

What is genetic quality?

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Mate choice is favored by indirect selection if choosy females mate with males of high genetic quality. We believe, however, that testing hypotheses about indirect selection has been constrained by how we conceptualize and therefore empirically measure male genetic quality. Here, we argue that genetic quality is the breeding value of an individual for total fitness. We can therefore learn little about genetic quality from measures of only a few fitness components. We explain breeding value for total fitness, drawing on concepts from life-history theory and quantitative genetics, and suggest how approaches incorporating these insights might result in empirical progress.

A trait can evolve both because of its direct effect on fitness (DIRECT SELECTION; see Glossary) and because it is genetically correlated with other fitness-related traits (INDIRECT SELECTION) [1]. The evolution of mate choice by direct selection is relatively uncontroversial, but the role of indirect selection is a source of ongoing debate [2,3]. Females are thought to derive an indirect fitness benefit when they choose to mate with males of high GENETIC QUALITY because offspring and future generations of descendants inherit both the genes underlying choice and the genes for quality [4,5]. Understanding indirect selection therefore presupposes an understanding of genetic quality.

Two broad types of genetic benefit might exist: those resulting from the general superiority of the genotypes of some males, and those resulting from interactions between the genes that offspring inherit from both parents (i.e. dominance and epistasis). There is increasing evidence that the latter 'genetic compatibility' benefits are important in many species [6]. General benefits (which arise as a result of additive genetic variation among males) have, however, been far more comprehensively studied. Here, we confine ourselves to discussing how additive genetic effects determine male general genetic quality.

It is common in studies of indirect selection to use one or a few fitness components as indices of genetic quality (e.g. survival [7–11], growth rate [8,9] or immunocompetence [12]). In our opinion, this approach is inherently limited in what it can tell us about male genetic quality because there are few *a priori* reasons to believe that the relationship between any given fitness component and TOTAL FITNESS is strong or even positive. For example, it is of no benefit to have offspring that live longer than average if this longevity benefit comes at a net cost to

reproduction and, therefore, total fitness. A multitude of life-history studies show that such tradeoffs between fitness components are common [13,14].

The use of the LIFETIME REPRODUCTIVE SUCCESS of an individual as an index of genetic quality is a vast improvement on the use of single fitness components and, in many cases, it provides a good approximation for

Glossary

Additive genetic variance (V_A): variance of breeding values among individuals in a population [33]; primary genetic cause of resemblance between relatives and, therefore, of the response of the population to selection.

Acquisition: ability of an individual to procure resources (energetic or essential nutrients) from the environment.

Allocation: how an individual partitions resources among different life-history components.

Best linear unbiased prediction (BLUP): general methodology used to predict the breeding value of an individual based on pedigree analysis [34].

Breeding value: sum of the additive effects of the genes of an individual on a given trait; can be measured by the mean value of the trait expressed by its progeny [33].

Condition: total pool of resources acquired by an individual. We follow Rowe and Houle [26] in equating the acquisition of resources with condition.

Direct selection: when there is a direct causal relationship between a trait and fitness, evolutionary change can occur through direct selection.

Environmental variance (V_E): all variation in a trait that is non-genetic in origin.

Genetic architecture: characterization of a phenotype in terms of the genetic and environmental effects and interactions that influence trait expression.

Genetic correlation: association between the alleles influencing two traits either because alleles at the same loci influence both traits (pleiotropy) or because of a statistical association between alleles at different loci that influence the expressions of each trait (linkage disequilibrium). When females mate with males with high breeding values for fitness, the alleles that determine mate choice become associated with alleles conferring high fitness in the offspring by linkage disequilibrium.

Genetic quality: breeding value for total fitness.

Genotype x environment interaction (GEI): extent to which genotype expression is influenced by the environment; typically visualized as reaction norms; non-parallel reaction norms are indicative of a significant GEI (Figure 1; Box 1).

Indirect selection: selection that operates on a trait as a consequence of direct selection operating on another, genetically correlated, trait; will operate on female choice when it is genetically correlated with fitness.

Lifetime reproductive success: number of offspring produced during an individual's lifetime.

Reaction norm: environmental sensitivity of a genotype. To measure reaction norms across a specific range of environments, individuals with a given genotype are reared in those environments (Figure 1; Box 1).

Restricted maximum likelihood (REML): method for estimating variances and covariances associated with random effects; performs better than other common methods (e.g. least squares) for unbalanced data.

Total fitness: a critically important concept with many different meanings [39]. Here, we conceive total fitness in a manner similar to personal fitness [39,40] as the number of descendants produced by an individual relative to the average produced by other individuals in the population. The most accurate estimates of fitness would enumerate the number of descendants an infinite number of generations into the future. This is, of course, intractable. It is important to count the output of both sons and daughter (i.e. grandchildren) when dealing with mate choice and sexual selection [3], because there can be considerable variation in the reproductive success of males (i.e. sons), and this can be positively or negatively genetically correlated with the fecundity of females (i.e. daughters).

Box 1. Measuring and interpreting genotype x environment interactions (GEIs)

A single trait measured in two different environments can be viewed in the same way as two traits measured within a single environment [33]. Consequently, estimating the genetic correlation across environments [and to test for genotype x environment interactions (GEIs)], requires estimates of among-family variance in both environments and the covariance of family means across environments [34]. The most commonly used technique is to split families or inbred lines (i.e. genotypes) among environments. For each genotype, one set of offspring is assayed in one environment and another set in the second environment. The variance components are then estimated and the across-environment genetic correlation calculated [34]. The significance of the interaction term provides an explicit test of whether the GEI is significantly greater than zero. Although most GEI studies only encompass two environments, the statistical procedures can readily be extended to multiple environments [34].

GEIs are often visualized by plotting the REACTION NORMS of genotypes (e.g. Figure 1, main text). Differences in trait expression within an

environment are indicative of additive genetic variation within that environment. Non-zero slopes of reaction norms indicate an effect of environmental variation. Reaction norms that are not parallel are indicative of GEI (Figure 1 b-d, main text). The environment in which genetic quality is measured can have an important influence on both the extent of genetic variation in quality and the rank order of genotypes. Under benign laboratory conditions with *ad libitum* food and no risk of predation, genetic variance in acquisition ability might be much smaller than that under field conditions. In three recent laboratory studies, variance in the expression of sexual traits was greatest in the poorest environment [21–23].

The importance of differential costs to honest sexual signaling [41,42] leads us to the testable prediction that genetic variation in signals of male quality will be greater in the environment in which they evolved than under benign laboratory conditions because, in harsh environments, poor-quality males are less likely to be able to bear the cost of signal expression.

total fitness. Indirect selection on choosiness is, however, driven by its effect on offspring performance and not all offspring are of equal value [15]. Kokko *et al.* [16] illustrate this problem by noting that a choosy female that pays a direct cost (fewer offspring) to mate with a more attractive male will leave more surviving descendents if the elevated mating success of her sons more than compensates for the fecundity costs that she and her choosy daughters suffer.

It is clear to us that there are problems with how the notion of fitness, and hence genetic quality, is both conceived and measured in studies of sexual selection. In the context of additive genetic effects and indirect selection, the genetic quality of a male can have only one meaning – his BREEDING VALUE for total fitness. Logistic demands often constrain empiricists to measure only one or a few fitness components in an attempt to understand male genetic quality. However, the use of individual fitness components as surrogate measures of total fitness can lead to inappropriate generalizations of how specific sires or genotypes affect offspring fitness. Here, we discuss several factors that could alter the sign and magnitude of the relationship between individual fitness components and total fitness, thereby complicating attempts to assess male genetic quality. Greater consideration of life-history theory and quantitative genetics might, however, provide a foundation for future empirical progress.

Genetic variation in total fitness

We believe that a thorough understanding of the sources of variation in total fitness is a crucial prerequisite to understanding male genetic quality. Ultimately, these sources of variation influence the nature of the relationship between fitness components and total fitness. We therefore focus on two processes that cause male genetic quality to vary: GENOTYPE X ENVIRONMENT INTERACTIONS (GEIs) and the ACQUISITION and ALLOCATION OF CONDITION.

Total fitness as a product of genotype x environment interactions

Until recently, most quantitative genetic studies on sexually selected traits have examined either the magnitude of ADDITIVE GENETIC VARIANCE (V_A) in a single

environment or the extent to which the heritability of male sexual traits is reduced by high environmental variation (which increases phenotypic variance) [17,18]. However, differences among individuals in total fitness (as in any other character) are inevitably the product of how their genotypes interact with the environment (Box 1, Figure 1). Recent studies explicitly designed to measure GEIs have therefore added considerable insight into the extent to which male genetic quality is repeatable across different environments [19–23].

Heritable variation in total fitness depends on the environment in which it is measured for two reasons. First, the relative expression of the many traits underlying total fitness can vary widely among genotypes across different environments. The amount of phenotypic variation in fitness attributable to genetic differences and the relative fitness of different genotypes are therefore strongly dependent on the environment [24]. Second, the adaptive value of traits varies among environments. For example, ambient light determines the direction of selection on the colourful ornamentation of male guppies in predictable ways because it affects how females and predators perceive colours [25].

Collectively, this means that the best genotype in one environment is not necessarily the best in another environment – a finding supported by several recent GEI studies [19–23]. It follows, then, that the best male to sire offspring in one environment is not necessarily the best in all environments. The extent to which the genetic benefits of mating with the most attractive males in one environment can be generalized to the wider range of environments in which populations naturally occur is an important area for future empirical study.

Total fitness and genetic variance in the acquisition and allocation of condition

Life-history theory distinguishes two sources of genetic variation that influence total fitness: variation in resource acquisition (i.e. condition) [26] and variation in the allocation of resources among fitness components. Relative levels of genetic variation in acquisition and allocation will strongly influence the GENETIC CORRELATIONS among

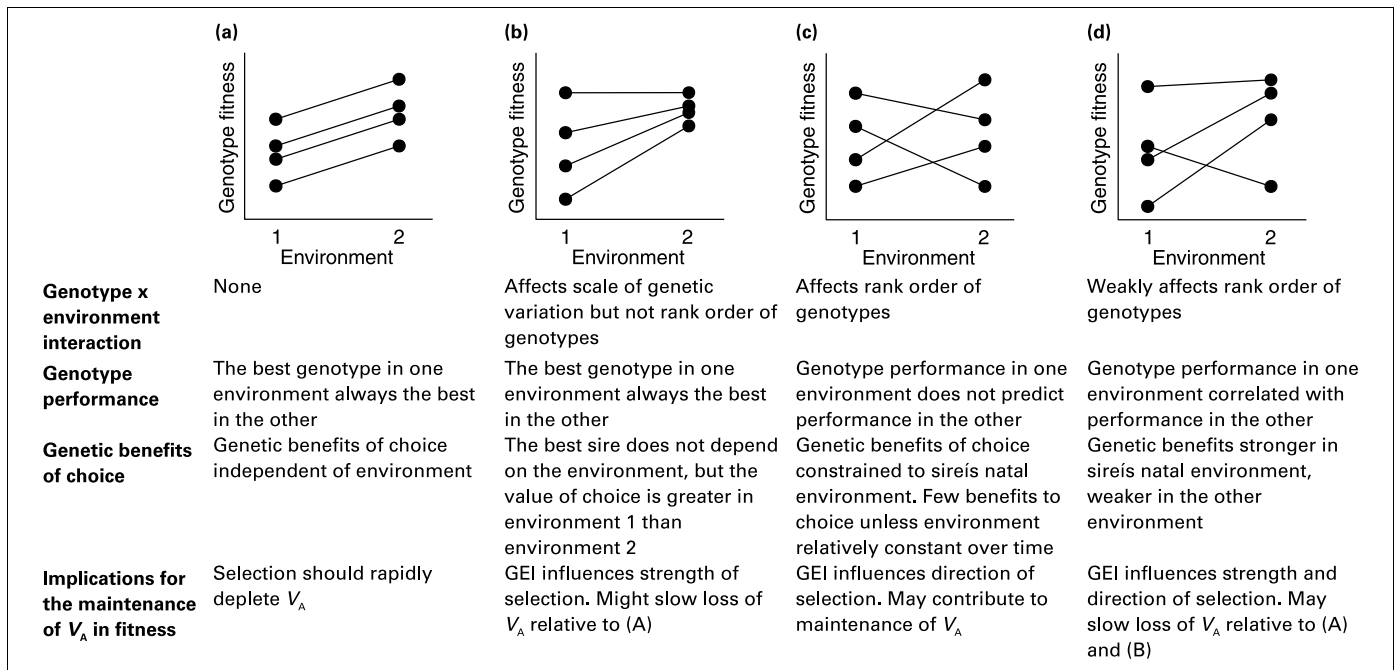


Figure 1. Hypothetical scenarios illustrating the possible effects of genotype x environment interactions (GEIs) on reaction norms of four genotypes in two environments. GEIs can influence the scale of within-environment genetic variation (b), the rank order of the genotypes (c) and (d), neither scale nor rank order (a) or both (not illustrated). In the context of genetic benefits of mate choice, effects on the scale of genetic variation within an environment influence the potential genetic benefits gained from mate choice in that environment. Effects on the rank performance of genotypes determine the extent to which sire genetic quality depends on the environment in which the offspring will develop.

fitness components [27,28]. Life-history traits tend to be condition dependent, so substantial genetic variation in acquisition will usually result in positive genetic correlations among fitness components: good acquirers perform well in all fitness measures [27–29]. Conversely, if there is mainly genetic variation in allocation, this will lead to genetically based tradeoffs [27,29]. Consequently, we expect a combination of positive and negative genetic correlations among life-history traits [13] with the value of specific correlations depending on the allocation pathways involved.

Genetic variation in the acquisition and allocation of resources is also influenced by GEIs. Condition is likely to be strongly affected by environmental factors, such as the availability of resources and the cost of acquiring them. In some environments, costs might be uniformly low (e.g. laboratory studies), whereas, in others, they might be strongly genotype dependent. Optimal allocation patterns might also vary among environments independently of any GEI for condition (e.g. invest less in a given trait in environments where it is more costly). In general, however, genotypic differences in acquisition across environments might directly affect allocation decisions, especially investment in sexually selected traits, because allocation strategies change depending on the condition of the male [26,30]; that is, GEI for condition can directly cause GEI for allocation. The combined effects of GEIs for the acquisition and allocation of condition to fitness components mean that the relationship between total fitness and any given fitness component might vary among environments. There is no *a priori* reason to assume that a given fitness component will be a good general index of male genetic quality.

Problems with the empirical tradition

There is much evidence that male attractiveness is correlated with displays and ornamentation that females assess when choosing mates [2]. To determine whether female choice confers indirect fitness benefits, behavioral ecologists have tested for associations between male attractiveness and various measures of offspring performance. However, the issues that we have just discussed expose several related problems for these tests: (i) specific male traits need not be correlated with general genetic quality; (ii) attractiveness might only be correlated with genetic quality in some environments; and (iii) studies of genetic benefits rarely have sufficient statistical power to obtain meaningful estimates of genetic correlations and GEIs.

Given the obvious difficulties in estimating total fitness, behavioral ecologists have long sought convenient phenotypic indicators of genetic quality. If such reliable markers exist, then testing whether indirect selection favors mate choice becomes a relatively simple task. However, a single fitness component will only indicate genetic quality when it is positively correlated with breeding value for total fitness. In many instances, this is unlikely to be so because individual fitness components are, themselves, subject to allocation tradeoffs [13,16]. Moreover, phenotypic plasticity in the allocation of condition among fitness components means that the magnitude and/or direction of the correlation between a fitness component and total fitness will change across environments. There is, therefore, no *a priori* reason to believe that a certain fitness component will reliably indicate fitness in any given population. There is some evidence for high genetic variation in acquisition [31], as assumed in the 'genetic capture' model for the maintenance of female choice [26]. If generally true, we

Box 2. The relative importance of V_A in the acquisition and allocation of condition in determining total fitness

Although breeding values for total fitness depend on additive genetic variance (V_A) in both the acquisition and allocation of condition to different life-history components, V_A in the acquisition of condition might be relatively more important to total fitness for the following reasons:

(i) Increased acquisition of resources (i.e. condition) is likely to elevate fitness in most environments. Thus, a signal of acquisition ability is likely to be a general indicator of quality. By contrast, a particular pattern of allocation can be adaptive in one environment but not in another.

(ii) Acquisition ability might also be a better predictor of fitness than is the strategy of allocation, because acquisition is under directional selection (i.e. for ever-increasing energy supplies) whereas allocation is under stabilizing selection (because too much or too little investment in any individual life-history trait is maladaptive) [27].

(iii) Acquisition of resources is influenced by a larger proportion of the genome than is allocation [26,27,31]. As a result, acquisition provides a larger mutational target than does allocation and should therefore harbor greater genetic variance in the face of selection (through mate choice).

(iv) One might expect there to be little genetic variance in allocation. Unless there are hidden costs, the optimal allocation strategy would be complete plasticity, with investment in each life-history trait in accordance with the current energy budget.

(v) If a large proportion of the segregating V_A in fitness in a population is due to allocation differences, any increment in investment in a costly sexual signal of quality will come at a net cost to other fitness components and, conceivably, to fitness itself. It is thus harder to see how females might obtain measurable fitness benefits from choice under such circumstances.

This view is supported by evidence that positive genetic correlations between life-history traits are more commonly reported than are negative ones [43], in spite of many studies being conducted in the benign conditions of the laboratory, where V_A in acquisition is likely to be reduced. This suggests that V_A in the acquisition of condition is more important than V_A in the allocation of condition in its effects on fitness and, thus, drives mate choice for indirect benefits.

expect mainly positive correlations between fitness components and genetic quality (Box 2). However, we cannot test the generality of the 'genic capture' model by assuming, rather than testing, whether V_A in acquisition is high. There is, therefore, little justification for using one or a few fitness components in critical tests of indirect benefits models.

The other important issue concerns the statistical power of empirical tests. Questions about genetic quality are inherently about the genetic (rather than phenotypic) correlations between male attractiveness and total fitness. Most published estimates have relatively small samples (e.g. median n (71 in 29 studies of the relationship between a sire trait and offspring viability [7]). Unfortunately, breeding designs with adequate power to test for significant genetic correlations need to be an order of magnitude larger than this [32,33].

Addressing the problems

The most important challenges faced by those studying the genetic benefits of mate choice are empirical. Total fitness is difficult (if not impossible) to measure and enormous effort is required to estimate breeding values [34]. To assess genetic quality, we must do both. At the very least,

empirical studies assessing the benefits of choosiness should estimate total fitness by counting the number of grandchildren produced, as this takes into account differences, which are due to sexual selection, in the mating success of sons and fecundity of daughters [3]. Ideally, sons should face realistic sexual competition so that sexually selected traits can influence the number of grand-offspring produced. To our knowledge, only a single study has examined fitness in terms of the number of grandchildren produced [35]. In this study, hybrid matings between the flycatchers *Ficedula hypoleuca* and *F. albicollis* significantly reduced parental fitness. The benefit of mate choice was, however, only apparent when the number of grandchildren produced was counted, because the reduced fitness in hybrid matings was due to the production of sterile sons.

The pervasiveness of GEIs means that descriptive statistics, such as heritabilities and genetic correlations, are context dependent and should ideally be estimated in the environment in which choice evolved. Statistical innovations in animal-breeding analysis, including RESTRICTED MAXIMUM-LIKELIHOOD (REML) estimation of variance components and BEST LINEAR UNBIASED PREDICTION (BLUP) of breeding values from detailed pedigrees, have proved useful in large and long-running studies of wild vertebrate populations (*Ficedula albicollis* [36] and deer *Cervus elaphus* [37]). Unfortunately these studies have not provided convincing evidence that total fitness is heritable. However, the alternate possibility that V_A in total fitness is actually relatively large cannot be excluded because the standard errors associated with estimates of V_A for total fitness are also large.

Whereas descriptive quantitative genetic studies are probably best performed in the field, laboratory experiments are an invaluable complement to test hypotheses about how signals of genetic quality are expressed under specific environmental conditions. In particular, there is still much scope for empirical studies to investigate the role of condition-dependent sexual traits in signaling male genetic quality [31]. There are good reasons to expect that V_A in the acquisition of condition is relatively more important to total fitness than is V_A in the allocation of condition. This might explain the more frequent occurrence of positive genetic correlations between major fitness components (Box 2). It might be tempting then to conclude that these traits will always be positively related to total fitness and thus reliably indicate male genetic quality.

Caution should still be taken, however, when assuming that condition-dependent traits will be positively correlated with total fitness, because their expression is also influenced by how condition is allocated to different fitness components. Furthermore, condition-dependent sexual signals might only reveal how the genotype of a male affects performance in the specific environment in which he developed. For example, in environments where female choice is a weaker force (e.g. because exercising choice is more costly [16]) condition-dependant sexual signals might be poor indicators of male fitness. In practice, the predictability of the environments faced by sires and their offspring, and the extent to which GEIs influence condition, will determine the potential genetic benefits of

female choice (Figure 1). If sires and offspring tend to share similar environments or if GEIs for genetic quality are small, male sexual signals of genetic quality might still reliably indicate offspring fitness. We therefore predict that choice is more likely to evolve in situations where ENVIRONMENTAL VARIANCE (V_E) and GEI effects on fitness are relatively small in magnitude. Careful quantitative genetic experiments examining the GENETIC ARCHITECTURE of fitness components, particularly the relative roles of V_A in the acquisition and allocation of condition, are needed before any single fitness component can be assumed to be a general index of male genetic quality.

Conclusion

Empirical attempts to test hypotheses about the evolution of mate choice by indirect selection have, until recently, largely involved documenting phenotypic relationships between sexual signals, mate choice and one or a few fitness components of chosen mates or their offspring. Building on the insights of Andersson [38] and Rowe and Houle [26] regarding the condition-dependent signaling of male quality, we believe that renewed examination of life-history theory and quantitative genetics offers the best way forward. Although there are numerous possible phenotypic indicators of genetic quality, there is only one meaningful definition: the breeding value of an individual for total fitness. We suggest that researchers should consider this point whenever they test hypotheses about the genetic benefits that maintain female choice. There are no obvious shortcuts to measuring fitness, and phenotypic correlations do not always predict genetic ones. On a positive note, calculating the relative contribution of variation in resource allocation and acquisition to the expression of sexual traits, especially when GEIs are explicitly tested for, will generate opportunities for many innovative new studies.

Acknowledgements

This work was funded by ARC grants to J.H., R.B. and M.D.J. and by a NSERC fellowship to L.F.B. We thank Jon Evans, Simon Griffith, Megan Head, Hanna Kokko, Jennifer Kelley, Tom Tregenza and three anonymous referees for valuable comments and discussions that greatly improved this article.

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