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 nonprovisioning 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; 1190b) 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 repond 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 plausible 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 metaanalysis 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