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REPORT

Fisherian and "good genes" benefits of mate choice: how (not) to distinguish between them

Hanna Kokko
Division of Environmental and Evolutionary Biology, Institute of Biomedical & Life Sciences, University of Glasgow, Glasgow G12 8QQ, U.K.
E-mail: h.kokko@bio.gla.ac.uk

Abstract

"Good genes" models of mate choice are commonly tested by examining whether attractive males sire offspring with improved survival. If offspring do not survive better (or indeed survive less well), but instead inherit the attractiveness of their father, results are typically interpreted to support the Fisherian process, which allows the evolution of preferences for arbitrary traits. Here, I show that the above view is mistaken. Because of life-history trade-offs, an attractive male may perform less well in other components of fitness. A female obtains a "good genes" benefit whenever males show heritable variation in quality, even if high-quality males invest so much in sexual advertisement that attractiveness has no positive correlation with any other life-history trait than male mating success itself. Therefore, a negative correlation between attractiveness and viability does not falsify good genes, if mating with a high-quality male results on average in superior offspring performance (mating success of sons included). The heritable "good genes" benefit can be sustained even if sexually antagonistic genes cause female offspring sired by high-quality males to survive and reproduce less well. Neglecting the component of male mating success from measurements of fitness returns from sons and daughters will bias the advantage of mating with a high-quality male downwards. This result may partly account for the rather weak "good genes" effects found in a recent meta-analysis.

Keywords

Fisher process, good genes process, mate choice, sexual selection.

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INTRODUCTION

One of the most fundamental problems of sexual selection is whether Fisher's process (Fisher 1930) sufficiently explains the evolution of extravagant sexual ornaments, or whether these signal high genetic quality of the bearer (e.g. Andersson 1994; Møller 1994; Höglund & Alatalo 1995). The latter, "good genes" model, is often rephrased as the "viability indicator model" (Andersson 1994), reflecting a presumed correlation between genetic quality and viability. It is hence widely assumed that the "good genes" model is falsified if mating with attractive males does not lead to improvements in offspring survival. Studies of sandflies *Lutzomyia longipalpis* (Jones *et al.* 1998) and guppies *Poecilia reticulata* (Brooks 2000) offer recent examples of such interpretations. For example, Brooks (2000) reports a negative genetic correlation between male survival and attractiveness in guppies, where attractiveness is measured in a mate choice experiment. Also, attractive males sire male offspring that suffer from high mortality yet are themselves more attractive. He concludes that "this result contradicts the predictions of indicator models [...] Only the most extreme handicap versions of indicator models could be consistent with this result, and only then if a positive genetic correlation between attractiveness and another fitness component negates the viability costs of attractiveness." Since no significant positive correlation was found between male attractiveness and female survival or fecundity, the evidence was interpreted to favour a Fisherian model of mate preferences (Brooks 2000).

Likewise, a recent meta-analysis seeks to measure the magnitude of a "good genes" effect by looking for improved offspring survival (Møller & Alatalo 1999). These authors state that "good genes" effects may be expressed as enhanced growth, fecundity or survival of offspring, but focus their analysis on survival as most published studies have concentrated on this trait, and because longevity is the major predictor of life-time reproductive success in many organisms (Clutton-Brock

1988; Newton 1989). Møller & Alatalo (1999) conclude that "good genes" benefits are present in many taxa, but in many cases the effect is small and results are possibly subject to publication bias.

Here, I will show that our focus on survival can seriously bias our interpretation of "good genes" benefits. Grafen's (1990) seminal paper proved that handicaps can work in the context of advertising individual quality. He makes the point that the handicap principle does not predict that high-quality males have higher net survival– the relationship between quality and net viability can be either positive or negative (Grafen 1990, p. 484; see also Getty 1998; Eshel *et al.* 2000). Below, I examine the consequences of this result in more detail.

What is the central prediction?

Fisher (1930; see also Lande 1981; Kirkpatrick 1982; Pomiankowski *et al.* 1991; Pomiankowski & Iwasa 1998) envisaged a self-sustaining process, whereby genes for a female preference for a male trait and genes for the trait itself become genetically correlated. The trait becomes exaggerated, until additive genetic variance for the trait is exhausted, or until costs of further exaggeration balance the mating benefit of possessing a trait more extreme than average (cyclic solutions are also possible; see Iwasa & Pomiankowski 1995; Pomiankowski & Iwasa 1998). Thus, if the Fisherian sexual selection has reached equilibrium, there is either no variation in the trait or the benefit of attractiveness is balanced through a viability cost of the ornament. This cost can be sketched as a trade-off between survival and mating success (Fig. 1a). Verbally, the "good genes" model appears to make the opposite prediction: high-quality individuals signal that they are able to survive despite their handicap (Zahavi 1975, 1977). While the logic of the argument was shown to be correct by Grafen (1990), the interpretation that net survival always remains higher in high-quality males is a verbal conjecture of the model that does not hold true mathematically (Grafen 1990).

The reason for this is that sexual advertisement is a life-history trait, subject to trade-offs with other traits. It is indeed increasingly recognized that life-history theory is essential for our understanding of sexual selection (e.g. Clutton-Brock *et al.* 1985; Partridge & Endler 1987; Møller 1989a, b; Schluter *et al.* 1991; Kokko 1997; Qvarnström 1997; Höglund & Sheldon 1998; Candolin 1999; Kokko *et al.* 1999b; Griffith 2000). In the current context, this is important since it pays for a female to mate with a male with "good genes" whenever males vary in genetic quality and quality is reflected in heritable fitness, even if there are negative correlations between life-history traits (Fig. 1b, c; see Kokko 1997, 1998). It is essential to realize that the "good genes" benefit may manifest itself in any life-history trait, including the mating success of male offspring (Eshel *et al.* 2000).

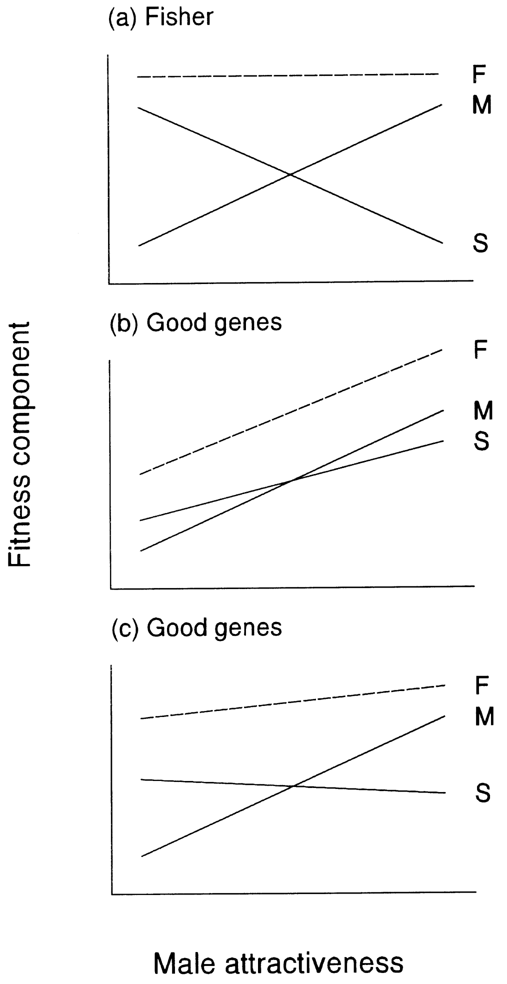

Figure 1 (a) At equilibrium, the Fisher process predicts that the mating benefit of attractiveness (M) is balanced by reduced survival (S), and the lifetime fitness (F) does not vary according to attractiveness. (b, c) The "good genes" process requires the maintenance of heritable variation in quality, so that attractive males are more fit. This is possible either with (b) positive or (c) negative correlations between attractiveness and survival.

Therefore, whilst positive correlations between attractiveness and other life-history traits provide evidence for "good genes" (Møller & Alatalo 1999), negative correlations are not sufficient evidence to the contrary. The crucial test between the "Fisherian" and "good genes" process is whether the *total* expected fitness returns from mating with an attractive male exceed the returns from an unattractive male. "Good genes" predictions are falsified only if they do not do so (as in Fig. 1a).

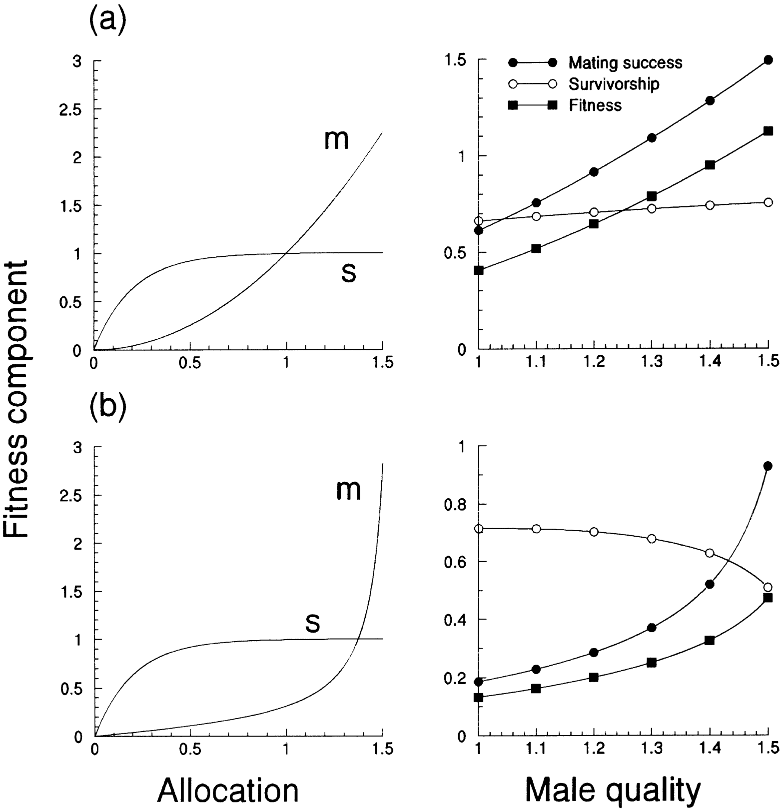

Figure 2 A numerical example where quality of males, q, varies from 1 to 1.5, and males invest a fraction a of quality into sexual advertisement and the remaining fraction $(1-a)$ into survival. Left panels: Benefits of mating success (m) and survival (s) according to the total amount allocated. Survival is measured as the expected lifespan. Right panels: Fitness components of males of varying quality, when allocations are optimal (males maximize their lifetime success for each quality). Fitness F is the product of lifespan and mating success, $w = sm$, which equals expected lifetime reproductive success (LRS). In (a), mating success increases with advertisement less sharply, $m = (aq)^2$, than in (b), $m = \tan(aq)$. In both cases, longevity s has diminishing returns ($s = 1 - e^{-5q(1-a)}$). In (b), quality is negatively correlated with longevity, but this is more than compensated by high mating success.

Figure 2 compares two life-history models where male mating success increases with allocation in sexual advertisement, either strongly (Fig. 2a) or very strongly (Fig. 2b). Fitness is measured as lifetime reproductive success (LRS), which is appropriate if we assume a temporally stable population regulated by offspring production (Brommer 2000). The returns from allocating resources either in survival or in mate acquisition determine the optimal patterns of investment for low- and high-quality males in these traits. The model predicts that when the success increases very strongly with allocation, high-quality males invest relatively more in mate acquisition, and thus have a shorter lifespan, than low-quality males (Fig. 2b).

Assuming heritable quality, Fig. 2(b) predicts that the fitness return through sons of the most attractive male exceeds the return from the least attractive male by a factor of 3.54. This is the result of 4.98 times as high mating success, which amply compensates for the fact that the lifespan of high-quality sons equals only 71% that of low-quality sons. Such inequality ("skew") in mating success is not atypically high. For example, studies on leks typically report that certain males are consistently favoured as mates, leading to a highly nonrandom distribution of matings (reviewed in Kokko *et al.* 1999a).

Such a strong fitness advantage through producing attractive, high-quality sons can also override substantial costs that may result from pleiotropic reductions in female viability or fecundity due to sexually antagonistic genes (Rice 1992, 1996). For example, if the lifespan of daughters of high-quality males is reduced to the same fraction of 71% as their sons (as in Fig. 2b), and their fecundity is, say, 50% lower than that of daughters of low-quality males, a female still increases her fitness by mating with the attractive male: each male offspring is 3.54 times as valuable, and each female is $0.5 \times 0.71 = 0.335$ times as valuable, when sired by the most vs. least attractive male. Assuming a 1:1 offspring sex ratio gives a total increase in fitness by a factor $(3.54 + 0.335)/2 = 1.94$, i.e. a 94% increase in fitness. Optimal sex ratio adjustment (Frank 1990; Godfray & Werren 1996; Sheldon 1998; Pen 2000) would favour biasing sex ratios of offspring according to paternal quality in such a setting, but this does not always seem to be possible, e.g. superb fairy-wrens *Malurus cyaneus* show evidence for sexually antagonistic genes but not for sex ratio adjustment (A. Cockburn, personal communication).

Whether or not sex ratios are adaptively adjustable, the above model shows that a preference for a male trait can be adaptive even if this damages the fitness of female offspring, and if life-history trade-offs cause highly attractive males to survive poorly. In both of the examples (Fig. 2a, b), attractiveness is an indicator of high genetic quality, even though attractiveness has in Fig. 2(b) no positive correlations with any other life-history trait than mating success itself.

DISCUSSION

"Good genes" models are not falsified by showing that survival correlates negatively with attractiveness. A female may still gain from mating with the attractive male, if the sons thus produced are of higher quality–even if they "choose" to allocate most of this quality into mate acquisition and not survival. The defining test between the presence and absence of "good genes" benefits is whether there is heritable variation in male fitness, which manifests itself in superior lifetime fitness returns from daughters and/or sons. The "classical" Fisherian process, by contrast, produces an outcome with no variation for heritable fitness, and it is indeed difficult to maintain if female choice incurs direct costs (Pomiankowski 1987; Pomiankowski *et al.* 1991).

Definitions of what "good genes" are good for vary, but a common interpretation (e.g. Kirkpatrick & Ryan 1991; Andersson 1994; Møller & Alatalo 1999) is that genetic quality must be realized in offspring viability or fecundity (mating success excluded from fecundity). This view is simply incompatible with theoretical results on condition-dependent handicaps that underlie the "good genes" mechanism (Grafen 1990; Kokko 1998; Eshel *et al.* 2000). Hence, we will only achieve a logically consistent definition of a "good genes" benefit when we cease to consider the "sexy son" benefit a monopoly of the Fisher process, and start to include the mating success of male offspring in fitness calculations (see also Eshel *et al.* 2000).

Studies that relate male mating success to their sons' mating success are rare (Wedell & Tregenza 1999). Studies that relate male attractiveness to the viability of offspring, especially during juvenile development, are more numerous. They show that attractive males, in fact, often produce offspring of high viability (reviewed in Møller & Alatalo 1999). This suggests that cases where condition dependence retains a positive correlation between net viability and attractiveness may be the norm. Yet, measuring attractiveness in the context of mate choice experiments, but leaving the correlation between mating success and attractiveness undetermined, will always bias the fitness estimates of attractive males (or their offspring) downwards. This bias makes us much more likely to reject scenarios of "good genes" erroneously, and may account for the overall small effect found in meta-analysis studies (Møller & Alatalo 1999).

Striving towards a lifetime, all-inclusive measurement of genetic quality is also necessary because genes that are good early in life are not always good later (Stearns 1992), and genes that are good for males are not always good for females (Rice 1992, 1996). As an example, Promislow *et al.* (1998) showed that the genetic benefit may manifest itself in improved survivorship of adult offspring rather than improved performance in juveniles. Studies such as Promislow *et al.* (1998) and Brooks (2000) provide a significant step forward in this respect, as they take pains to estimate many fitness components of offspring of both sexes. Yet, even these studies have ignored the mating success of male offspring. It is currently unclear if, and by how much, an inclusion of this benefit will increase our estimates of the heritability of fitness. Current theoretical considerations (Burt 1995; Kirkpatrick & Barton 1997) suggest that heritability should not rise much above what was found by Møller & Alatalo (1999). One should note that in species with negative correlations between components of fitness, including all components in fitness calculations, may also decrease the value of heritability from an incomplete estimate.

It is not the easiest task to estimate empirically the correlation between a male's mating success and his attractiveness, especially since the latter can only be inferred indirectly, and special care must be taken to avoid circular argumentation. Yet, as the above model shows, all components of offspring success, including expected mating success of male offspring, must be included in fitness calculations, before we can truly distinguish between "good genes" or "Fisherian only" processes. Indeed, the latter may be considered unlikely, when mating success of male offspring is included in studies of sexual selection (Eshel *et al.* 2000).

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BIOSKETCH

Hanna Kokko is interested in interactions between individual behaviour, life-history theory and population dynamics. Her work focuses especially on conflicts that underlie sexual selection, social behaviour and space use strategies.

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