Sexual selection for indicators of intelligence
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Abstract

Many traits in many species have evolved through sexual selection specifically to function as 'fitness indicators' that reveal good genes and good health. Sexually-selected fitness indicators typically show (1) higher coefficients of phenotypic and genetic variation than survival traits, (2) at least moderate genetic heritabilities, and (3) positive correlations with many aspects of an animal's general condition, including body size, body symmetry, parasite resistance, longevity, and freedom from deleterious mutations. These diagnostic criteria also appear to describe human intelligence (the g factor). This paper argues that during human evolution, mate choice by both sexes focused increasingly on intelligence as a major component of biological fitness – both for its heritable genetic benefits and its relevance to parenting ability. Many human-specific behaviors (such as conversation, music production, artistic ability, and humor) may have evolve principally to advertise intelligence during courtship. Though these mental adaptations may be modular at the level of psychological functioning, their efficiencies may be tightly intercorrelated because they still tap into common neurophysiological and mutation-load variables associated with fitness itself. Although the g factor (like the superordinate factor of fitness itself) probably exists in all animal species, humans evolved an unusually high degree of interest in assessing each other's intelligence during courtship and other social interactions – and, consequently, a unique suite of highly g-loaded mental adaptations for advertising their intelligence to one another through linguistic and cultural interaction. This theory makes five novel predictions that could be tested with standard factor-analytic, behavior-genetic, psychometric, and evolutionary psychology methods.

Introduction: Sexual selection for fitness indicators

During sexual courtship, animals often advertise the quality of their genes, bodies, and minds, in order to attract the best possible mate (Cronin, 1991; Miller, 1997, 1998). The peacock's tail, the elk's antlers, and the nightingale's voice all evolved through sexual selection as 'fitness indicators': traits specifically evolved to advertise good genes, good health, and/or good psychological functioning (Andersson, 1994). This paper argues that many human mental traits evolved through sexual selection as fitness indicators, to advertise a particular component of fitness called 'intelligence', also known as the g factor.

When choosing sexual partners, animals have particularly high incentives to favor partners with above-average 'fitness' (heritable genetic quality). In genetic terms, low fitness corresponds not so much to 'genetic load' (the number of fully recessive mutations on single-gene Mendelian traits – which tends to be phenotypically invisible), but to the number of mildly harmful, partially recessive mutations on the many genes ('quantitative trait loci') underlying complex polygenic traits – which tends to be clearly manifest in phenotypic functioning.

The whole point of fitness indicators is to advertise differences in heritable fitness between individuals. This gives them some unusual features as biological adaptations, compared to ordinary survival adaptations (Miller, in press). Survival adaptations tend to be genetically and developmentally canalized to create the optimal phenotype, leading to low apparent heritability and minimal differences between conspecifics. By contrast, fitness indicators evolve to be costly, complex displays that are so difficult to grow, maintain, and produce that only the highest-fitness individuals can afford to produce them in the optimal, most sexually-attractive form. Whereas survival adaptations tend to minimize between-individual differences, fitness indicators tend to amplify them dramatically (Pomiankowski & Moller, 1995; Rowe & Houle, 1996).

The evolution of most survival adaptations can be modelled using standard optimization theory, but the evolution of fitness indicators can only be modelled using a form of evolutionary game theory called signalling theory (Bradbury & Verhencamp, 1998). A central lesson from modern signalling theory is that fitness indicators must have high marginal costs in order to be reliable, or else low-fitness pretenders would be able to afford an impressive display as easily as a high-fitness signaller (Grafen, 1990; Johnstone, 1995). This is called 'the handicap principle' (Zahavi, 1997): fitness indicators typically impair survival (they are 'handicaps'), but increase sexual attractiveness and hence reproductive success. They are analogous to conspicuous consumption (Veblen, 1899): a wasteful display of luxury that reliably reveals an individual's wealth because the poor cannot afford the waste.

Fitness and intelligence

'Fitness' is a statistical abstraction across the efficiency levels of many different adaptations serving different survival and reproductive functions. The 'g factor' is a statistical abstraction across the efficiency levels of many different mental adaptations. How are these two constructs related?

So far, biologists have not used factor analysis to analyze fitness in the same way that psychometricians have used it to analyze human intelligence. Fitness cannot be measured directly, but biologists have developed a number of moderately reliable measures that probably correlate positively with general biological fitness, including body size, body mass, body symmetry, and low parasite load (Moller & Swaddle, 1997). I conjecture that, given a large representative sample of mature individuals from a particular species, and a number of different fitness measures of proven reliability, the correlation matrix between all such fitness measures will usually contain all positive entries – the same sort of positive manifold discovered by Spearman in 1904, in relation to the *g* factor. Given this positive manifold of fitness measures, it would be possible to use standard factor analysis methods to recover a general fitness factor, which could be called the *f* factor (for a similar idea, see Houle, this volume).

> **Prediction 1**: Factor analysis of reliable fitness measures obtained from a large representative sample of individuals from any wild species will reveal a general fitness factor, an *f* factor, analogous to the *g* factor in psychometrics. This *f* factor will account for a substantial proportion of between-individual variance in the fitness measures, and will prove moderately heritable under normal ranges of environmental conditions.

This prediction is implicit in most modern biological research on sexual selection and fluctuating asymmetry (e.g. Moller & Swaddle, 1997; Furlow et al., 1997), but is worth making more explicit. The *f* factor prediction is quite different from the standard assumption in behavioral ecology that trade-offs between traits should give rise to negative correlations between many fitness measures.

The *f* factor ('fitness') would probably be superordinate to the *g* factor ('intelligence'), just as the *g* factor is superordinate to the spatial intelligence factor and the verbal intelligence factor. (Obviously, such hierarchies of factors can only be recovered through hierarchical factor analysis, which does not force lower-order factors to be orthogonal to one another.) If *f* is superordinate to *g*, then we might more parsimoniously explain why human intelligence is positively correlated with so many biological traits such as height, health, longevity, and bodily symmetry (see Jensen, 1998; Furlow et al., 1997): all of these traits, including intelligence, are tapping into a general fitness factor.

> **Prediction 2**: The *g* factor will prove subordinate to the *f* factor. That is, individual differences in 'intelligence' partly reflect individual differences in biological fitness that are not specific to psychological or neurophysiological functioning.

If *g* is subordinate to *f*, we should be careful about interpreting correlations between *g* and measures of social, economic, or reproductive success (e.g. Lubinski, this volume): such correlations should be attributed to the effect of 'intelligence' on life outcomes only if the subordinate *g* factor accounts for significant variance in those measures beyond that which is accounted for by the *f* factor itself. Likewise, any behavior-genetic study claiming to find a quantitative trait locus associated with human 'intelligence' (e.g. Chorney et al., 1997; see McGuffin, this volume) should demonstrate that the locus has *g*-specific effects, and not just a generally positive effect on fitness.

Now, consider the implications of predictions 1 and 2 from the viewpoint of sexual selection theory. An animal choosing a sexual partner is trying to select the individual with the highest possible heritable fitness, corresponding to the f factor. If the g factor is a major component of f (i.e. if the g factor itself has a high f-loading in this particular species), then g makes a convenient fitness indicator. This implies that any behavioral capacity with a high g-loading may also have a reasonably high f-loading. That is, any behavior that requires high 'intelligence' can function as a fitness indicator in sexual selection. If g has a high f-loading, then the mechanisms of mate choice should evolve to favor courtship displays and behaviors with high g-loadings. Behaviors that are particularly indicative of high 'intelligence' should prove particularly attractive.

> **Prediction 3**: If g has a high f-loading, mate choice mechanisms should favor courtship behaviors with high g-loadings, as cues of heritable fitness. Generally, a mental trait's sexual attractiveness should correlate positively with its g-loading.

Evolutionary psychology research suggests that intelligence is a major criterion of human mate choice. Buss (1989) found that, across all 37 cultures he investigated, intelligence was the second-most-desired trait in a sexual partner (kindness was the most desired). Although males are not very choosy about the intelligence of short-term sexual partners, both sexes become equally, and extremely, choosy about the intelligence of long-term sexual partners (Kenrick et al., 1990). The method of correlated vectors (Jensen, 1998, this volume) also shows that assortative mating is very focused on g-loaded mental traits. For example, spouses correlate more highly for their vocabulary sizes (a highly g-loaded trait) than they do for digit span (a modestly g-loaded trait).

Sexual selection for g-loaded intelligence-indicators

Courtship behaviors evolve in response to the pressures of mate choice. If mate choice mechanisms in a particular species are favoring highly g-loaded behaviors as fitness indicators, then sexual selection would shape those behaviors according to the standard predictions of fitness indicator theory. The behaviors should evolve to have higher marginal costs, higher coefficients of genetic and phenotypic variation, higher complexity, and higher f-loadings (by virtue of ever-higher g-loadings).

Elsewhere, I have argued that many of our uniquely human mental traits evolved mainly through sexual selection, due to the mate choices made by ancestral males and females (Miller, 1998, 1999, in press). These traits may include our capacities for language, art, music, generosity, creativity, and humor. Here, I am emphasizing that these capacities may have evolved to advertise biological fitness principally through their ability to advertise intelligence: their f-loadings may be carried almost entirely by their g-loadings. In other words, our most distinctive mental traits may have evolved not so much because they yielded some survival advantage during the Pleistocene, but because they were sexually attractive fitness indicators that yielded reproductive advantages.

> **Prediction 4**: Most of our uniquely human mental abilities should show particularly high g-loadings and f-loadings, compared to more ancient mental capacities common to other great apes, primates, or mammals. Like other sexually selected fitness indicators, they should also show higher coefficients of genetic variation and phenotypic variation, and at least moderate heritabilities.

Though we often attribute high intelligence to someone capable of impressive verbal, visual, or musical behavior, it is not so clear whether the link between intelligence and fitness is consciously understood. However, very little about mate choice is consciously mediated, nor need it be. Presumably peahens do not consciously appreciate that a large, symmetrical peacock tail indicates a lower than average number of mildly deleterious, partially recessive mutations on genetic loci associated with fitness – they only need to feel attracted to such tails, and evolution keeps track of the correlations.

If sexual selection favored intelligence-indicators, why is there no sexual dimorphism in the _g_ factor?

Because males and females of any mammalian species share almost all of the same genes (except those on the tiny Y chromosome), we would not expect any sexual dimorphism in the _f_ factor itself, which is basically just average genetic quality across the entire genome. Fathers selected through mate choice for high fitness would produce high-fitness daughters, not just high-fitness sons. Insofar as the _g_ factor is highly _f_-loaded, this may help explain why there appears to be no sexual dimorphism in the _g_ factor (Jensen, 1998). Even if sexual selection were driven entirely by female choice favoring highly intelligent males, as long as the _g_ factor depended on genetic variation at mostly autosomal loci, average _g_ would increase in both sexes at the same rate. Darwin's 'Law of Equal Inheritance' expressed the same idea (see Lande, 1987).

However, sexual selection theory would still predict sexual dimorphism in the public behavioral manifestations of intelligence, because the reproductive benefits of such displays would always be higher for males than for females given some degree of polygyny. (Also, the marginal costs of such displays would be higher for females, given the competing demands of pregnancy and maternal care.) Demographic data on the production of costly, difficult, public displays of intelligence, such as painting pictures, writing novels, producing jazz albums, and publishing philosophical speculations, reveals a very strong dimorphism, with males producing about ten times more displays than females, and male display rates peaking in early sexual maturity, corresponding to the peak of courtship effort (Miller, 1999).

> **Prediction 5**: Despite the sexual equality in the _g_ factor itself, the human display behaviors that show the highest sexual dimorphism should show the highest _g_ loadings, functioning as the most effective displays of intelligence. Likewise, the display behaviors that show the sharpest peak in young adulthood (at the peak of courtship effort) should show the highest _g_ loadings.

How can the _g_ factor be reconciled with evolutionary psychology's massive modularity hypothesis?

Evolutionary psychologists have argued that evolution would have produced human minds composed of hundreds of distinct psychological adaptations, each dedicated to solving a particular problem of survival or reproduction under ancestral conditions (Cosmides & Tooby, 1994; Tooby & Cosmides, 1990; Pinker, 1997). This 'massive modularity' argument goes well beyond Howard Gardner's (1983) 'multiple intelligences' theory, which posited only seven distinct faculties. But like Gardner's theory, the

massive modularity view seems difficult to reconcile with the existence of the *g* factor. If the mind has so many parts, why should the efficiencies of those parts be positively inter-correlated, such that they yield such a robust *g* factor?

I agree with Ian Deary (this volume) and Arthur Jensen (1998) that we must distinguish between the species-typical human cognitive architecture (which many be massively modular), and the factor-analytic structure of individual differences in cognitive functioning (which yields a unitary *g* factor). This distinction is obvious in the case of fitness itself: to claim that there is an *f* factor in a particular species (which can capture individual differences in general health and condition) is not to claim that a typical individual of that species is composed of just one bodily organ. The *f* factor is not a single gene or a single physical organ, and the *g* factor ('intelligence') is not a psychological organ. Rather, the *g* factor arises because each mental organ taps into the same basic set of genetic and neurophysiological variables (Jensen, 1998; this volume). The existence of the *g* factor leaves completely open the question of how many psychological adaptations comprise human nature; it is not inconsistent with a highly modular mind.

A more interesting question is why we attach the honorific label of 'intelligence' to some of our modular psychological adaptations, and not to others. For example, why did Gardner (1983) choose the seven 'intelligences' (linguistic, logical-mathematical, spatial, musical, body-kinesthetic, interpersonal, intrapersonal) that he did? His explicit criteria for distinguishing an intelligence from a non-intelligence are almost identical to the criteria that modern evolutionary psychologists (e.g. Pinker, 1997) use to distinguish any modular, psychological adaptation from anything else. According to Gardner's explicit criteria, dozens of psychological adaptations (including species-typical capacites for face recognition and social inference) should qualify as 'intelligences'. However, Gardner alludes to an implicit criterion that actually does all the work: an 'intelligence' is psychological adaptation that shows large individual differences, and that is socially valued across cultures. In my terms, he has picked out some of the highly *g*-loaded intelligence indicators, and what he calls 'socially valued', I would call 'sexually attractive'. (Whenever social scientists talk about 'social status', evolutionary psychologists see the footprints of sexual selection). Likewise, the evidence that Robert Sternberg (1988) cites for his 'triarchic theory' of intelligence – the fact that 'intelligence' to ordinary people connotes practical, social, and academic forms of intelligence – suggests that there are practical, social, and academic types of intelligence-indicators, some genetically evolved, and some culturally learned.

However, the notion of intelligence-indicators raises some problems for a strong version of the massive modularity view. If each psychological adaptation was totally modular at all levels of description (genes, developmental pathways, brain circuits, cognitive operations), then there would be no such thing as the *g* factor (negating the idea of an intelligence-indicator), and no module could function as a very good fitness indicator either. Indicators are most reliable when they have some intrinsic correlation with the variable they are indicating, by virtue of sharing some lower-level biological processes. Total mental modularity would make intelligence-indicators totally unreliable: efficiency in one behavioral domain would have no correlation with efficiency in other domains.

In fact, if sexual selection favored certain psychological adaptations specifically as intelligence-indicators, then those adaptations should be specifically designed to have a high degree of functional overlap with many other psychological adaptations – at least at

the genetic, developmental, and neurophysiological levels, if not at the cognitive and behavioral levels. The main way for an intelligence-indicator to evolve a high *g*-loading would be to recruit a large number of genes, developmental pathways, and brain circuits into its operation. Typically, this might be accomplished by evolving a very high degree of psychological complexity that draws upon a wide range of cognitive operations and mental representations. Conversation, art, music, and humor do precisely that. According to this theory of intelligence-indicators, the psychological complexity of such behaviors evolved not because complex survival problems demanded complex solutions, but because complex courtship displays are more easily disrupted by low fitness and low intelligence, and therefore make better indicators of both.

Why is intelligence still heritable after all these years?

If the *g* factor is subordinate to the *f* factor, then the surprisingly high heritability of human intelligence may reflect the heritability of fitness itself across many species.

According to traditional population genetics, fitness should not remain heritable in any species at evolutionary equilibrium, because selection should remove any alleles that result in below-optimal fitness. However, molecular genetic research since the 1960s has shown surprisingly high amounts of fitness-related genetic variation in wild populations. Also, sexual selection theory since the 1980s has emphasized that optimal fitness is a moving target, due to co-evolution between any species and its pathogens, parasites, predators, and competitors. Moreover, the constant hail of mutations often keeps species from converging to optimal fitness, even when the fitness optimum is stable (see Eyre-Walker & Keightley,1999; Kondrashov, 1995). Apparently, fitness remains at least moderately heritable in most species most of the time, and this is why mate choice mechanisms still bother to pay attention to fitness indicators (see Charlesworth, 1987; Pomiankowski & Moller, 1995; Moller & Swaddle, 1997; Rowe & Houle, 1996).

From this perspective, the continuing heritability of human intelligence may be a special case of the heritability of fitness itself, which is the evolutionary norm. But there is another effect called 'genic capture' (Rowe & Houle, 1996) that may account for the especially high heritability of sexually-selected fitness indicators, including intelligence-indicators. Insofar as intelligence-indicators are favored because they advertise general fitness, intelligence-indicators should evolve to recruit an ever larger number of genes and developmental pathways into their operation, so they reveal more information about the quality of an individual's genome. In particular, they should increase their 'mutational target size': their vulnerability to harmful mutations, wherever they occur (Rowe & Houle, 1996). (This follows the handicap principle: the easier a trait is to mess up through mutations, inbreeding, injury, or disease, the better a fitness indicator it makes, and the more it will be favored by sexual selection). The human brain apparently depends upon a very large proportion of the human genome, which gives it a wonderfully large mutational target size, from sexual selection's viewpoint. (Of course, if every human gene were expressed in the human brain, the *g* factor might be identical to the *f* factor.) This leads to some final predictions that molecular genetics methods should be able to test within a few years:

> **Prediction 6**: A mental trait's *g*-loading should correlate positively with the number of quantitative trait loci upon which it depends

Prediction 7: the g-score indicated by a mental trait should correlate negatively with the number of mutations affecting those loci

Prediction 8: a mental trait's g-loading should correlate positively with its f-loading

Prediction 9: a mental trait's g-loading and f-loading should both correlate positively with its heritability.

The theory of sexual selection for intelligence-indicators might not turn out to have the virtue of truth, but at least it has the virtue of falsifiability.

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