

Sexual selection and mate choice in evolutionary psychology

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Abstract The importance of mate choice and sexual selection has been emphasized by the majority of evolutionary psychologists. This paper assesses three cases of work on mate choice and sexual selection in evolutionary psychology: David Buss on cross-cultural human mate preferences, Randy Thornhill and Steve Gangestad on the link between mate preferences and fluctuating asymmetry, and Geoffrey Miller on the role of Fisher's run-away process in human evolution. A mixture of conceptual and empirical problems in each case highlights the general weakness of work in evolutionary psychology on these issues.

Keywords Evolutionary psychology · Mate choice · Sexual selection · Human evolution · Mate preferences · Optimality

The inherent plausibility of the hypothesis that mate choice is a common feature of the sexual behavior of animals should make us especially cautious and critical in our evaluation of attempts to demonstrate its occurrence in nature

(Halliday 1983: 3).

Introduction

Two aspects of human life in particular have featured prominently in evolutionary psychology: (1) the link between one's biological sex and one's behavior, and (2) the dynamics of intergender relations, specifically in the context of what evolutionary psychologists refer to as "human mating," which encompasses (for reasons described below)

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all sorts of behavior which one might not immediately associate with mating (e.g., getting a good job.)

Much of the research on sexual dimorphism and mating conducted on nonhumans has appealed to the family of theories which make up the field of sexual selection. Similarly, evolutionary psychologists have found sexual selection theories to be felicitous in accounting for ostensibly widespread gendered behaviors among humans. Theories in the field of sexual selection, it is supposed, shed light upon human sex differences and the upshots of those differences for reproduction.

In this paper I examine three cases in which sexual selection models have been employed by evolutionary psychologists. The first part of the paper deals with the well-known and perennially influential work of David Buss on cross-cultural mate preferences and their implications for our evolutionary past. I then turn to a large ongoing project directed by Steve Gangestad and Randy Thornhill which investigates the link between mate preferences and certain physical characteristics. I end with a critique of Geoffrey Miller's work on the putative role of Fisher's "runaway" process in human evolution.

Buss busted

The year 1989 was an important one for the study of human behavior. That year saw the publication David Buss's report in *Behavioral and Brain Sciences* on the results of an exceptionally broad study entitled "Sex Differences in Human Mate Preferences: Evolutionary Hypotheses Tested in 37 Cultures," which contained data concerning human mating preferences for 10,047 individuals in 37 different cultures located in 33 countries. Buss's strategy for detecting mate preferences was to administer a survey which asked people to provide information about a number of personal features which Buss believes have been shown to be theoretically important to mate choice. This study would be the foundation for Buss's immensely popular (1994; rev. 2003) book, *The Evolution of Desire*, as well as for countless subsequent articles. Most importantly, Buss's (1989) study has achieved a paradigm-like status in evolutionary psychology, and continues to serve as a major resource for many different types of work in other subfields within psychology and the social sciences generally.¹

It is undoubtedly the enduring influence of Buss's study which explains why it remains—and *ought to remain*—one of the targets of contemporary critiques of evolutionary psychology. Until the inadequacy of Buss's work as a piece of evolutionary investigation is properly, clearly, and widely understood, researchers will persist in using it as a well from which to draw their own conclusions about human evolutionary history. Toward this end, I present in this section a very basic but wide-ranging criticism of the way in which Buss claims to have tested evolutionary hypotheses regarding sex differences in human mate preferences.

One of the central foci of Buss's work is the distinction between "long- and short-term mating," which he considers to be "core components of the human strategic repertoire" (Buss 1998: 411). He asserts (*ibid*: 412) that women with a preference for a "reliable man willing to commit to her" were selected for because "the resources, aid, and protection" which those men provided caused her to have "children who survived and thrived."

¹ A Google Scholar search revealed over 500 citations of *The Evolution of Desire* and "Sex Differences in Human Mate Preferences" since 2000.

Let us suppose Buss has actually demonstrated that women have a preference for reliable men who are willing to commit to them. Let us suppose even further that he has satisfied that most difficult of requirements and shown variation in this preference to have a genetic basis. The only question left to ask is, has Buss demonstrated that women's reproductive success is augmented by a nonrandom pattern of choosing men who are "reliable" in terms of providing resources, aid, protection, etc.—i.e., that the preference for reliable men "solved key reproductive problems" (*ibid*: 412; see also Buss 2003: 19–48).

Buss offers us no actual data on reproductive success of women either with a preference for reliable men or without a preference for reliable men. Of course, we *at least* need these two data sets in order to evaluate his claim that these two types of women differ with respect to their reproductive success. In place of the necessary data, Buss submits the "discovery" that women "place a premium on a man's social status, his ambition and industriousness, and his older age—qualities known to be linked with resource acquisition," (Buss 1998: 422) as well as love, which "some [unnamed: CH] studies have found...signals commitment of a host of reproductively valuable resources" (*ibid*: 420).

Thus, the preference for "reliable" men turns out to be a composite of preferences for qualities "known" to be linked with resource acquisition, combined with a preference for men who love them, because love "signals commitment of...reproductively valuable resources." Whether there is a reliable link between a man's love and his willingness to furnish a woman with resources, as well as whether the resources Buss cites are "reproductively valuable," are assertions requiring demonstration but which Buss simply assumes are true. In particular, showing that some resource is "reproductive valuable" requires exactly the same kind of demonstration as does showing that Buss's putative preference for reliable men is adaptive—viz., a demonstration of differences in reproductive success *in humans* resulting from the focal variable (i.e., the valuable resource or the preference). Problems only multiply when we consider that the female preference for reliable, resource-giving men is supposed to have evolved sometime during the Pleistocene, thus making measurement of the relevant reproductive success differentials impossible.

Buss engages in a priori assessment of fitness effects combined with a comparison to behavior in other taxa to which he imputes adaptive significance—throughout his work on human mate choice. But apart from a few "just so" stories, we have nothing linking Buss's data on contemporary human behavior to a history of selection—direct or indirect—of the preferences he claims to have discovered.

Randy Thornhill and Steve Gangestad on fluctuating asymmetry

I now turn to a critical assessment of a well-regarded project directed by evolutionary psychologist Randy Thornhill and Steve Gangestad which examines the link between human mate preferences and fluctuating asymmetry using a form of optimality analysis (outlined in detail below). After a brief discussion of the concept of optimality analysis in evolutionary biology, I describe and explain an instance in which it has been used quite convincingly. I then use the exemplary features of this instance, along with a demonstration of the general weakness of Thornhill and Gangestad's model itself, to show why Thornhill and Gangestad's work should fail to persuade us to believe anything which has been alleged on its behalf concerning evolved mate preferences. The extent to which the

structure of Thornhill and Gangestad's study resembles that of lots of other work in evolutionary psychology is noteworthy, and, in addition, allows the significance of my comments to extend beyond this single case.

Optimality modeling

We can divide optimality models into roughly two types—those that make quantitative predictions and those whose predictions are qualitative. Quantitative predictions offer the opportunity for a clear test of the accuracy of the model; we simply see whether the observed numerical values match the predicted values within a suitable confidence interval. A sterling example of the quantitative sort is Parker's predictions for copulation duration in male dung flies. Incorporating a variety of parameters, Parker predicted that if males were optimally designed in this respect, then copulation would last 41 min.²

Qualitative models predict that the data will show a general trend of some kind. Because of the lack of precision endemic to qualitative predictions, it is (or at least, *ought* to be) more difficult to generate confidence in their probative value. To be sure, qualitative predictions do not immediately spell “doom” for a model, so long as the predictions would, if true, be “sufficiently striking” (Parker and Maynard Smith 1990: 31). Alternatively, researchers can make several independent qualitative predictions. In this case, the probative value of the model increases with each independently confirmed prediction (Brown 2001: 151).³ Whether quantitative or qualitative, the power of optimality models to provide evidence for adaptation is dependent upon two factors: (1) the fine-grainedness of the predictions derived from the model; and (2) the uniqueness of those predictions.

Case study: sex ratios across fig wasp species

Herre et al. (2001) investigated the actual sex ratio responses of 15 species of fig wasp to different selective factors as compared with the predictions of local mate competition theory (LMC). Female fig wasps (“foundresses”) lay their eggs inside the fruit of fig trees and subsequently die there, with the normal number of foundresses per fruit (1–3) differing across species. Based on quantitative figures derived from LMC, Herre et al. made two predictions: (1) that decreases in the number of foundresses per fruit will be associated with increases in the degree of female bias in the sex ratio; and (2) that for a given number of foundresses, more inbred species will be associated with increases in a brood's female-bias (Herre et al. 2001: 197).

The results: “there is qualitative and in some cases quantitative agreement between theoretical predictions and the sex ratio response of the fig wasps” (*ibid*: 208). Not only are the basic qualitative trends confirmed, but in some cases the actual sex ratios correspond precisely to the numerical values predicted by the theory. This is indeed impressive, but it's unclear whether we ought to consider the case closed—the wasps really *are* optimally

² The observed mean value was actually 36 min. Kitcher (1985: 138–141) discusses different approaches to resolving the discrepancy between observed and predicted values.

³ See Earman (1992) for a Bayesian explanation of the ability of several independent predictions to raise the posterior probability of a hypothesis.

designed in the manner predicted by LMC—or press Herre et al. to give some account for the quantitative deviations.

To some extent, the authors have made up our minds for us. They're sensitive to the quantitative failure and devote considerable discussion as to how to resolve the matter. Their preliminary solution is to subsume the deviations under the original theory in the following manner. Species vary with respect to how many foundresses typically occupy an individual fruit. As we move away from the conditions with which a species is most familiar, the observed sex ratios begin to deviate from the 95% confidence interval. Thus, the observed values are closest to the predictions in the situations (in terms of number of foundresses) encountered most often by a given species of wasp, which is what we would expect to be the case if a species is optimally designed for its native environment (*ibid*: 203). Rather than being satisfied with the general qualitative fit of the data to LMC, then, Herre et al. use theoretical considerations associated with LMC to explain the cases in which quantitative fit breaks down.

Case study: extrapair copulation and fluctuating asymmetry

An extrapair copulation (EPC) is defined as copulation with any partner other than one's current long-term mate, with the term length required for sexual partners to qualify as a "pair" differing depending on the species. EPCs are often characterized by short-term sexual encounters with little or no material or parental investment on the part of the male. For this reason among others, the function of EPCs has been a source of considerable debate in behavioral ecology. For if the female is not receiving any material or parental benefit in exchange for access to her reproductive capacities, why grant the male access at all? One popular explanation suggests that the benefits received by the female come in the form of "good genes" for her offspring. The EPC male's high genetic quality is thus thought to explain why the female consents to a copulation in the absence of material or parental investment.

The term "fluctuating asymmetry" (FA) is used to describe "a random non-directional departure from perfect bilateral symmetry" (Maynard Smith and Harper 2003: 4). One line of thought in evolutionary biology holds that the degree of bilateral symmetry exhibited by an organism can provide indirect evidence of that organism's genetic quality. The extent to which an organism's left and right halves are symmetrical is thought to vary directly with the degree of stability of the organism's developmental processes. Developmental stability is in turn thought to be partly determined by genetic quality, with high genetic quality resulting in developmental processes that are highly stable and low genetic quality resulting in relatively unstable processes. On this view, then, a low degree of bilateral asymmetry should indicate high genetic quality, or "good genes."

Based on the theoretical considerations involving EPC and FA, Gangestad and Thornhill made two predictions about EPCs among humans: first, that "men's number of EPCs would correlate negatively with their fluctuating asymmetry;" and second, that "men's number of times having been an EPC partner of a woman would negatively correlate with their fluctuating asymmetry" (Gangestad and Thornhill 1997: 69).

Assessment

The authors' choice to limit their predictions to the qualitative sort might be taken as suggestive, given that quantitative predictions could have been made. For example, they

could have specified a value or range of values of FA corresponding to a man's number of times having EPCs and having been an EPC partner. This would have given us a clear idea of what to expect if natural selection was to have played a dominant or important role in shaping women's preference for EPCs and a clear idea of what constitutes, in Orzack and Sober's (1994: 367) words, "an unacceptable match between theory and data." Testing those predictions would have been easy (after all, FA measurements *were* quantitative), and a good fit would have been impressive. Moreover, as in the wasp study, any trend in deviations from the quantitative predictions could have potentially shed light upon why we failed to see an exact match.

Unfortunately, since the predictions of the model are not quantitative, we are forced to assess how surprising it would be if they turned out to be true, given common sense. Here, as in the majority of evolutionary psychological models, we find that the predictions fail to rise above the platitudinous. If symmetrical faces are considered to be more attractive than asymmetrical ones, then it would seem to follow plainly from common sense that men with low FA will be preferred over men with high FA for the obvious reason that more attractive men should be expected to be preferred over less attractive men. The idea that women prefer attractive men over unattractive men is hardly surprising, and certainly not the kind of prediction which, if true, should inspire confidence that our model is correct.

A possible reply on behalf of evolutionary psychologists would be to suggest that a general preference for symmetry might itself have an adaptive explanation behind it. That's true enough, but it is similarly true that a preference for symmetry can be explained by the fact that a wide range of taxa are attracted to environmental novelty and that symmetry is relatively novel in natural environments (Enquist and Arak 1994). It is simply not possible to distinguish between these two hypotheses using the evolutionary psychology methodology.

This brings us to the second evaluative question—viz., are the predictions of the model unique? The predictions certainly appear to be "consistent with the notion that 'good genes' sexual selection has partly forged the design of human psychological adaptations that underlie mating" (Gangestad and Thornhill 1997: 84). Unfortunately, the authors fail to make the obligatory distinction between being *consistent* with a model and providing *support* for that model. By themselves, the predictions, if true, would not allow us to distinguish between a selective process which has designed females to prefer men with "good genes" versus general sensory bias in favor of symmetry. If women prefer symmetry regardless of which object they are perceiving, they will naturally tend to prefer symmetrical men over asymmetrical ones. In fairness to the authors, they do acknowledge that their "research cannot rule out all other explanations" (Gangestad and Thornhill 1997: 84). But they do not attempt to provide a basis for why *their* model should be preferred over *any* alternative, and the reader is left wondering what other than mere consistency with their own model is motivating the authors' belief that the model has been supported by their findings.

At any rate, Gangestad and Thornhill found qualitative agreement with their predictions: men with relatively low FA—in their words, "men who show evidence of developmental stability" (*ibid*: 83)—were more likely to have sex with people other than their long-term mate, and they were more likely to be the person with whom women had extra-pair sex. Again, there's no surprise here, and no light is shed on the underlying reasons for women's preference for men with low FA by wheeling out some fuzzy associations with evolutionary theory. What *is* surprising is the casualness with which the authors convert "men with relatively low FA" to "men who show evidence of developmental stability." Aside from the questionable association between FA and developmental stability

(see below), the authors provide no basis for thinking that men who show evidence of developmental stability per se are more likely to engage in and be sought out for EPCs. Even if FA *were* a reliable indicator of developmental stability, it is an entirely open question whether, in general, men who show evidence of developmental stability exhibit the predicted associations with EPCs. There is no mention of other potential proxies for developmental stability and their associations with EPCs.

The link between developmental stability and fluctuating asymmetry

The preceding discussion of FA points to another component of optimality models which is often overlooked in evolutionary psychological practice—the truth of assumptions. In the Gangestad and Thornhill model, the predictions are derived from a few primary assumptions, most of which are not made explicit. Here I will discuss what I take to be the most important assumption of their model—viz., that developmental quality is accurately represented by FA.

Let me first briefly outline the argument for the idea that an organism's FA is a cue to its developmental quality. Because bilaterally symmetrical traits (e.g., ears) are likely to be controlled by the same gene or gene complex, under perfect developmental conditions the left and right halves should be perfectly symmetrical, having received the same set of developmental inputs. When there is some developmentally relevant perturbation, left and right halves should deviate from perfect symmetry to the extent that their developmental inputs differ.

Many biologists' interest in FA lies in the belief that it is an indicator of the organism's ability to withstand developmental perturbation, an ability which is determined by their genetic quality. It is assumed that the degree of symmetry exhibited between the organism's left and right halves is representative of the degree of fidelity maintained by the organism's developmental processes in the face of developmental perturbations such as pathogens, mutations, and environmentally induced stress factors like temperature shifts (Gangestad and Thornhill 1997: 72; Kruuk et al. 2003).

There are a number of phenomena we should expect to see if FA is truly representative of high genetic quality (which is usually understood in terms of viability). First, FA should vary directly with the severity of environmental stress (Kruuk et al. 2003: 102). Second, FA should be negatively associated with the degree of multilocus heterozygosity, on the assumption that heterozygosity, *ceteris paribus*, provides for better phenotypic condition than does homozygosity. (Plainly, inbred individuals are characteristically of lower phenotypic quality, which is a function of the increased homozygosity of their genotype due to inbreeding).⁴ Third, the FA of a given trait thought to be subject to sexual selection should be heritable. This follows directly from the notion that differences in FA are caused by genetically based differences in developmental stability (Kruuk et al. 2003: 102).⁵

A recent review of the few experiments which have actually tested for associations between FA and various stresses in a number of species found there to be no consistent relationship between FA and developmental perturbations (Bjorksten et al. 2000). In addition, a formidable study on FA in the antlers of red deer *Cervus elaphus* found no evidence to support the idea that there is an association between FA and factors known to

⁴ Lewontin (1974)

⁵ See Kruuk et al. (2003: 102) for additional phenomena to be expected from the assumed relationship between FA and genetic quality.

affect the fitness of *C. elaphus* (Kruuk et al. 2003). Most importantly, concerning what we should expect to see if low FA is associated with high genetic quality (see above), the study demonstrated each of the predictions to be false (i.e., no consistent relation to developmental perturbations, no consistent relation to inbreeding, and “no evidence of additive genetic variation [i.e., heritability: CH] underlying FA” [*ibid*: 111]). Thus they concluded that there was “no evidence to suggest” that FA is “useful as any sort of indicator...and so is presumably a poor indicator of developmental stability” (*ibid*: 111, my emphasis).

Now, Kruuk et al. *did* find that FA in antler length was negatively related to breeding success. And, perhaps interestingly, the only empirical support Gangestad and Thornhill provide for the idea that FA is indicative of developmental quality is reference to a number of studies which show a negative association of FA with mating success (a principal determinant of reproductive success). But where Gangestad and Thornhill use this correlation as evidence for an association between low FA and individual condition, Kruuk et al. concluded that “FA in antler length” may “be important because of the function of antlers, rather than because it reflects individual condition” (Kruuk et al. 2003: 110) specifically *because* they could not find a consistent relationship between FA and either condition itself or known determinants of condition in red deer. Kruuk’s et al. inability to find direct evidence for FA as an indicator of condition led them to believe that the negative association between FA and breeding success which they had found was just a byproduct of some other causal process (e.g., that more symmetrical antlers, for mechanical reasons, give red deer an advantage in antler-locking contests which bear a direct causal relation to mating opportunities [Kruuk et al. 2003: 110]). In this case, direct tests of the argument for why low FA indicates developmental stability—the major assumption of the Gangestad and Thornhill study—showed that argument to be unsupported by the actual evidence.

Geoffrey Miller on runaway sexual selection

One of the best discussions of sexual selection in evolutionary psychology occurs in Geoffrey Miller’s (2000) *The Mating Mind*. Miller’s comments here are among the most wide-ranging and conceptually sophisticated of evolutionary psychologists who have appealed to sexual selection models for the purpose of understanding human behavior. Most notable, I think, is the attention Miller gives to two topics which have dominated discussions in the field of sexual selection for the last 25 years but which have received scarcely a mention by evolutionary psychologists: (1) Fisher’s “runaway” process, and (2) the role of sensory bias in mate choice. Despite the degree of attention Miller gives to these matters, his discussion ultimately reveals weaknesses in his grasp of both conceptual and empirical issues associated with runaway and an unexplained adaptationist deviation from orthodoxy in the literature on sensory bias.

Let us first review the mechanics of runaway. Imagine a population which in its initial state G_1 contains females of type P_1 , who mate indiscriminately, and equal amounts of T_1 and T_2 males. At G_2 , a female is born with a chance mutation P_2 which causes in her a preference of strength a_2 to mate with males of type T_2 over males of type T_1 (such that in a choice between two males she is a_2 times more likely to mate with T_2 males than she is to mate with T_1 males, where $a_2 > 0$). Some of the female offspring of the initial P_2T_2 mated pair possess P_2 through genetic inheritance, and the male offspring of this pair similarly inherit T_2 . In the third generation G_3 , T_2 males enjoy an increase in their chances of mating

success, as there are more P_2 females now than in previous generations. Whereas T_2 males in G_1 enjoyed a likelihood no better than chance of mating with either P_2 females or P_1 females, in G_3 they retain their chance likelihood of mating with P_1 females but *augment* their chances of mating with P_2 females, thus increasing their overall chances of mating. Consequently, in G_4 there will be proportionately more T_2 males than there were in G_3 —i.e., selection for T_2 males has been generated by the preference in P_2 females. In addition, the nonrandom pattern of mating between T_2 males and P_2 females creates a nonrandom positive association between the allele responsible for the male trait and the allele responsible for the female preference such that an individual carrying one allele will tend to carry the other (what is called “gametic phase disequilibrium” or “linkage disequilibrium” [Kirkpatrick 1987: 74–75], my emphasis), and selection for the male trait will thus drag the female preference to a higher frequency.⁶In turn, the increased frequency of P_2 females generates even stronger selection for T_2 males, which increases the frequency of P_2 females, and so on and so forth until the either all genetic variation in population is exhausted or, in cases where the male trait becomes increasingly exaggerated because of peak shifts in the female preference, there is a selective backlash against the conspicuousness of the male trait (Andersson 1994: 35; Fisher 1958: 152; Lande 1981).

Runaway has a number of interesting and important features.⁷ First, the runaway process is an *inevitable* consequence of the co-occurrence of genetic variation in female preferences and preferred male traits (Kokko et al. 2002: 1338; Lande 1981). Second, runaway can occur even when the costs of T_2 are “nearly lethal” to its possessor (Kirkpatrick 1982: 9) and can continue even to the point where T_2 is so costly to males that the species is driven to extinction. Third, even where T_2 reduces survival, both it and the preference for it (i.e., P_2) can persist in the case where a new female preference for males who are “optimally designed” with respect to viability is introduced into the population (Kirkpatrick 1982). Consequently, *it does not follow as a matter of logic that females who prefer high-viability or “high quality” males will have higher reproductive success than females who prefer relatively low-viability males* (Arnold 1983: 88–89; Mark Kirkpatrick [pers. comm.], my emphasis). If the preference for the less viable male type is sufficiently strong, the long life enjoyed by the “high quality” male will not be of much use to him since other males are much more attractive to females. Lastly, although Fisher originally described the runaway process in terms of “further development” (i.e., exaggeration) of the sexually selected male trait (Fisher 1958: 152), that male traits should increase in conspicuousness is not a

necessary outcome of Fisher’s hypothesis of runaway sexual selection...[T]his theory can accommodate, but does not predict, the exaggeration of male traits under sexual selection (Ryan 1990: 169. See also Arnold 1983: 83–84).

Nor does it predict that females will evolve to *prefer* ever-greater exaggeration of male traits, although it can accommodate that result as well (Ryan 1994: 194).

Runaway and adaptationist accounts of preferences

We can use the basics of Fisher’s runaway process to expose a ubiquitous mistake in work on the evolutionary psychology of human mating, namely the a priori assumption that

⁶ Good explications of the process by which certain alleles can become correlated (as well as the process of runaway in general) are provided by Arnold (1983: 77–79) and Shuster and Wade (2003: 79–81).

⁷ Explanations of the features mentioned here, where not included, can be found in the references provided.

“high quality” males will as a matter of logic be selected for over “lower quality” males. One of the more instructive passages occurs in Miller’s revisionist account of sensory bias. His views on sensory bias represent a radical departure from traditional discussions of the topic in that he sees what is normally considered either an arbitrary fundamental orientation of the nervous system (such as the swordtail’s preference for swords [Basolo 1995, 1996]) or a default attraction to (say) louder calls (because they are easier to detect) (Endler 1992: 125) as actually having “evolved to help animals choose good sex partners” (Miller 2000: 147). To wit, “[m]ost sensory biases are consistent with what we would expect from adaptive decision-making machinery that evolved for mate choice” (*ibid*: 147). Traditional thinking in the field of sensory bias has shortchanged “viewers” by presuming that their attraction to “larger, brighter, and more symmetric visual ornaments” is based merely upon sensory biases, failing to realize that “[l]arge, healthy, well-fed, intelligent animals can produce” those kinds of traits (*ibid*: 147). Notes Miller, “As far as I know, there is no example of a sensory bias that leads animals to favor sexual partners that are smaller, less healthy, less energetic, and less intelligent than average” (*ibid*: 147). Thus, the “hidden adaptive logic” behind so-called sensory biases unveils itself: “larger, brighter, and more symmetric visual ornaments” as well as “louder, deeper, more frequent, and more varied songs” are actually “fitness indicators” representing the advertiser’s quality through the magnitude of his advertisement (*ibid*: 147). This much should be intuitive, suggests Miller, adding that “[i]f sensory biases led animals to choose lower-fitness animals over higher-fitness animals, I suspect that the biases would be eliminated rather quickly” (*ibid*: 147).

Genetic modeling of sexual selection does not confirm Miller’s suspicions. In fact, it directly contradicts them. As we have seen, it follows analytically from the most basic Fisherian runaway model (as well as from other kinds of models)⁸ that a preference which causes (say) females to prefer “lower-fitness” (i.e., lower viability) animals over “higher-fitness” (i.e., higher viability) animals can spread and *persist* in a population, even when a preference for “optimal” (in terms of viability) males is introduced. Not only that, according to the basic model the preference which initiated runaway will itself become exaggerated, causing males to have even *lower* viability. Miller presumably is aware of this feature of runaway. However all of this gets tossed aside in pursuit of “hidden adaptive logic.”

The mistaken belief that a preference for a “higher-fitness” male will, as a matter of logic, replace a preference for a “lower-fitness” male is widespread in the evolutionary psychological literature (see the numerous examples in Buss [2003], including one mentioned above). There can be little doubt that this is an instance of the general assumption that the “adaptive” will, *ceteris paribus*, replace the “nonadaptive.” The preference for “higher-fitness” males is intuitively perceived as adaptive, and the reasoning seems obvious: it is better to prefer males with higher fitness than to prefer males with lower fitness; therefore, in the limit preferences for higher-fitness males will replace those for lower-fitness males.

The intuitive appeal of this argument coupled with its complete wrong-headedness makes this an especially instructive case. There is a consensus among workers in sexual selection that if the preference for higher-fitness males spreads in a population, it is not because the *preference itself* is adaptive. In the case where the *preference* is adaptive, the higher fitness of preferred males would be incidental to the evolution of the preference,

⁸ E.g. Servedio and Kirkpatrick’s (1996) mate choice copying model, where the copying allele spreads even when it causes females to copy a choice for low-viability males.

which is due to increased fecundity. Rather, the reason the preference for higher-fitness males will spread is because of the linkage which arises due to assortative mating. If anything, the preference for higher-fitness males is *maladaptive* when there is direct selection acting upon it in the manner which Miller suggests. Consider: the preference for higher-fitness males causes linkage, which results in the female being pulled away from the natural selection optimum which would have obtained in the absence of linkage disequilibrium (Kirkpatrick 1996: 2134).

Demonstrating runaway

If we want to show that a trait reflects runaway activity at some time in the past, we will need to gather support for predictions for the long-term or end results of a runaway process. Because the direction in which male traits will develop as a result of runaway is completely unpredictable, it is nearly impossible to know what we might look for in the way of phenotypic properties which could indicate that runaway was responsible for the current state of a particular male trait. At present, no proposals have been offered in this regard, and there is little hope among researchers that this situation will change (Heisler et al. 1987: 109; Kirkpatrick and Ryan 1991: 37).

Actually, it is not quite accurate to say that there are *no* proposals for uncovering whether the runaway mechanism has shaped some aspect of the population in a past selection regime. Since writing his dissertation on the evolution of the human brain via runaway sexual selection, Geoffrey Miller has come to question whether the runaway process could thoroughly explain the brain's/mind's progression. Below I will review both Miller's reasons for believing that runaway was involved as well as his reasons for ultimately "burying" runaway as a candidate explanation (Miller 2000: 98).

Evidence in favor of runaway: traces of an unpredictable process

One of the reasons Miller thinks we have cause to suspect the influence of Fisher's runaway process on the mind is that this trait shows indications of being the result of an "evolutionarily unpredictable" process (*ibid*: 98). The reader can get a feel for what unpredictability looks like by observing

the diversity of sexual ornamentation in closely related species. Of a dozen species of bowerbirds, no two construct the same style of courtship nest. Of three hundred species of primate, no two have the same facial hair color and style." (77)

all of which are symptomatic of "[r]unaway's unpredictability" (77).

The orthodox response to the unpredictability of runaway has been the pessimism mentioned above with respect to being able to form expectations about what the outcome of a process governed by runaway will look like and, therefore, whether we can know if runaway was involved in the formation of a particular evolutionary endpoint.

One possible way out of this difficulty, as suggested by Miller, is to claim that the runaway process allows us to form certain sorts of expectations about its outcome in the same way that dice-rolling allows us to form certain sorts of expectations about its outcome (such as distribution samples). The question then becomes whether the kinds of things Miller is claiming to be evidence of the influence of runaway follow logically from the assumptions of runaway models.

Unfortunately, the items Miller offers in support of the notion that runaway was partly or entirely responsible for this or that feature of the natural world simply do not follow from the logical framework of the runaway process. But even if they did, the kinds of things he offers as indicative of runaway can be accommodated by any of the other major models of sexual selection. Indeed, most theorists see it as an essential goal of *any* model of sexual selection that it be capable of explaining the kind of diversity which Miller takes as evidence specifically of runaway. For example, Grafen's (1990a, b) model was designed to explain that diversity while axiomatically *excluding* any type of runaway effect. So Miller's examples are no more symptomatic of runaway than they are of any of the other theoretically possible modes of sexual selection (or of lots of other sorts of evolutionary processes, for all we know).

Evidence against runaway: directional evolution

One thing which leads Miller to reject the idea that runaway was involved in the evolution of the mind is the rapid directional increase in the size of the human brain.

Pure runaway cannot explain it, because runaway does not have any intrinsic bias toward larger ornament size, higher ornament cost, or greater ornament complexity (ibid: 81; see also 98).

Again, Miller gets the conceptual features of runaway roughly correct. There is no inherent bias in a runaway process which would necessarily cause the brain to consistently increase in size, cost, or complexity, and the mind to increase in intelligence. But it does not follow from this that we can *reject* the influence of runaway whenever we notice a directional trend. Runaway does not logically entail that a male trait will increase, but an increase is certainly *consistent* with runaway. After all, part of runaway's original mandate was to explain directional increases in male traits (Fisher 1958). The only way that the directional increase in brain size would rule out runaway as a candidate explanation would be if some logical feature of runaway actually *prevented* directional change from taking place. It simply does not follow from the fact that runaway has no "intrinsic bias" toward large brains that it cannot *accommodate* the evolution of larger brains. To repeat the quoted passage from Ryan (1990), "this theory can accommodate, but does not predict, the exaggeration of male traits under sexual selection."

Conclusion

I think what the preceding discussion has shown is that the significance attributed by evolutionary psychologists to sexual selection and mate choice in human evolutionary history is entirely out of proportion to the quality of work produced in this area. Balancing the scales would involve (among other things) (1) replacing commonsense, qualitative predictions with *surprising* qualitative, or, preferably, quantitative ones; (2) a better representation of available explanatory frameworks and a better grasp of the associated conceptual issues; and (3) closer attention to empirical work on potentially related features of nonhuman taxa. One important feature of much of the work on mate choice and sexual selection in nonhumans is a willingness to entertain hypotheses which assign no viability-enhancing (or in any way adaptive) role to mate preferences or secondary sex character-

istics. Evolutionary psychologists would do well to pursue these sorts of hypotheses in their own work.

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