

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.<sup>2</sup> 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.<sup>3</sup>

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.<sup>4</sup> 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