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Mate Choice for Genetic Benefits: Time to Put the Pieces Together

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Abstract

It is thought that mate choice allows individuals to obtain genetic benefits for their offspring, and although many studies have found some support for this hypothesis, several critical questions remain unresolved. One main problem is that empirical studies on mate choice and genetic benefits have been rather piecemeal. Some studies (1) aimed to test how mate choice affects offspring fitness, but have not examined whether the benefits are because of genetic effects. Other studies tested whether mate choice provides (2) additive or (3) non-additive genetic benefits and only a few studies (4) considered these genetic effects together. Finally, some studies (5) examined whether the *potential* benefits that might be gained from mate choice are due to additive genetic effects vs. non-additive effects, and although they found evidence for both, they did not examine whether mate choice is relevant. Furthermore, previous studies have usually not controlled for non-genetic sources of variation in offspring fitness. Thus, there remain gaping holes in our understanding, and it is the connections among the research approaches that now need more attention. We suggest that studies are needed that measure non-genetic effects, the potential benefits from both additive and non-additive genetic effects, and also determine whether mate choice exploits these potential benefits. Such integrative studies are necessary to put the pieces together and clarify the role of genetic benefits in the evolution of mate choice.

Mate choice may function to provide genetic benefits to the choosing parent. Genetic benefits may be especially important for mate choice in non-resource-based breeding systems, in which males only provide females with sperm and the only possible benefits of choice are genetic (Trivers 1972; Andersson 1994). Two types of genetic benefits from mate choice have been suggested. First, mate choice may allow individuals to confer alleles that increase survival and⁄or reproductive success of offspring ('good genes') (Trivers 1972; Iwasa et al. 1991; Kokko et al. 2006). This idea assumes that there is additive genetic variation in fitness and that the choosing parent is able to assess the heritable genetic quality of potential mates. Second, mate choice can allow individuals to enhance offspring fitness by creating favourable combinations of the maternal and paternal genes or genomes ('genetic compatibility' and 'incompatibility avoidance') (Trivers 1972; Yamazaki et al. 1976; Zeh & Zeh 1996). We consider incompatibility avoidance (Zeh & Zeh 1996) and preferences for genetic compatibility (Penn 2002; Mays & Hill 2004; Neff & Pitcher 2005) to be ends of one continuum, as both serve to enhance

non-additive genetic benefits to offspring, and we refer to them collectively as choice for non-additive genetic benefits (Neff & Pitcher 2005; Puurtinen et al. 2005). Mate choice for non-additive genetic benefits requires that females are able to discriminate their own species, kin or assess their own genotype and that of potential mates, and that there is non-additive genetic variation in fitness (Zeh & Zeh 1996, 1997; Tregenza & Wedell 2000; Penn 2002). These two types of genetic benefits lead to different predictions with respect to the details of the sexual selection process. In particular, when additive genetic variation is more important, mate choice is expected to converge on the high quality individuals that are the best mates for any member of the choosing sex, whereas when non-additive genetic variation is more important, there is no overall best mate as choice of an individual depends upon its own genotype (Mays & Hill 2004; Neff & Pitcher 2005; Puurtinen et al. 2005, 2009).

There is a large and growing body of studies addressing the consequences of mate choice to offspring fitness, and evidence for potential additive and non-additive benefits of mate choice are also abundant (for reviews see Hunt et al. 2004; Mays & Hill 2004; Neff & Pitcher 2005; Kempenaers 2007; Puurtinen et al. 2009). However, studies linking some critical questions about mate choice for genetic benefits are lacking. Our main concern here is that the studies on mate choice for genetic benefits are fragmented, as (1) studies linking the areas of additive and non-additive genetic benefits in the context of sexual selection are scarce, (2) the two types of genetic effects have rarely been directly related back to mate choice and (3) there is a lack of comprehensive studies using suitable model organisms (*sensu* Owens 2006). While recent theoretical papers have drawn attention to the importance of integrating the research fields of additive and non-additive genetic benefits (Colegrave et al. 2002; Neff & Pitcher 2005, 2008; Lehmann et al. 2006; Fromhage et al. 2009; Puurtinen et al. 2009), here we explain in more detail, and from an empirical point of view, why previous studies have been too fragmentary and suggest how a more integrated methodological framework will improve our understanding of mate choice for genetic benefits.

We give a brief overview on empirical studies addressing mate choice for genetic benefits, giving examples from recent literature. This is not an exhaustive literature review and we do not aim to provide quantitative or qualitative evaluations about the results of previous research. The purpose of this paper was to provide a classification of previous empirical studies of mate choice for genetic benefits, and point out the advantages as well as the methodological and other limitations of each type of approach. Furthermore, we aim to show how the links between the various types of approaches could be fruitfully explored. As we see no reason why genetic benefits of mate choice should depend on the mechanism biasing paternity, we do not distinguish between pre-copulatory and post-copulatory choice, and give examples of studies from both types of sexual selection. We finally suggest an experimental approach that integrates key aspects of mate choice for genetic benefits and propose taxa which would be especially promising model organisms in studies of mate choice for genetic benefits.

The empirical studies on mate choice for genetic benefits can be classified into five separate categories based on their primary aims and methodology. The first category of studies looks at the consequences of mate choice to offspring performance, the second examines whether sexually selected traits in parents predict offspring performance, the third relates mate choice and offspring fitness to estimates of parental compatibility (e.g. genetic dissimilarity of parents), the fourth explores mate choice for secondary sexual traits vs. estimates of parental compatibility, and the fifth aims to disentangle the potential additive and non-additive genetic benefits of mate choice. Finally, we suggest a sixth approach that will simultaneously assess mate choice for additive and non-additive genetic benefits. See Fig. 1 for a schematic presentation of all six types of approaches.

Empirical Approaches to Genetic Benefits of Mate Choice

Consequences of Mate Choice to Offspring Fitness

A number of studies have experimentally tested the effects of mate choice on offspring performance (Drickamer et al. 2000, 2003; Sandvik et al. 2000; Gowaty et al. 2003; Bluhm & Gowaty 2004; Anderson et al. 2007; Cothran 2008; Casalini et al. 2009). The experimental methods generally consist of individual mate preference assays, followed by assigning individuals to either a preferred or a random/non-preferred mate and recording reproductive success and offspring performance.

One advantage of these studies is that all possible sensory cues can be used in mate choice, instead of confining selection to one or a few more-or-less arbitrary traits chosen by the experimenter, and
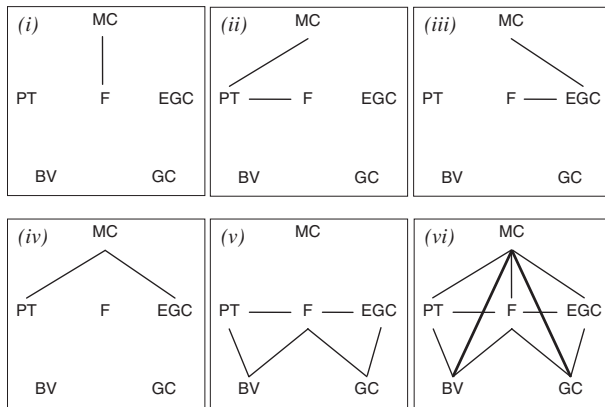
Fig. 1: Schematic presentation of empirical studies on genetic benefits of mate choice. Lines represent connections studied by the different approaches, thick lines in panel *vi* represent the information emerging from the proposed integrated approach: (*i*) studies on consequences of mate choice to offspring fitness; (*ii*) studies on phenotypic traits predicting offspring fitness; (*iii*) studies on the relationship between estimates of parental compatibility, mate choice and offspring fitness; (*iv*) studies on simultaneous mate choice for indicators of additive and non-additive genetic benefits; (*v*) studies disentangling potential additive and non-additive benefits of mate choice; (*vi*) an example of an integrated experimental design. See text for full description of each panel. MC, mate choice; PT, phenotypic trait (expression of sexually selected traits, body size, dominance, attractiveness); F, fitness (measures of offspring performance); EGC, estimators of genetic compatibility (surrogates for genetic compatibility of parents, e.g. genetic dissimilarity, dissimilarity at MHC loci, etc.); BV, parental breeding value for fitness; GC, genetic compatibility of parents.

therefore, false negatives are less likely, and the results are more ecologically relevant. The limitation of this type of studies is that differential maternal allocation to offspring of the preferred mate has never been controlled for. Parental allocation of resources to offspring can vary according to the attractiveness of the mate, and the benefits conferred to offspring may not be genetic (Burley 1988; Gil et al. 1999; Cunningham & Russell 2000; Sheldon 2000; Kotiaho et al. 2003; Gowaty et al. 2007; Loyau et al. 2007; Harris & Uller 2009; Magrath et al. 2009). Although there is large variation in overall estimates, genetic benefits from choice are generally thought to determine a smaller proportion of variance in offspring fitness than maternal effects (Møller & Alatalo 1999; Johnsen et al. 2000; Jennions et al. 2001; Wedekind et al. 2001; Penn et al. 2002; Rudolfsen et al. 2005; but also see Meagher et al. 2000; García-González & Simmons 2005; Neff & Pitcher 2005). Consequently, while these studies often show an increase in the viability of offspring because of mate choice, they do not unambiguously show genetic benefits and likely

overestimate the magnitude of these benefits (Sheldon 2000; Kotiaho et al. 2003).

Phenotypic Traits Predicting Offspring Fitness

The main goal of these studies was to identify parental traits, such as frog's calls, that correlate with mating success and experimentally test whether the parental traits are also related to offspring fitness (e.g. Boake 1985; Hoikkala et al. 1998; Welch et al. 1998; Iyengar & Eisner 1999; Sheldon et al. 2003; Evans et al. 2004a; Forsman & Hagman 2006; Klappert & Reinhold 2007; Wedekind et al. 2008a). The benefit of these studies is that they can reveal genetic correlations between sexually selected traits and fitness, which can then explain the evolution and maintenance of possibly costly preferences for such traits. A few studies did not look at an isolated secondary sexual traits, but male attractiveness itself and its correlation with offspring fitness (Jones et al. 1998; Wedell & Tregenza 1999; Fedorka & Mousseau 2004; Head et al. 2005; Rundle et al. 2007).

In these studies, previous general results on mating preferences or attractiveness scores are related to variation in offspring performance. Thus, individuals of the choosing sex are mated to partners that should generally be preferred (successful) or not preferred (unsuccessful), even although there may generally be large inter-individual variation in these preferences (e.g. Forstmeier & Birkhead 2004), with not all females preferring the one 'best male' (Andersson 1994). The use of such previously established mating preferences (aptly termed 'population-level preferences' by Wagner 1998) or attractiveness scores precludes all possibilities for mate choice for 'compatibility' benefits. A sexual partner artificially assigned to an individual may be of high genetic quality, but incompatible with its partner at the same time. Also, the cost-benefit balance of mate choice may depend on the condition, physiological state or social status of the choosing individual (e.g. Clemens et al. 2005; Hebets et al. 2008; Ilmonen et al. 2009). Also, potential confounds from differential allocation (see above) have been considered in only a few of these types of studies (e.g. Parker 2003; Evans et al. 2004b). Direct benefits of mate choice are also often ignored, even though these generally have larger effect sizes than indirect benefits (Kirkpatrick & Barton 1997; Arnqvist & Kirkpatrick 2005; but see Møller & Jennions 2001; Head et al. 2005). The detection of additive genetic benefits from mate choice may be hindered if non-additive effects or

the state of the choosing individuals are ignored (false negatives), and may be over or underestimated if differential allocation or direct effects are important (false positives or negatives).

Estimates of Parental Compatibility Predicting Mate Choice and Offspring Fitness

Other studies aim to test whether individuals can increase their fitness by choosing mates that are more genetically compatible than the alternatives. Species recognition and inbreeding avoidance appear to be common, and other examples may include particular loci, such as major histocompatibility complex (MHC)-dependent mating preferences (Penn 2002). These studies usually classify individuals as offspring from 'compatible' or 'incompatible' matings based on some genetic marker and evaluate their performance, or test whether mate choice can be linked to patterns in the genetic markers used (Garner & Schmidt 2003; Cohen & Dearborn 2004; Lampert et al. 2006; Simmons et al. 2006; Forsberg et al. 2007; Sherborne et al. 2007; Thunken et al. 2007; Evans et al. 2008; Firman & Simmons 2008; Schwensow et al. 2008; Sherman et al. 2008; Gillingham et al. 2009; Jamieson et al. 2009; Szulkin et al. 2009). Sometimes both of these two steps are performed, but, unfortunately, usually on different occasions, and using different groups of individuals (for an exception see Pitcher et al. 2008). The rationale behind most studies is that matings with genetically similar individuals should be avoided, as inbreeding generally decreases fitness.

These studies allow quantifying non-additive genetic benefits that are potentially obtained from mate choice and explore the relationship between mate choice and genetic markers associated with these benefits. Surprisingly many studies, however, find no evidence for inbreeding avoidance or even find that genetically similar individuals are favoured in mate choice. This may be a result of inclusive fitness benefits that may favour incestuous matings even in the face of appreciable inbreeding depression (Parker 1979; Smith 1979; Waser et al. 1986; Kokko & Ots 2006), a non-linear relationship between genetic similarity and fitness-consequences (Puurtinen et al. 2009), or weaknesses of the applied experimental approaches. Similarly to studies in the previous group, the neglect of potentially present additive genetic benefits, direct benefits of mate choice and differential maternal allocation may often conceal non-additive genetic effects or create spurious genetic effects.

Simultaneous Mate Choice for Indicators of Additive and Non-Additive Genetic Benefits

Three studies have experimentally investigated simultaneous mate choice for indicators of additive and non-additive genetic benefits. Roberts & Gosling (2003) investigated the extent to which domesticated female house mice (*Mus domesticus*) based their preferences for males' urinary scent marks on the males' genetic compatibility (MHC-dissimilarity) vs. genetic quality, which they assumed is indicated by high rates of scent-marking. They found that both traits influenced female preferences, but MHC-dissimilarity only had an effect when the amount of males' scent-marking was controlled. Subsequent studies indicated that scent-marks honestly reflect males' health and condition (Zala et al. 2004), and genetic resistance to infectious diseases (Zala et al. 2008). Taken together, these findings support the good genes hypothesis and suggest that MHC only plays a role when females assess males of similar social status or quality. Neff et al. (2008) studied mate choice in Chinook salmon (*Oncorhyncus tshawytscha*) in relation to male size and colour as well as genetic relatedness and MHC class IIB alleles, and found that male phenotype and MHC-alleles of the parents affected mating patterns. Liljedal et al. (2008) studied post-copulatory sexual selection in Arctic charr (*Salvelinus alpinus*) in relation to sperm quality, male colouration, male genetic heterozygosity and genetic overlap with the female. In their study, fertilization success was positively affected by sperm velocity and genetic similarity between parental individuals.

While such studies investigating mate choice for traits indicating additive and non-additive genetic benefits simultaneously can help determine the relative importance of the two (Mays & Hill 2004), none of these studies have directly quantified the effects of actual mate choice on offspring fitness. If mating preferences and offspring fitness patterns are examined separately, the effect of individually varying mate preferences on offspring fitness may remain unclear.

Disentangling Potential Additive and Non-Additive Genetic Benefits of Mate Choice

Whereas almost all previous studies cited above were concerned with either additive or non-additive genetic effects of mate choice, a number of studies have examined these effects simultaneously when looking at the consequences on offspring fitness (e.g.

Evans et al. 2007; Bilde et al. 2008; Dziminski et al. 2008; for a review see Puurtinen et al. 2009). These studies apply an artificial breeding design where reciprocal crosses between two sets of animals are performed (Lynch & Walsh 1998), which makes it possible to quantify variation in offspring performance due to additive vs. non-additive genetic effects. Additive and non-additive genetic effects are assessed simultaneously based on the main effects and the interactions of parental identities, respectively. A few studies have further related variation in offspring fitness to male ornamentation (Wedekind et al. 2001, 2008b; Rudolfsen et al. 2005; Pitcher & Neff 2007), dominance (Jacob et al. 2007) or MHC genotypes (Pitcher & Neff 2006).

These studies are able to test the potential benefits of mate choice for additive- and non-additive genetic benefits. Crucially, however, none of these studies have tested for actual mate choice that may realize the measured potential genetic benefits, which means that it is unclear whether their findings are relevant to mate choice.

Putting the Pieces Together: An Example of an Integrated Experimental Design

The above groups of studies have all delivered important insights into specific areas within the framework of mate choice for genetic benefits. However, it remains largely unknown how these areas relate to each other, what their relative importance is and, ultimately, how additive and non-additive genetic benefits might together shape the evolution of mate choice. If we aim to understand this, it will be crucial to conduct mate choice tests and assess both additive and non-additive genetic effects while using the same individuals, thereby avoiding problems associated with the previous approaches.

As a first step, prior to matings, mate choice experiments need to be performed with sires and dams to elucidate mating preferences at the individual level. The same group of an ecologically relevant number of individuals of one sex should be offered for choice to several individuals of the other sex. Several groups of males and females may be used to increase sample sizes. Possible direct benefits of choice need to be controlled or at least quantified to allow measuring mating preferences for partner attributes (Kirkpatrick & Barton 1997; Arnqvist & Kirkpatrick 2005; Kotiaho & Puurtinen 2007).

As a second step, experimental matings should be conducted and, to avoid under- or overestimating genetic benefits of mate choice because of genotype-by-environment interaction, offspring fitness will have to be measured in the natural or at least multiple semi-natural environments (Meagher et al. 2000; Welch 2003; Mills et al. 2007; Ilmonen et al. 2008; Zhou et al. 2008). This is best done by performing all possible crosses between two sets of individuals (e.g. North Carolina Design II; Lynch & Walsh 1998; also see Ivy 2007), and measuring offspring viability and reproductive success (Kokko et al. 2003, 2006; Taylor et al. 2007). Statistical analysis of this mating design yields estimates for male additive genetic quality, female quality (including maternal effects) and the compatibility of male and female pairs (see Puurtinen et al. 2009 for details of the analysis). By combining information about mate choice with the estimates of the male and female quality and pair compatibility, it becomes possible to determine if mate choice targets additive genetic quality or genetic compatibility, or perhaps a combination of both. Note that this analysis looks at true genetic benefits as expressed in offspring fitness, not surrogates such as secondary sexual traits or genetic dissimilarity.

As a third step, it will be interesting to correlate measures of paternal additive genetic quality with presumed indicators of genetic quality, such as expression of secondary sexual traits, to see if these indicators correlate with true male genetic quality. Similarly, it will be interesting to see the relationship between molecular estimates of genetic compatibility and estimates of the true genetic compatibility of the parents obtained from the breeding design.

This approach would solve most of the problems described above, even if it is feasible for only a limited range of organisms. We suggest that the step that needs to be taken now is studying model systems with the least influence of confounding factors, even if results on one species are not always fully applicable to other taxa. Externally fertilizing species with no parental care and no post-copulatory mate choice would be ideal model organisms. A short lifespan would also be advantageous for the measurement of fitness. Many fishes and anuran amphibians fulfil these requirements, and they also cover a wide range of mating systems and life histories, thereby allowing a certain level of generalization. More integrative studies on such model organisms will help provide more rigorous tests of mate choice for genetic benefits, and, ultimately, allow for estimating how much of the potentially achievable genetic benefits are actually realized by choice in natural populations.

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