

Evolution of Life-History Trade-Offs in Mate Attractiveness and Health: Comment on Weeden and Sabini (2005)

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J. Weeden and J. Sabini's (2005) finding of small to no relation between traits rated as attractive in a mate and health of that mate might be interpreted as consistent with C. Darwin's (1859) proposal that these traits are arbitrary signs of beauty. However, such a conclusion would be premature. A combination of consistent empirical findings with nonhuman species and theoretical reasons argues for a continued search for honest signals of genetic fitness and reproductive health in human mate choices. Moreover, (a) even quite small relationships can be important when viewed across generations, and (b) traits that make a potential mate attractive at one age can result in poor health or early death at a later age. These life-history trade-offs greatly complicate the empirical study of attractiveness–health relations, and their potential importance has been underestimated by J. Weeden and J. Sabini.

Keywords: life history, health, attractiveness, trade-offs

Weeden and Sabini (2005) have provided a useful review of (a) physical attractiveness as judged by members of the opposite sex and (b) the relationship between judged attractiveness and a variety of health outcomes. These relationships are of theoretical importance because they are informative about the potential influence of mate choice and reproductive competition—sexual selection—on the evolution of related traits. Weeden and Sabini's review addresses issues specifically associated with choice of mates, which for most species involves female choice. Darwin (1859) proposed that associated male traits, such as a colorful plumage, are displays of “beauty to charm the females” (p. 199) and do not necessarily signal male health. Wallace (1892), in contrast, argued that female choice was more strongly influenced by the “bodily vigor” (p. 750) of the male than by his physical beauty.

Despite these intriguing and testable hypotheses regarding the function of traits that influence mate choices, the study of sexual selection lay dormant for 100 years after publication of Darwin's (1871) masterwork on the topic. In recent decades, these hypotheses have recaptured the attention of the scientific community (Andersson, 1994; Trivers, 1972), and corresponding research has revealed that mate choice is more nuanced than implied by either Darwin's (1859) or Wallace's (1892) proposals. In the following sections, I illustrate a few of these nuances as they relate to the results of Weeden and Sabini's (2005) review. In the first section,

I overview the importance of honest signals as related to mate choice and provide a context for interpreting the magnitude of any attractiveness–health relations. In the second section, I focus on trade-offs between the development of attractive traits at one age and potential health costs at a later age.

Evolution of Honest Signals

I start with discussion of why many traits rated as attractive are likely to evolve as “honest” signals of a mates' genetic health or reproductive behavior. In the second section, I place the strength of these relations in an evolutionary context.

Good Genes and Honest Signals

Although the issues continue to be studied, in nonhuman species many traits associated with female and male choice of mating partners are honest signals of a potential mate's physical, reproductive, or genetic health (Amundsen, 2000; Andersson, 1994; Roulin, Jungi, Pfister, & Dijkstra, 2000). As described below (see Evolution of Health-Related Trade-Offs section), one mechanism that may influence the expression of honest signals and link them to health is the interplay between sex hormones and various components of the immune response, although these relations are complex and not yet fully understood (Buchanan, 2000). It is also likely that a relation between hormones, immune responses, and sexually selected traits will be not fully expressed and thus not easily detected in populations that are not under stress, and this applies to most of the samples assessed in Weeden and Sabini's (2005) review, as they acknowledged. For this reason, as well as the overall pattern of findings with nonhuman species, the search for mate-choice indicators of physical and genetic health in humans should not be abandoned, despite the largely mixed or null results reported by Weeden and Sabini.

For the study of nonhuman species, one assumption underlying much of the contemporary work is that mate choice is guided by reliable signals of a potential mate's physical health, behavioral

Editor's Note. The authors of the target article for this comment, “Physical Attractiveness and Health in Western Societies: A Review” (Weeden & Sabini, 2005), were given an opportunity to react to this commentary but chose not to.—HC

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competence, or genetic superiority (e.g., Hamilton & Zuk, 1982). The concept is broadened with Zahavi's (1975) proposal that many sexually selected traits are a handicap in the sense that the development and maintenance of these traits come at some cost to the individual. Selection would favor the evolution of any such handicap because only superior mates could incur such costs, or stated differently, inferior mates would not be capable of deception by faking good health, for instance. Handicaps are thus called *honest* signals of the mates' genetic and phenotypic condition.

As an example, the plumage coloration and other sexually selected traits of the males of many bird species sometimes vary directly with degree of parasite infestation, with infected males sporting duller displays than their healthier counterparts. Zuk, Thornhill, and Ligon (1990) infected a group of male red jungle fowl chicks (*Gallus gallus*) with a parasitic worm (*Ascaridia galli*) and compared their growth and later success in attracting mates with a group of unaffected males. Affected males grew more slowly than their healthy peers, and in adulthood, their sexually selected characteristics were more adversely affected by the parasitic worm than were other physical characteristics. The comb on males is one such sexually selected trait, and the comb of affected males was smaller and duller than that of unaffected males. Many other physical characteristics, such as ankle length, did not differ across these groups. A mate-choice experiment demonstrated that unaffected males were preferred 2 to 1 relative to their affected cohorts and that female choice of mates was related to sexually selected traits but not to other traits.

One mechanism relating these signals and male fitness is the potential for testosterone to suppress immune functions and vice versa (Folstad & Karter, 1992; Hamilton & Zuk, 1982). Infestation with parasites leads to an increase in immune system activity, which, in turn, can suppress the secretion of testosterone. The resulting decline in testosterone levels then results in poorly developed secondary sexual characteristics. Moreover, increases in testosterone levels, as are necessary for the development of secondary sexual characteristics in males, can suppress the effectiveness of the immune system, which then increases risk of disease. Experimental and field studies indicate high testosterone levels only selectively increase risk of infestation by parasites (e.g., Saino, Møller, & Bolzern, 1995; Zuk, Johnsen, & Maclarty, 1995), as predicted by Zahavi (1975) and good-genes models. Specifically, immunosuppression is more evident in low-quality than in high-quality males, as would be expected if secondary sexual characteristics are condition-dependent indicators of male quality and the focus of female choice of mating partners.

The results of field and experimental research on nonhuman species are by no means always consistent with predictions of the good-genes model (Weatherhead, Dufour, Lougheed, & Eckert, 1999), and the relation between female hormones and the development of traits that influence male choice remains to be fully explored. Nonetheless, the balance of empirical results and the understanding of potential hormonal mechanisms make this a more viable area of work on human attractiveness and health than some readers might infer from Weeden and Sabini's (2005) review, despite their careful acknowledgments of the limits of the review.

Selection Coefficients

Although most of the predicted attraction–health relations reviewed by Weeden and Sabini (2005) were not confirmed or the results were mixed, two consistent findings did emerge. Waist-to-hip ratio and body mass index influence men's ratings of women's attractiveness, and these two traits are predictive of women's health. The global attractiveness of women's faces as rated by men is also related to health outcomes, but the magnitudes of all of these relations are small. As a result, Weeden and Sabini suggested the importance of any attractiveness–health relations may be overstated. However, when viewed from the lens of evolution, small relations can be very important, because these effects can multiply across generations.

In recent decades, field biologists have been explicitly studying the relation between heritable variation in many potentially adaptive traits and the correlation between individual differences in these traits and survival and reproductive outcomes. Mousseau and Roff (1987) conducted a comprehensive review of the heritable variability of the morphological (e.g., body size), behavioral (e.g., mating display), physiological (e.g., cardiovascular capacity), and life-history (e.g., age of maturation) traits that covary with survival and reproductive outcomes in wild animal populations. The analysis included 1,120 heritability estimates across 75 species. Although the magnitude of the heritability estimates varied across species, contexts, and phenotypes, their analysis indicated that “significant genetic variance is maintained within most natural populations, even for traits closely affiliated with fitness” (Mousseau & Roff, 1987, p. 188). The median heritability estimates were .26 for life-history traits, .27 for physiological traits, .32 for behavioral traits, and .53 for morphological traits.

Kingsolver and colleagues (2001) recently reviewed field studies of the relation between the types of traits analyzed by Mousseau and Roff (1987) and survival and reproductive outcomes in wild populations. Across species and traits, the median effect size indicated that being one standard deviation above (e.g., late maturation) or below (e.g., early maturation) the mean was associated with a 16% increase in survival (e.g., surviving to next breeding season) or reproductive (e.g., number of offspring) fitness. If the heritability of any such trait was only .25, “then selection of this magnitude would cause the trait to change by one standard deviation in only 25 generations” (Conner, 2001, p. 216). In terms of absolute magnitude these are small effects, but in terms of evolutionary significance the effects can be quite important.

The potential importance of these small effects can be illustrated with Weeden and Sabini's (2005) finding that the weighted correlation between women's rated facial attractiveness and various health outcomes was .15 (their Table 2). A correlation of this magnitude represents a standardized effect size of 0.30. Mealey, Bridgstock, and Townsend (1999) found an intraclass correlation of .74 for rated facial attractiveness across monozygotic twin pairs, which provides an upper bound for heritability of the combination of cues that contribute to facial attractiveness. If one makes a conservative assumption that two thirds of the similarity between the twins is due to shared environment, then the heritability for global facial attractiveness would be .24. The mechanisms relating heritable variation in facial attractiveness and heritable variation in health outcomes are not well understood, and thus no estimates of the strength of the genetic correlation can be made at this time. For

the sake of illustration, I will assume this correlation is small. If the genetic correlation is equivalent to an effect size of 0.30 or a correlation of .15, then using the same assumptions (i.e., the same pattern across generations) as Conner (2001), women with high rated facial attractiveness would achieve a one-standard-deviation advantage in health relative to women of average rated attractiveness in 45 generations. If the correlation between attractiveness and health is .20 then the effect would occur in 35 generations. These values are only for the purpose of illustrating the point that even seemingly small advantages can represent important relations from an evolutionary perspective.

Evolution of Health-Related Trade-Offs

Weeden and Sabini (2005) acknowledged that life-history trade-offs may confound assessment of relations among mate choice, attractiveness, and health, but the importance of these trade-offs was understated. Physiological processes, growth rate, behavioral biases, and other traits that result in improved survival or reproductive prospects at one point in the life span may have more deleterious affects at a later point in the life span (G. C. Williams, 1957). As an example, testosterone contributes to sex differences in growth rate, cardiac morphology and capacity, muscularity, skeleton strength, and many other traits (Stauffer & Leinwand, 2004; Tanner, 1990). Some of these traits, such as muscularity, were noted by Weeden and Sabini as contributing to women's ratings of men's attractiveness, and there are likely to be related traits, such as physical endurance, that were not assessed but may also contribute to rated attractiveness. Muscularity, cardiac capacity, and so forth, develop rapidly during puberty and peak during early adulthood in men (Fletcher et al., 1995; Tanner, 1990). This is the same point in the life span when physical male-male competition for social dominance, resource control, and ability to attract mates is at its peak (Geary, 1998; Wilson & Daly, 1985). In many traditional societies today (Chagnon, 1988) and almost certainly throughout human evolution (Keeley, 1996; Zerjal et al., 2003) the outcome of this competition and women's mate choices has had evolutionary consequences.

These hormonally influenced advantages of certain men's physical traits, as well as correlated behaviors (e.g., risk taking), during early adulthood appear to contribute to a variety of health risks later in life, including increased risk for hypertension and renal disease (Reckelhoff, Fortepiani, Yanes, & Cucchiarelli, 2004), certain forms of heart disease (Stauffer & Leinwand, 2004), and a significantly increased risk of premature death resulting from these conditions (e.g., Adams et al., 1999). The human pattern of earlier mortality for males than females (Arias, 2004) is the same pattern evident in other species in which reproductive competition is more intense among males than females (Allman, Rosin, Kumar, & Hasenstaub, 1998) and is almost certainly a reflection of evolved life-history and reproductive trade-offs. In short, many traits that facilitate evolved forms of male-male competition and are related to female choice may be honest signals during early adulthood but may be unrelated or inversely related to health later in life.

These trade-offs complicate any analysis of the relation between attractiveness and health, and they may explain some of the mixed findings found by Weeden and Sabini (2005). As they noted, there is a tendency for male body type to be associated with risk of heart disease. Men who show a combination of higher than average

levels of body fat (endomorphism) around the midsection and chest and higher than average levels of lean muscle mass (mesomorphism) have increased risk of heart disease, especially before the age of 50 (Damon, Damon, Harpending, & Kannel, 1969; Malina, Katzmarzyk, Song, Theriault, & Bouchard, 1997). Aspects of this common male pattern of muscle and fat distribution are influenced by sex hormones, including testosterone (Mayes & Watson, 2004; Tanner, 1990), and contribute to men's attractiveness. Young women rate young men who are moderately mesomorphic and have a larger chest than waist as physically attractive (Beck, Ward-Hull, & McLear, 1976; Maisey, Vale, Cornelissen, & Tovee, 1999), but men with this body type are more likely than other men to accumulate upper body fat as they age (S. R. P. Williams et al., 2000). The combination of mesomorphism and upper body fat is associated with increased risk for heart disease in middle age and later in life. Damon et al. (1969), for instance, found that chest depth—a trait that young women find attractive in young men—was positively correlated with risk of heart disease in middle age.

The patterns are consistent with G. C. Williams's (1957) prediction of life-history trade-offs whereby traits that confer advantage in reproductive competition early in life come at a cost of increased risk of later morbidity and early mortality. These trade-offs contribute to the maintenance of heritable variation in sexually selected traits and will keep small the magnitude of the relation between these traits and health and other survival or reproductive outcomes. These trade-offs combined with Weeden and Sabini's (2005) mixing studies that assessed men's attractiveness in early adulthood (largely college samples) with studies that often assessed correlations between these traits and health later in life make their mixed findings for the relations among men's physical attractiveness and health very difficult to interpret. Potential relations between attractiveness and men's health may in fact not be assessable given current data. This is because life-history trade-offs may vary within men; some men are likely to pay a high long-term price for an early competitive advantage. In theory, men with "good genes" are those who not only have the physical traits that women find attractive and that facilitated reproductive competition during human evolution but who also do not pay as heavy a long-term cost as other men. The question is: Are there physical or other markers early in adulthood that distinguish men who will remain healthy from men who will ultimately pay a high price for early competitiveness, and are women sensitive to the likely subtle differences between these men when the men are young adults?

Conclusion

Weeden and Sabini (2005) have provided an important and very useful review of the relation between traits that influence human mate choices and the relation between these traits and a potential mate's health. These are issues that have been debated and ignored in cycles over the past 150 years but have once again captured the attention of life scientists. With the exception of the finding that women's health is predicted by a few traits that influence male choice, such as global facial attractiveness and body mass index, Weeden and Sabini largely reported null or mixed results. The overall pattern fits Darwin's (1859) predictions that many traits associated with the evolution of "beauty" are arbitrary. In any event, relations between beauty and health are likely to be subtle and difficult to study, and thus null or mixed results for humans are

not too surprising at this point in time. Trade-offs between reproductive competitiveness at one age and risks to health at a later age (G. C. Williams, 1957) will keep the magnitude of attractiveness and health relationships small and sometimes hard to detect. However, life-history trade-offs combined with research on mate choices and health in nonhuman species make this area a much more attractive, so to speak, endeavor for the study of human health and mate choices than some readers may assume on the basis of Weeden and Sabini's review. Life-history trade-offs and potential handicaps in the expression of attractive traits in particular make the issues more subtle than can be assessed given much of the current data but at the same time provide a solid theoretical foundation for guiding future work with humans.

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