

## **Aesthetic fitness: How sexual selection shaped artistic virtuosity as a fitness indicator and aesthetic preferences as mate choice criteria**

By Geoffrey Miller

Published as:

Miller, G. F. (2001). Aesthetic fitness: How sexual selection shaped artistic virtuosity as a fitness indicator and aesthetic preferences as mate choice criteria. *Bulletin of Psychology and the Arts* 2(1), 20-25. Special issue on Evolution, creativity, and aesthetics.

### **Abstract**

Aesthetic ornamentation in other species almost always results from sexual selection through mate choice, and sexually-selected ornaments usually function as indicators of fitness – good health, good brains, and good genes. This paper suggests that human art capacities evolved in the same way, with aesthetic judgement evolving in the service of mate choice. This theory draws on the biological aesthetics of Darwin, Nietzsche, Veblen, Boas, Gombrich, and Zahavi, and on the example of bowerbird courtship. It revives the traditional emphasis on virtuosity in ornamental and representational art, in contrast to the runaway creativity celebrated by Modernist art theory. It suggests that aesthetic judgement evolved as a functional part of social and sexual cognition, not as a side-effect of perceptual psychology.

In Darwin's (1871) view, natural beauty arose through competition to attract a sexual partner. His process of sexual selection through mate choice – the struggle to reproduce, not to survive – drove the evolution of visual ornamentation and artistry, from flowers through bird plumage to human self-adornment. Moreover, Darwin saw animal and proto-human nervous systems as fully capable of aesthetic judgement, used largely in the service of choosing their sexual partners. However, when Darwin's sexual selection theory fell into disfavor among Victorian biologists (Cronin, 1991; Miller, 2000a), so did his radically naturalized and sexualized aesthetics.

This paper tries to revive Darwin's view of visual aesthetics and artistry as products of sexual selection through mate choice. It does so in light of the revival of sexual selection theory in evolutionary biology (e.g. Andersson, 1994), especially new ideas about the role of sexual ornamentation as a reliable indicator of an animal's health, fertility, fitness, and genetic quality (Johnstone, 1995; Miller, 2000a, b,c,d,e; Zahavi & Zahavi, 1997). In this view, the fine arts are just the most recent and pretentious manifestations of a universal human instinct for visual self-ornamentation, which in turn is a manifestation of sexual selection's universal tendency to ornament individuals with visual advertisements of their fitness. Thus, the human capacity for visual artistry is viewed here as a 'fitness indicator', evolved like the peacock's tail and the bowerbird's bower for a courtship function.

### **Art as an adaptation**

The adaptationist approach taken here considers human visual art in the functionalist framework of evolutionary biology and evolutionary psychology. Adaptationism entails identifying biological adaptations and investigating their adaptive functions – that is, the ways in which their survival or reproduction benefits outweighed their costs in ancestral generations.

Probably no particular type of human art or aesthetic style can be considered a genetically encoded adaptation. That is the wrong level of description. Rather, we should focus

on the level of psychological adaptations: evolved, domain-specific mental capacities that may include perceptual, cognitive, emotional, motivational, learning, and motor control sub-systems (Buss, 1999; Tooby & Cosmides, 1990). It is only at this level that evolutionary psychology has some hope of integrating the ultimate (evolutionary-functional) and proximate (reductionistic) study of psychological adaptations. Also, the adaptationist approach emphasizes selection pressures over phylogeny: if art evolved in our lineage over the last one or two million years, there is little reason to expect proto-art abilities in living non-human primate such as chimpanzees, which split off from us at least 5 million years ago (c.f Lenain, 1995; Whiten, 1976).

The capacity to produce visual art and self-ornamentation appears to be a genuine evolutionary adaptation unique to our species of primate (Dissanayake, 1992). It fits many criteria for recognizing adaptations (see Buss, 1999; Tooby & Cosmides, 1990). It is ubiquitous across human groups, cultures, and history. Art-making and art-viewing are pleasurable, and pleasure is an evolutionary hallmark of psychological adaptation. Artistic production entails costs in time, energy, effort, and skill, and such costs are rarely expended without some adaptive rationale. Humans are much better at producing and judging art than any artificial intelligence program or any other primate. Art is not 'innate' in the sense of fully functioning at birth (almost no psychological adaptations are), but art is relatively fun and easy to learn, compared to evolutionarily novel skills such as following APA format.

The fitness indicator theory of art outlined in this paper is not new. Similar ideas were expressed not only by Charles Darwin (1871), but also by Friedrich Nietzsche (1883-1888/1968), Thorstein Veblen (1899), Frans Boas (1955), Ernst Gombrich (1977, 1982), Amotz Zahavi (1975, 1978; Zahavi & Zahavi, 1997), Frederick Turner (1991), Fraser Neiman (1997), Marek Kohn (1999), and Camilla Power (1999). The fitness indicator theory has also been used in my previous work on art (Miller, 1999a, 2000a), music (Miller, 2000b), creativity (Miller, 1997a), mate choice (Miller, 1997b, 1998a,b), and the evolution of human mental traits as indicators (Miller, 2000c,d,e).

### **Art as a product of sexual selection**

If art is an adaptation, what possible function could it have served? From the viewpoint of current animal communication research, art is a signalling system. There is a signaller (the maker of the art), and a set of receivers (who perceive the work of art). The prototypical functions for animal signals include long-range sexual attraction, short-range sexual courtship, sexual rivalry, territorial conflict, begging by offspring to solicit parental investment, warning signals to deter predators, and alarm signals to alert relatives of danger (Bradbury & Vehrencamp, 1998).

Out of these standard functions for signalling, sexual selection for courtship produces the most complex and aesthetically pleasing signals (Darwin, 1871; Cronin, 1991; Miller, 2000a). Insofar as we praise human art for its complexity and aesthetic value, it seems reasonable to focus on sexual courtship as the most likely adaptive function of human art-production – at least in prehistory, if not in modern society.

Sexual selection is not just a theory of sex differences. Sexual selection emerges in any sexually-reproducing species as a result of competition within each sex to attract sexual partners of the opposite sex (for overviews see Andersson, 1994; Cronin, 1991; Miller, 2000a). Darwin (1871) distinguished two kinds of sexual selection: aggressive rivalry and mate choice. Rivalry, especially between males, tends to produce weapons, such as sharp teeth, large horns, and strong muscles. Mate choice, especially by females, tends to produce ornaments, such as colorful tails, innovative sounds, and musky smells. In Darwin's view, mate choice is mediated by animal nervous systems, so it is mid-way between natural selection (selection on survival ability, mostly by the inanimate environment) and artificial selection by human breeders. This

mediation by animal senses and preferences is what gives mate choice such aesthetic power in evolution.

From 1871 until the turn of the 20<sup>th</sup> century, Darwinian aesthetics was an active area of theorizing. Darwin (1871) himself viewed the human visual arts as an outgrowth of an instinct for body ornamentation. He pointed out that males in most cultures indulge in much more self-adornment than females, as predicted by his sexual selection theory. (He understood that men of his own culture ornamented themselves with country estates and colonial treasures rather than tattoos and penis sheaths). Herbert Spencer argued that sexual selection produced most of the beauty in nature and culture, while Max Nordau posited a neurophysiological link between reproductive urges and artistic creativity, which Sigmund Freud appropriated in this theory of art as sublimated sexuality. Friedrich Nietzsche developed an especially intriguing and little-appreciated biological aesthetics in The Will to Power, in the section titled 'The will to power as art'. Nietzsche (1883-1888/1968, p. 421) also accepted a sexual display function for the visual arts, writing "Artists, if they are any good, are (physically as well) strong, full of surplus energy, powerful animals, sensual; without a certain overheating of the sexual system a Raphael is unthinkable."

Other theorists who were less open to sexual selection theory, such as Alfred Russel Wallace, had more trouble understanding the adaptive benefit of art, given its high time and energy costs but limited survival utility. For example, in The Beginnings of Art, Ernst Grosse (1897, p. 312) argued that natural selection would "long ago have rejected the peoples which wasted their force in so purposeless a way [i.e. making art-works], in favor of other peoples of practical talents; and art could not possibly have been developed so highly and richly as it has been". Throughout the 1890s, Darwinian art theorists H. Balfour, A. C. Haddon, and Felix Clay also struggled to find credible non-sexual functions for art.

Misled by Herbert Spencer's phrase 'survival of the fittest', many theorists of this era suggested that art's high cost and apparent uselessness implied the futility of Darwinian analysis. Darwinian aesthetics also languished because most Victorian biologists were unwilling to follow Darwin in granting female animal brains any power to choose their mates by aesthetic criteria. This patronizing attitude to animal aesthetic tastes was reinforced by the rise of Behaviorism in early 20<sup>th</sup> century psychology. Although Darwin gave strong evidence for the importance of female mate choice in producing male ornaments, biologists after Darwin focused almost exclusively on male rivalry, rejecting the possibility of female choice (Cronin, 1991, Miller, 2000a). For over a century, sexual selection was seen as a process where active, competitive males struggled for "possession" of passive females, by acquiring territories and status, and repelling rivals. Ornaments were usually interpreted as species-recognition signals, to help animals avoid mating with the wrong species. Only in the last couple of decades has the picture changed, with a mass of support for Darwin's mate choice hypothesis in thousands of experimental and theoretical studies (e.g. Andersson, 1994; Bradbury & Vehrencamp, 1998). Sexual selection is now recognized as a major factor in the evolution of animal bodies, brains, signals, social interactions, and species.

What sort of evidence could support this sexual selection theory of art? One clue would be an example of convergent evolution: the independent evolution of art-like abilities in another species through sexual selection. Bower-birds offer strong evidence along this line.

### **Bowerbirds: The Darwinian aesthetics of the extended phenotype**

Bowerbirds are native to New Guinea and Australia. Each of the 18 species constructs a different style of display site or bower. Bowers are constructed only by males, and only for courtship (Borgia, 1986). Each male constructs his nest by himself, then tries to attract females to copulate with him near it. Females fly around searching for the most visually impressive bower, and copulate with the best bower-builders. Males that build superior bowers can mate with up to ten different females per day; bad bower-builders attract no females (Borgia, 1986,

1995, 1997; Lenz, 1994). Once inseminated, the females go off on their own, build their own small cup-shaped nests, lay their eggs, and raise their offspring by themselves with no male help (like Picasso's mistresses). Just as sexual selection on ornamental plumage drove speciation among the closely related Birds of Paradise, changes in bower fashion probably drove the proliferation of bowerbird species (Borgia, 1997; Uy & Borgia, 2000). This evidence confirms Darwin's (1871) view that bowers evolved as courtship ornaments, through sexual selection by female choice. Functionally, bowers attract females to copulate by advertising male fitness, and they have no survival function.

Structurally, bowers are large and complex, show bilateral or radial symmetry, are decorated colorfully, and require a great deal of time, energy, material, and skill to construct. For example, the Golden Bowerbird of northern Australia, though only 9 inches long, builds a sort of roofed gazebo up to 9 feet high, many times its own body size and weight. Males fly around searching for the most brilliantly colored natural objects (such as berries, snail shells, and flowers), bring them back to their bowers, and arrange them carefully in clusters of uniform color. When the berries and flowers lose their color after a few days, the males replace them with fresh material. Females mate preferentially with males who construct larger, better quality, and more highly ornamented bowers (Borgia, 1985, 1986, 1995; Lenz, 1994). Immature males build unimpressive bowers, and it requires several years of practice (and survival in a hostile environment) before high-quality bowers can be achieved. The bower can be considered the 'extended phenotype' of the male bower-bird (Dawkins, 1982): a genetically evolved, species-specific artefact constructed outside the individual's body, but very much in the service of the individual's genes.

In fact, recent evidence shows that the cognitive challenge of bower-construction was the major selection pressure driving the evolution of brain size in bowerbirds. Madden (2001) found a correlation around .80 between bower complexity and relative brain size across 10 species of bowerbirds and four non-bowerbirds (such as the closely related catbirds). Sexual selection for bower complexity almost doubled male brain size. For example, after controlling for body size, the brains of a complex bower-builder *C. lauterbachii* were 80% larger than those of the catbird *A. melanotis*. This is not quite as dramatic as the tripling of brain size in art-making humans compared to non-artistic chimpanzees (Miller, 2000a), but impressive nonetheless. Madden's (2001) study was the first to show expansion of overall brain size in response to sexual selection pressures, and the first to show a relationship between brain size and the complexity of an aesthetic display constructed outside the body. In this light, Madden's work suggests there was convergent evolution not only between bowers and human art, but between bower bird brains and human brains.

As Darwin (1871) realized, bowers are one of the best examples of sexual selection through mate choice, and also one of the only examples of animal art. Bowers show that mate choice can create complex psychological adaptations for constructing aesthetic ornamentation beyond an animal's body. Bowers also illustrate the idea that mate choice favors fitness indicators. The aesthetic quality of a bower is a reliable indicator of good skill, a good brain, and good genes, and female bower-birds have evolved the aesthetic discernment to judge bowers in order to get the best genes (heritable fitness) for their offspring. In social cognition terms, their aesthetic tastes allow them to make fitness-attributions through the bower, as it were, to the bower-builder behind. This point leads us to fitness indicator theory.

### **Fitness indicator theory**

In recent years, biologists have found that many sexually-selected traits function as reliable indicators of reproductively important traits such as age, health, fertility, social status, and genetic quality (Andersson, 1994; Cronin, 1991; Johnstone, 1995; Zahavi & Zahavi, 1997). Collectively, these traits determine the individual's expected Darwinian fitness, so indicators of these traits can be called 'fitness indicators' (Miller, 2000a,b,c,d,e). By choosing sexual

partners with high-quality fitness indicators, animals are more likely to get healthy partners, competent parents, and good genes for their offspring.

For example, the peacock's tail works as a fitness indicator because unhealthy, weak peacocks cannot grow very large colorful, symmetric, well-preened tails. Even if they could, their encumbering tails would make it even more difficult to escape from predators such as tigers. The result is that the size of a (surviving) peacock's tail correlates positively with the peacock's age, health, and heritable fitness (Petrie, 1994). By mating with a large-tailed peacock, peahens are getting good genes that will give their offspring survival and reproductive advantages.

Indicators are usually subject to the 'handicap principle' (Zahavi, 1975; Zahavi & Zahavi, 1997) that they must have high costs in order to be reliable. Cheap, easy-to-grow, easy-to-maintain indicators could be faked too easily by unhealthy, unfit individuals, so the indicator would lose its value as a signal, and receivers would evolve to ignore it. Technically, the key feature is that the indicator must have a higher relative marginal costs to an unfit animal than it does to a highly fit animal (Grafen, 1990). It took biologists 20 years to understand and accept Zahavi's (1975) handicap principle, but it has recently become a major theme in sexual selection research (Johnstone, 1995).

Handicaps have the counter-intuitive feature that the more vulnerable they are to disruption (by poor nutrition, injury, parasites, pathogens, genetic inbreeding, high mutation load, or socially subordinate status), the more useful they are as fitness indicators. Vulnerable traits amplify the apparent variance in phenotypic quality across individuals (Hasson, 1990). They take small differences in genetic quality, nutritional state, general health, or intelligence, and turn them into dramatic differences in ornament quality – including the quality of courtship behavior such as bower-building or art-production. In this way, they make individual differences more visible to mate choice, amplifying the power of sexual selection to shape both ornament quality and underlying fitness (Rowe & Houle, 1996; Houle, 2000).

Evolutionary psychology has revealed that many cues of human physical beauty function as fitness indicators. These cues include height, facial symmetry, facial averageness, facial indicators of sex hormone levels, male upper-body musculature, and female waist-to-hip ratio (see Etcoff, 1999; Gangestad & Thornhill, 1997; Manning, Scutt, Whitehouse, & Leinster, 1997; Thornhill, 1998; Thornhill & Grammer, 1999). For example, men are sexually attracted to low waist-to-hip ratios in females, and a low female waist-to-hip ratio really does correlate with youth, fertility, and health (Singh, 1995). This research concerns aesthetic tastes, not just sexual psychology. Insofar as the human form has been considered the prototype of beauty in every culture, this research shows the utility of using fitness indicator theory to understand the adaptive logic behind visual beauty.

### **Indicators of genetic quality**

Fitness indicators often advertise good genes, not just good bodies and brains. By 'good genes', biologists usually mean a genotype that has a low number of expressed deleterious mutations. Mutation is a major problem for every species. New mutations are always arising, and since they hurt much more often than they help, they are continually eroding fitness. For example, Eyre-Walker and Keightley (1999) estimated that in our hominid ancestors over the last several million years, there have been on average 1.6 new, harmful, expressed mutations per individual per generation. This exceeds the mutation rate that natural selection alone could counter-act (Crow, 1999; Kondrashov, 1995). So how do species resist a 'mutational meltdown' (Ridley, 2001)? Some biologists believe that sexual selection for indicators of genetic quality is a major factor in allowing complex, long-lived species to persist in the face of mutation's entropic power (e.g., Atmar, 1991; Michod & Hasson, 1990; Pomiankowski & Moller, 1995; Rowe & Houle, 1996). Indeed, many biologists believe that

limiting the propagation of harmful mutations may be the reason why sexual reproduction evolved in the first place (Ridley, 1993).

Indicators of genetic quality can be bodily traits, or behavioral traits such as bird song, bower-building, or human art-production. Behaviors are often better fitness indicators simply because brains are so complex, so hard to grow, so costly to maintain, and so easy to disrupt, compared to other organs (Miller, 2000a). For example, a songbird's singing ability is a potent fitness indicator. The number of different songs a male can sing (his 'song repertoire') correlates positively with his age, with the size of the brain area specialized for song learning, with his reproductive success, and with the health and survival likelihood of his offspring; this is why females prefer large-repertoire males (Catchpole & Slater, 1995; Hasselquist, Bensch, & von Schantz, 1996).

Which behavioral traits would be most valuable as good-genes indicators? Some behaviors summarize much more information about an individual's genotype, by depending on more complex neurogenetic developmental pathways, which can be disrupted by mutations on a much larger set of genetic loci (Houle, 2000; Miller, 2000e; Rowe & Houle, 1996). Mate choice should evolve to focus on complex, challenging behaviors that amplify minor differences in genetic quality between individuals into massive, easily-noticed differences in the relative qualities of their courtship behavior – such as art-production.

This leads to an important point about assessing whether art is an adaptation. Some evolutionary psychologists have suggested that genuine psychological adaptations should show low phenotypic variance (small individual differences) and low heritability, because selection should have eliminated maladaptive genetic variation. These criteria make sense for traits that evolved under natural selection for survival, but they do not make sense for sexually selected fitness indicators (Miller, 2000c,d,e). If art evolved under sexual selection as a fitness indicator, then we should expect large, conspicuous individual differences in artistic ability, and at least moderate heritability. Moreover, if artistic ability evolved to advertise other underlying mental and personality traits, we should expect substantial phenotypic correlations between artistic ability and those other traits. Thus, although art ability might be modular at the level of adaptive design, it might not appear very independent in a factor analysis of mental abilities. In fact, if artistic ability evolved as an indicator of the fitness component known as general cognitive ability ('intelligence'), then we would expect it to show a very high correlation with intelligence – such that it would be easy to mistake for an evolutionary side-effect of 'domain-general human intelligence' (Miller, 2000e).

### **Art-works as fitness indicators**

From the viewpoint of fitness indicator theory, maybe our aesthetic preferences evolved to favor art-works that could only have been produced by a high-fitness artist. Art-objects may be displays of their creator's fitness, and may be judged as such. As with the sexual ornaments on our bodies (Gangestad & Thornhill, 1997), perhaps beauty boils down to fitness.

To be reliable, fitness indicators must be difficult for low-fitness individuals to produce (Zahavi, 1975; Grafen, 1990; Johnstone, 1995). Applied to human art, this suggests that beauty equals difficulty and high cost. We find attractive those things that could only have been produced by people with attractive, high-fitness qualities such as health, energy, endurance, hand-eye coordination, intelligence, creativity, access to rare materials, the ability to learn difficult skills, and lots of free time.

An art-work's beauty reveals an artist's virtuosity. This is an old-fashioned view of aesthetics, but that does not make it wrong. Throughout most of human history, the perceived beauty of an object has depended very much on its cost in terms of time, energy, skill, or resources. Objects that were cheap and easy to produce were almost never considered beautiful. As Thorstein Veblen (1899, p. 80) pointed out in The Theory of the Leisure Class, "The marks of expensiveness come to be accepted as beautiful features of the expensive

articles". Likewise, Franz Boas (1955) found that in most cultures he studied, "goodness and beauty are the same" (Boas, 1955, p. 356), with goodness denoting the patient, resourceful, and creative application of high skill and high intelligence. In his view, this thirst for virtuosity explains our preferences for regular form, symmetry, perfectly repeated decorative motifs, smooth surfaces, and uniform color fields – which are all difficult to produce under pre-modern conditions, but easy to assess (also see Gombrich, 1982). Thus, our sense of beauty was shaped by evolution to embody a tacit awareness of what is difficult versus easy, rare versus common, costly versus cheap, skillful versus slovenly, and fit versus unfit.

From this sexual selection viewpoint, the artist's challenge is to demonstrate his or her fitness by making something that a lower-fitness sexual rival could not make. Almost anything can be made aesthetically, because anything can be made with special care that would be difficult to imitate by one who was not so careful. This fits with Dissanayake's (1992) view of making art as 'making special'. Fitness indicator theory explains why our aesthetic tastes are so culturally flexible at one level, yet so invariant in their underlying emphasis on virtuosity. Just as sexual selection can make almost any body surface more elaborate and complex as a visual ornament, resulting in a diversification of visual ornamentation across species, our sexually-selected aesthetic tastes can favor the elaboration or 'making special' of almost any object according to almost any set of challenging norms or rules, resulting in the diversification of visual styles across human cultures. This also explains why most people rejected the 20<sup>th</sup> century Modernist styles (such as abstract expressionism or conceptual art) that self-consciously rejected virtuosity as a criterion of artistic importance (Miller, 2000a). Fitness indicator theory helps us understand why 'art' is an honorific term that connotes superiority, exclusiveness, and high achievement in almost any domain of skill, whether pottery or psychotherapy.

Beauty conveys truth, but it is a truth about the artist's individual fitness, not about the human condition in general. Compared to human language, the non-representational visual arts seem very poor as communication media. Yet compared to human language, all animal signalling systems in all other species that have ever evolved seem very poor at communicating propositional information about the external world. The primary function for almost all animal signalling systems is to convey fitness information about the signaller, not information about the world (Bradbury & Vehrencamp, 1998). In this sense, the absence of distinct propositional meaning in most of the human visual arts is biologically normal, and language is the bizarre exception.

Since the rise of evolutionary psychology around 1990, several thinkers have applied sexual selection theory, biological signalling theory, the handicap principle, and related ideas to understand the human arts. Constable (1997) analyzed verse poetry as a system of verbal handicaps that constrain vocabulary choice, thereby making poetry a more effective intelligence-indicator. Kohn (1999) viewed the Acheulian hand-axe as a sexually-selected part of the *Homo erectus* extended phenotype, and as a reliable fitness indicator. Power (1999) analyzed the origins of cosmetics, especially the use of red ochre, using the handicap principle. Neiman (1997) analyzed the construction of Mayan pyramids as costly, wasteful displays, and Frank (1999) did likewise in analyzing runaway American consumerism. Zahavi has also applied his handicap principle insightfully to human aesthetics (Zahavi, 1978; Zahavi & Zahavi, 1997).

### **Developmental stability and artefact regularity**

How can we apply fitness indicator theory to understand specific aesthetic tastes and artistic styles? This section develops a brief example. Many physical beauty cues advertise a component of fitness known as 'developmental stability', which may have some interesting analogs in the visual arts. Developmental stability refers to an individual's ability to grow organs in their optimal, species-typical form, despite the disruptive effects of genetic mutation

and environmental stressors (Gangestad & Thornhill, 1997). Body symmetry is one convenient way to measure developmental stability in the lab – and in the wild. Because perfect bodily symmetry is so hard to produce but so easy to assess perceptually, many visual ornaments in many species have evolved to show off their bilateral symmetry.

This fitness-indicating power of symmetry holds equally well for artefacts. The ability to produce an art-work that incorporates perfectly symmetric elements (bilaterally or radially) is a potent indicator of artistic skill (Gombrich, 1982; Kohn, 1999; Washburn, 1999). This may be why we find beautiful those ornamental art-works that incorporate symmetric motifs. More generally, the regular repetition of ornamental motifs across a decorated surface, without noticeable errors, functions as a potent indicator of artistic skill (Gombrich, 1982), and was respected as such in all cultures until the invention of mechanized production (Boas, 1955).

At a more abstract level, representational art follows the same indicator logic as body symmetry and ornamental regularity. Accurate visual representations of recognizable objects are very easy to assess (given our excellent visual memory), but very hard to produce (given the challenge of suppressing our depth perception circuitry to see with the ‘innocent eye’ required in painting). This may be why accurate representations have been considered aesthetically impressive in every human culture, at least until the invention of photography (Gombrich, 1977). Only since then have students been taught to suppress our natural tendency to equate artistic merit with representational accuracy.

### **Aesthetic judgement as a branch of social psychology**

The fitness indicator theory of aesthetics suggests that the perception of beauty in an art-work is normally just the first step in a chain of inference that reaches all the way into our mechanisms of social cognition and social attribution. Aesthetic judgement normally entails some attribution to the artist of intelligence, creativity, skill, maturity, imagination, conscientiousness, and agreeableness – or their opposites. These in turn are taken, unconsciously, as inputs into other social assessment systems, principally mate choice, but also systems for evaluating offspring, relatives, friends, allies, and individuals in other biologically significant social roles.

Perhaps the psychological study of aesthetics should be re-considered as a branch of social attribution research, rather than a branch of perceptual psychology. Our ability to judge beauty as a fitness indicator is part of our ‘social rationality’ (Gigerenzer & Todd, 1999), a set of inference heuristics for making biologically significant decisions about other individuals on the basis of observable behavioral cues. The question for empirical psychologists should not be whether such inferences are logically warranted (they rarely are), but whether they have some pragmatic utility, by virtue of relying on cues (such as fitness indicators) that have objective cue validity in Brunswik’s (1956) sense.

It makes sense to separate art-work from artist only in our modern urban societies, in which art-works are commodified, transported, preserved, traded, and mechanically reproduced through photography and printing. When we seek the evolutionary origins of art, we should remember that any art-work our prehistoric ancestors would have been able to see, would have probably been made by a living individual with whom they could have interacted socially or sexually. The artist was never far from his or her work, or else the work could not have functioned as the artist’s extended phenotype.

This is bad news for arm-chair aesthetic theorists. It means we should stop looking for formal determinants of beauty in art-works themselves, and start looking for correlations between (1) variation in the design details of art-works produced by representative samples of real people, (2) variation in the underlying fitness components (e.g. intelligence, personality, health) of those same people, and (3) variation in the beauty ratings assigned to those art-works by other people – preferably young, single, opposite-sex people in the same mating market (for other empirical predictions, see Houle, 2000; Miller, 2000a,c,d,e). In my view, Brunswikian



social psychology, not the formal mathematical analysis of exemplary art-works, is the royal road to understanding human aesthetic judgements.

### **Sexual selection, sex differences, and sexual motives**

Sexual selection often produces sex differences, but not always. In socially monogamous species such as humans and most birds, both sexes tends to be choosy, and both sexes evolve sexual ornamentation (Kirkpatrick, Price, & Arnold, 1990; Miller, 2000a). For this reason, a sexual selection theory of art evolution need not imply higher male art-production ability and higher female aesthetic-judgement ability. Although males have produced vastly more public art in agricultural and industrial societies (Miller, 1999a), the sexual dimorphism in art output among prehistoric hunter-gatherers may have been smaller. In any case, sexual selection is likely to have produced more dimorphism at the level of artistic motivation than at the level of artistic capacity, given the overlapping perceptual and cognitive abilities required to produce and to appreciate art (Miller, 2000a).

If art evolved through sexual selection to serve a courtship function, we are not likely to be consciously aware of that function. A peacock's tail need not know that it evolved for a sexual-attraction function, and neither do our brains. Contra Freud, a sexually-selected instinct for making aesthetically pleasing ornamentation need not have any connection with a sexually-selection desire to copulate, even at an 'unconscious' or 'subconscious' level. The proper biological function of art (which must concern survival or reproduction somehow) must not be confused with the proximate individual motivations for producing art (which may include making money, inspiring religious devotion, or challenging patriarchy). No part of the human nervous system needs to keep track of the fact that beautiful art-works often led to successful reproduction; evolution kept track for us.

### **Conclusion**

After a century of neglect and obscurity, Darwin's (1871) sexual selection theory has been revived, and its psychological and aesthetic dimensions are becoming better appreciated. This paper has argued that there is a reasonable null hypothesis about human art considered as a biological adaptation: It evolved through sexual selection to serve the same courtship functions as almost all other examples of organic beauty and complex behavioral signals observable in nature. Such ornamentation often evolves as a reliable, costly indicator of the signaller's good health, good brain, and good genes. This leads to the further proposal that many design features of art function as indicators of the artist's virtuosity, creativity, intelligence, conscientiousness, and other important heritable mental and physical traits. This 'aesthetic fitness' view suggests that aesthetic judgement is a natural part of mate choice and social cognition, in which an art-work is viewed as the extended phenotype of the artist.

## Appendix: 34 predictions of the aesthetic fitness indicator theory

[Note: this appendix could not be included in the published version of the paper, due to space limitations.]

The fitness indicator view of aesthetic judgement and artistic production is, like most real mid-level hypotheses in evolutionary psychology, eminently testable (see Ketelaar & Ellis, 1999). Indeed, one major advantage is that it can be tested using many of the same empirical methods that have already been used in animal communication research (see e.g. Andersson, 1994; Bradbury & Vehrencamp, 1998; Catchpole & Slater, 1995; Johnstone, 1995). The hypothesis that a behavioral trait has evolved through sexual selection as a fitness indicator leads to the 34 predictions below. They are generic to fitness indicators, but in the context of this paper on the visual arts, the 'trait' would be art production ability (presumably controlling for instruction and practice), and the 'mate choice criterion' would be aesthetic value-judgments about artistic merit. Not all 34 predictions need be supported for the hypothesis to hold true, but the more the better. For a fuller explanation of how these predications relate to the theory, see Miller (2000a,b,c,d).

1. phenotypic variance: the trait should vary significantly between individuals in the species. Without variance there is no way for mate choice to use the trait as an indicator
2. perceivability: variation in the trait should be perceivable, directly or indirectly, consciously or unconsciously, by the opposite sex, in a way that could potentially influence mate choice.
3. stability: individual variation in the trait should be at least somewhat stable across time and situations. If the trait value varied capriciously across time and situations, there would be no incentive for mate choice to use it as a criterion. For subjectively judged traits such as the aesthetic merit of an art-work, there should be decent test-retest reliability for any sexually relevant judge (e.g. any single, opposite-sex person in the same local mating market as the actual producer of the art-work), and decent inter-subjective agreement (positive correlation between ratings) between such judges
4. significant cost: the trait should incur a significant cost to produce, as measured in energy, time, risk, or nutritional resources. This positive cost prediction suggests that, holding an individual's fitness constant, there is a trade-off between the trait (such as art-production) and other survival and reproduction tasks. However, this trade-off can be very difficult to measure except experimentally, because in practice, inter-individual differences in overall fitness can swamp the intra-individual trade-offs between different fitness components (see Johnstone, 1995; Rowe & Houle, 1996; Houle, 2000). Thus, correlational studies will probably not reveal a negative correlation (trade-off) between art production and other fitness components such as longevity or fecundity, and are thus inappropriate ways of measuring costs.
5. the condition-dependent handicap condition: the relative marginal cost of producing the trait should be lower for higher-fitness individuals. This is the key technical condition of Zahavi's (1975) handicap principle, as interpreted by Grafen (1990). It could be tested with cognitive neuroscience methods, by showing that, holding constant the quality of art-work produced in a brain imaging study, higher-fitness individuals should burn less glucose in the brain areas devoted to art production than lower-fitness individuals -- glucose burn rate here being the index of the marginal cost of the cognitive activity.
6. experimental condition-dependence: if the behavioral trait evolved as an indicator of current phenotypic quality (i.e. good condition), then the trait should be highly sensitive to experimental increases or decreases in an individual's condition (see Jacobs, 1996). For example, food deprivation or experimentally induced hypoglycemia – both of which reduce the glucose available to the brain – should particularly impair sexually-selected trait quality (e.g. art-production ability) relative to behavioral traits that evolved under natural selection for survival.

7. positive correlation with fitness measures: variation in the trait should correlate with known components of fitness, such as health, longevity, fertility, fecundity, body size, body symmetry, social status, intelligence, low mutation load, and genetic outbreeding (for methodological examples, see Gangestad & Thornhill, 1997, Sluming & Manning, 2000). Note that assessing this correlation would require a broad, representative sample of individuals, not a restricted-range sample such as university students or professional artists
8. positive fitness-factor loading: more specifically, if phenotypic variation in many traits is measured from a broad, representative sample of people, and if all phenotype correlations between such traits are calculated and put into a correlation matrix, and if that correlation matrix is subject to hierarchical factor analysis, a top-level 'general fitness factor' should emerge (analogous to the *g* factor in psychometrics) – see Houle (2000) and Miller (2000). If this general fitness factor does emerge, then variation in the trait (e.g. artistic ability) should show a significant positive loading on that factor. This positive fitness-loading could be taken as the Brunswikian 'cue validity' of the trait as a fitness-indicator.
9. positive correlation with other preferred mental and personality traits: if the trait evolved as an indicator of neurological fitness, it should positively correlate with brain size, regularity of brain development, information-processing efficiency, general cognitive ability (see Jensen, 1998), and perhaps some of the 'Big Five' personality traits that are favored in mate choice, such as openness, agreeableness, conscientiousness, and low neuroticism.
10. social attribution based on trait value: if prediction 8 holds (i.e. the trait has some objective cue validity as an indicator of psychometric and personality traits), then mate choice systems should have evolved to make the appropriate social attributions on the basis of observed trait values. In the visual arts, this implies that art-works by socially relevant individuals (not necessarily strangers) should provoke attributions about the artist's intelligence, creativity, and character in opposite-sex observers. In cognitive neuroscience terms, aesthetic judgment tasks given these social conditions should activate cortical areas known to be involved in social attribution.
11. favored in mate choice: when choosing sexual partners, and all else being equal, individuals should prefer to mate with those who show high-quality forms of the trait, i.e. forms that correlate positively with other measures of fitness. This prediction does not imply that the trait under investigation should have a higher importance than other well-established mate choice criteria such as kindness, intelligence, physical attractiveness, or social status (see Buss, 1999) – only that it be taken into consideration, and that the preference should be in the 'right' (i.e. positively fitness-correlated) direction.
12. favored especially by ovulating females: traits that function as good-genes indicators, but that have high costs in other domains such as parenting, should be particularly favored by females during the ovulatory phase of the menstrual cycle (for choosing short-term extra-pair partners), and less favored at other times (when choosing good parents is more important). Applied to the visual arts, this prediction implies that women should become more aesthetically discerning during ovulation, more inclined to view art-works as manifestations of male talent, and perhaps more inclined to view art ability as genetically heritable.
13. increased offspring number: individuals with high trait values (especially males) should produce more offspring, at least in societies without contraception. Since many of these additional offspring may result from extra-pair copulations, they may be difficult to detect without doing DNA paternity tests on all offspring in a particular population.
14. assortative mating: in species with social monogamy such as ours, individuals should assortatively mate with respect to the trait, because the competitive mating market should ensure that high-fitness individuals prefer each other by virtue of the trait, leaving lower-fitness individuals no choice but to settle for each other (see Johnstone, 1997; Miller, 2000a; Sloman & Sloman, 1988).

15. higher rates of extra-pair copulation: individuals (especially males) with high trait values should be more likely to have extra-pair copulations (affairs) outside their primary relationships, due to their higher sexual attractiveness. For the evolutionary logic behind this, see Barash (2001) and Birkhead (2000).
16. lower rates of being cuckolded: The sexual partners of individuals (especially males) with high trait values should be less likely seek extra-pair copulations with other partners (see Barash, 2001; Birkhead, 2000).
17. mate-guarding: individuals in relationships should guard their mates from exposure to individuals with high trait values, to discourage extra-pair copulation with such individuals. Also, social interactions with individuals who have higher trait values on the putative fitness indicator (e.g. respected artists) should provoke more intense sexual jealousy in partners (see Buss, 2000).
18. derogation of trait quality in sexual competitors: if the trait is used and valued in courtship, same-sex rivals should selectively derogate each other with respect to trait quality (see Buss & Dedden, 1990). In the visual arts, this may entail impugning the skill or creativity manifest in artworks produced by potential rivals.
19. gossip about trait values: in social species such as ours, in which mate choice often includes collective decision-making involving family and friends, gossip about potential mates should focus some attention on the trait that is claimed to be a fitness indicator. High trait values should be recognized and praised.
20. alternative mating strategies: individuals low in trait quality should more often pursue alternative mating strategies that attempt to circumvent mate choice by the opposite sex, including increased use of sexual harassment and sexual coercion (see Thornhill & Palmer, 2000).
21. genetic correlation between trait and preference: if mate choice was shaping the trait over recent evolutionary history, we should expect to see a positive genetic correlation between trait quality and choosiness with respect to the trait (see Jennions & Petrie, 1997). This is because there is typically some genetic variation not only in sexually-selected traits, but also in sexual-selective preferences (Bakker & Pomiankowski, 1995). In the visual arts, this would imply positive phenotypic and genotypic correlations between art production ability, aesthetic discernment, and the relative importance attached to art ability in mate choice.
22. conspicuous courtship display: during courtship, individuals should conspicuously (if unconsciously) display the trait to the opposite sex. This could be measured across different time-scales, comparing courtship to non-courtship situations across minutes, hours, days, ovulation cycles, or seasons.
23. higher trait mean in males: assuming sexual selection operated more strongly on males, as it almost always does (Darwin, 1871; Andersson, 1994), sexual selection should have favored higher mean trait values in males. Note that for behavioral traits such as art production, this need not imply higher male cognitive abilities underlying the trait, only higher motivation to produce the behavior in social situations that could potentially attract mates.
24. higher trait variance in males: in species that evolved with some degree of polygyny and some frequency of extra-pair copulation, the higher male variance in reproductive success should favor a risk-seeking pattern of trait expression, such that male trait values show higher variance than female trait values (see Pomiankowski & Moller, 1995). That is, there should be more male artistic geniuses but also more talentless males who are hopeless at art.
25. young-adult peak in trait expression: for sexually selected behavioral traits, trait expression should peak in young adulthood, at the peak of mating effort. It should be low before puberty, should increase rapidly thereafter, and should decline gradually as individuals shift their time and energy from courtship to parenting. This demographic profile appears to hold true for several genres of painting (Miller, 1999a).

26. strategic investment in trait based on self-assessed talent: in species such as humans that have several different kinds of behavioral courtship displays (e.g. language, art, music, ideology), there are different sexual/status niches (Barkow, 1989). Juveniles should assess their relative talent in each behavioral domain and invest time and effort in building skills preferentially in their highest-talent areas. This specialization in distinct status niches should be more intense among males than females, further amplifying male variance in the trait value, and reducing phenotypic correlations in skill across behavioral domains, despite the genotypic correlations in capacity that may exist.
27. positive heritability: if the trait is an indicator of good genes, it should prove genetically heritable in twin and adoption studies, or using other behavior-genetic methods
28. increased heritability after puberty: if the trait is costly and evolved under sexual selection, the genes underlying the trait should become more expressed only after sexual maturity, perhaps in response to sex hormones. This should lead to higher trait heritability in adults than in children, as has been found with general cognitive ability (Plomin et al., 2000).
29. genetic correlation with fitness: if the trait is an indicator of good genes, then it should not only correlate phenotypically with the general fitness factor (prediction 8 above); it should also show positive genetic correlation with that factor (see Houle, 1992, 2000).
30. high CVa: if the trait is an indicator of good genes, it should also fulfil the more technical condition of showing a high coefficient of additive genetic variance, denoted CVa by evolutionary geneticists (see Pomiankowski & Moller, 1995; Rowe & Houle, 1996). Note that measurement of this coefficient in the domain of visual arts would require development of a true ratio scale for artistic ability.
31. genetic inbreeding should reduce trait quality: if the trait is a good-genes indicator, the offspring of sibling or cousin marriages should show reduced trait values, due to the expression of deleterious homozygous mutations.
32. large mutational target size: if the trait evolved as a good-genes indicator, it should depend on a large number of genes, and thereby summarize a lot of information about individual's mutation load, since more genes give a larger sample size of possible mutation sites (Rowe & Houle, 1996). Molecular genetic investigation of the trait should reveal that a large number of quantitative trait loci (QTLs) affect the trait, rather than a small number of Mendelian genes.
33. heterogeneity in QTLs across groups: if the trait is a good-genes indicator that has been subject to mate choice in recent evolutionary history, then any deleterious mutations that impair trait quality should be removed fairly quickly by sexual selection. They should therefore have a short evolutionary half-life, and be restricted to local populations. This should lead to between-group heterogeneity in the quantitative trait loci (QTLs) underlying genetic variance in the trait. That is, the genetic loci that create heritable variation in the trait in one family or ethnic group should often be different from those that create heritable variance in other families and ethnic groups (for an introduction to quantitative genetics, see Lynch & Walsh, 1998).
34. offspring viability: if the trait is a good-genes indicator, individuals with higher trait values should produce healthier, higher-fitness offspring (e.g. see Hasselquist, Bensch, & von Schantz, 1996).

## References

- Atmar, W. (1991). On the role of males. Animal Behavior, *41*, 195-205.
- Boas, F. (1955). Primitive art. New York: Dover.
- Borgia, G. (1986). Sexual selection in bowerbirds. Scientific American, *254*(6), 92-100.
- Borgia, G. (1995.) Complex male display and female choice in the spotted bowerbird: specialized functions for different bower decorations. Animal Behavior, *49*, 1291-1301.
- Borgia, G. (1997). Comparative behavioural and biochemical studies of bowerbirds and the evolution of bower-building. In M. L. Reaka-Kudla, D. E. Wilson, & E. O. Wilson (Eds.), Biodiversity II (pp. 263-276). Washington, D.C.: Joseph Henry Press.
- Bradbury, J. W., & Vehrencamp, S. L. (1998). Principles of animal communication. Sunderland, MA: Sinauer.
- Brunswik, E. (1956). Perception and the representative design of psychology experiments. Berkeley, CA: U. California Press.
- Buss, D. M. (1999). Evolutionary psychology: The new science of mind. New York: Allyn & Bacon.
- Catchpole, C. K., & Slater, P. J. B. (1995). Bird song: Biological themes and variations. Cambridge, UK: Cambridge U. Press.
- Constable, J. (1997). Verse form: A pilot study in the epidemiology of representations. Human Nature, *8*, 171-203.
- Cronin, H. (1991). The ant and the peacock: Altruism and sexual selection from Darwin to today. Cambridge, UK: Cambridge U. Press.
- Crow, J. F. (1999). The odds of losing at genetic roulette. Nature, *397*, 293-294.
- Darwin, C. (1871). The descent of man, and selection in relation to sex (2 vols.). London: John Murray. (Reprinted in 1981 by Princeton U. Press.)
- Dawkins, R. (1982). The extended phenotype: The gene as the unit of selection. Oxford, U.K.: W. H. Freeman.
- Dissanayake, E. (1992). Homo Aestheticus: Where art comes from and why. New York: The Free Press.
- Etcoff, N. (1999). Survival of the prettiest: The science of beauty. New York: Doubleday.
- Eyre-Walker, A., & Keightley, P. D. (1999). High genomic deleterious mutation rates in hominids. Nature, *397*, 344-346.
- Frank, R. (1999). Luxury fever: Why money fails to satisfy in an era of excess. New York: Free Press.
- Gangestad, S. W., and Thornhill, R. (1997). Human sexual selection and developmental stability. In J. A. Simpson and D. T. Kenrick (Eds.), Evolutionary social psychology (pp. 169-195). Mahwah, NJ: Erlbaum.
- Gigerenzer, G., & Todd, P. M. (Eds.). (1999). Simple heuristics that make us smart. Cambridge, MA: MIT Press.
- Gombrich, E. H. (1977). Art and illusion: A study in the psychology of pictorial representation (5<sup>th</sup> ed.). London: Phaidon Press.
- Gombrich, E. H. (1979). A sense of order: A study in the psychology of decorative art. Ithaca, NY: Cornell U. Press.
- Grafen, A. (1990). Biological signals as handicaps. J. Theoretical Biology, *144*, 517-546.
- Grosse, E. (1897). The beginnings of art. New York [no publisher indicated].
- Hasselquist, D., Bensch, S., & von Schantz, T. (1996). Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. Nature, *381*, 229-232.
- Hasson, O. (1990). The role of amplifiers in sexual selection: An integration of the amplifying and Fisherian mechanisms. Evolutionary Ecology, *4*, 277-289.

- Houle, D. (2000). Is there a g factor for fitness? In G. Bock, J. A. Goode, & K. Webb (Eds.), The nature of intelligence, Novartis Foundation Symposium 233 (pp. 149-170). Chichester, UK: John Wiley.
- Johnstone, R. A. (1995). Sexual selection, honest advertisement and the handicap principle. Biological Review, *70*, 1-65.
- Kirkpatrick, M., Price, T., & Arnold, S. J. (1990). The Darwin-Fisher theory of sexual selection in monogamous birds. Evolution, *44*(1), 180-193.
- Kohn, M. (1999). As we know it: Coming to terms with an evolved mind. London: Granta.
- Kondrashov, A. (1995). Contamination of the genomes by very slightly deleterious mutations: Why have we not died 100 times over? J. Theoretical Biology, *175*, 583-594.
- Lenain, T. (1995). Ape-painting and the problem of the origin of art. Human Evolution, *10*, 205-215.
- Lenz, N. (1994). Mating behaviour and sexual competition in the regent bowerbird *Sericulus chrysocephalus*. Emu, *94*, 263-272.
- Lynch, M., & Walsh, B. (1998). Genetics and analysis of quantitative traits. Sunderland, MA: Sinauer.
- Madden, J. (2001). Sex, bowers and brains. Proc. R. Soc. London B, *268*, 833-838.
- Manning, J. T., Scutt, D., Whitehouse, G. H., & Leinster, S. J. (1997). Breast asymmetry and phenotypic quality in women. Evolution and Human Behavior, *18*, 1-13.
- Michod, R. E., & Hasson, O. (1990). On the evolution of reliable indicators of fitness. American Naturalist, *135*, 788-808.
- Miller, G. F. (1997a). Protean primates: The evolution of adaptive unpredictability in competition and courtship. In A. Whiten & R. W. Byrne (Eds.), Machiavellian Intelligence II: Extensions and evaluations (pp. 312-340). Cambridge, UK: Cambridge U. Press.
- Miller, G. F. (1997b). Mate choice: From sexual cues to cognitive adaptations. In G. Cardew (Ed.), Characterizing human psychological adaptations, Ciba Foundation Symposium 208 (pp. 71-87). Chichester, UK: John Wiley.
- Miller, G. F., & Todd, P. M. (1998a). Mate choice turns cognitive. Trends in Cognitive Sciences, *2*, 190-198.
- Miller, G. F. (1998b). How mate choice shaped human nature: A review of sexual selection and human evolution. In C. Crawford & D. Krebs (Eds.), Handbook of evolutionary psychology: Ideas, issues, and applications (pp. 87-129). Mahwah, NJ: Lawrence Erlbaum.
- Miller, G. F. (1999). Sexual selection for cultural displays. In R. Dunbar, C. Knight, & C. Power (Eds.), The evolution of culture (pp. 71-91). Edinburgh, UK: Edinburgh U. Press.
- Miller, G. F. (2000a). The mating mind: How sexual choice shaped the evolution of human nature. New York: Doubleday.
- Miller, G. F. (2000b). Evolution of human music through sexual selection. In N. L. Wallin, B. Merker, & S. Brown (Eds.), The origins of music (pp. 329-360). Cambridge, MA: MIT Press.
- Miller, G. F. (2000c). Mental traits as fitness indicators: Expanding evolutionary psychology's adaptationism. In D. LeCroy & P. Moller (Eds.), Evolutionary perspectives on human reproductive behavior, Annals of the New York Academy of Sciences, Volume 907 (pp. 62-74). New York: New York Academy of Sciences.
- Miller, G. F. (2000d). How to keep our meta-theories adaptive: Beyond Cosmides, Tooby, and Lakatos. Psychological Inquiry, *11*, 42-46.
- Miller, G. F. (2000e). Sexual selection for indicators of intelligence. In G. Bock, J. A. Goode, & K. Webb (Eds.), The nature of intelligence. Novartis Foundation Symposium 233 (pp. 260-275). Chichester, UK: John Wiley.
- Neiman, F. D. (1997). Conspicuous consumption as wasteful advertising: A Darwinian perspective on spatial patterns in classic Maya terminal monument dates. In G. A. Clark

- & C. M. (Eds.), Rediscovering Darwin: Evolutionary Theory in Archaeological Explanation. Archaeological Papers of the American Anthropological Association, No. 7, pp. 267-290.
- Nietzsche, F. (1883-1888/1968). The will to power. New York: Vintage. (Trans. W. Kaufmann & R. J. Hollingdale from Nietzsche's notebooks 1883-1888).
- Petrie, M. (1994). Improved growth and survival of offspring of peacocks with more elaborate trains. Nature, *371*, 598-599.
- Pomiankowski, A., & Moller, A. (1995). A resolution of the lek paradox. Proc. R. Soc. London B, *260*, 21-29.
- Power, C. (1999). 'Beauty' magic: The origins of art. In R. Dunbar, C. Knight, & C. Power (Eds.), The evolution of culture (pp.92-112). Edinburgh, UK: Edinburgh U. Press.
- Ridley, Matt. (1993). The red queen: Sex and the evolution of human nature. New York: Viking.
- Ridley, Mark (2000). Mendel's demon: Gene justice and the complexity of life. London: Weidenfeld & Nicholson.
- Rowe, L., & Houle, D. (1996) The lek paradox and the capture of genetic variance by condition dependent traits. Proc. R. Soc. London B, *263*, 1415-1421.
- Singh, D. (1995). Female health, attractiveness, and desirability for relationships: Role of breast asymmetry and waist-to-hip ratio. Ethology and Sociobiology, *16*, 465-481.
- Thornhill, R. (1998). Darwinian aesthetics. In C. Crawford & D. Krebs (Eds.), Handbook of evolutionary psychology (pp. 543-572). Mahwah, NJ: Erlbaum.
- Thornhill, R., & Grammer, K. (1999). The body and face of woman: One ornament that signals quality? Evolution and Human Behavior, *20*, 105-120.
- Tooby, J., & Cosmides, L. (1990). The past explains the present: Emotional adaptations and the structure of ancestral environments. Ethology and sociobiology, *11*, 375-424.
- Turner, F. (1991). Beauty: The value of values. Charlottesville, VA: U. Virginia Press.
- Uy, J. A. C., & Borgia, G. (2000). Sexual selection drives rapid divergence in bowerbird display traits. Evolution, *54*, 273-278.
- Veblen, T. (1899). The theory of the leisure class. New York: Macmillan.
- Washburn, D. (1999). Perceptual anthropology: The cultural salience of symmetry. American Anthropologist, *101*, 547-562.
- Whiten, A. (1976). Primate perception and aesthetics. In D. Brothwell (Ed.), Beyond Aesthetics: Investigations into the Nature of Visual Art (pp. 18-40). London: Thames and Hudson.
- Zahavi, A. (1975). Mate selection: A selection for a handicap. J. Theoretical Biology, *53*, 205-214.
- Zahavi, A. (1978). Decorative patterns and the evolution of art. New Scientist, *19*, 182-184.
- Zahavi, A., & Zahavi, A. (1997). The handicap principle: A missing piece of Darwin's puzzle. Oxford, UK: Oxford U. Press.

### Author Notes

This work was supported in part by a Leverhulme Trust grant to Lord Michael Young of the Institute of Community Studies, London.