences vary across their menstrual cycle in ways revealing special design; and (5) the importance of applying market phenomena to understand the complex dynamics of mating. In addition, they have led us to qualify or expand three several positions: (a) we now believe that men possessing indicators of genetic fitness may provide more direct benefits than others when female demand for extra-pair and short-term sex is very low; (b) we contend that both men and women should track ecological cues to make mating decisions; and (c) we acknowledge that more work on female orgasm is needed. The commentators have identified many potentially productive avenues for future theoretical and empirical investigation. We thank them for offering their expertise, insight, and criticism.

NOTES

1. There may be other reasons for male mating effort to increase in response to increased extrinsic mortality. Males investing in offspring may tolerate higher levels of extra-pair paternity with increased mortality (due to a life history trade-off; Mauck et al. 1999). Extra-pair mating may thus have a lower cost for females, which may increase female demand for extra-pair partners and, as a consequence, male mating effort for extra-pair sex.

2. Michelle Cristiani offered this suggestion. Paul Andrews has developed a model of the signaling of intent that informed this section as well.

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Letters "a" and "r" appearing before authors' initials refer to target article and response, respectively.

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