

An introduction to genetic quality in the context of sexual selection

Trevor E. Pitcher · Herman L. Mays Jr.

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Abstract This special issue of *Genetica* brings together empirical researchers and theoreticians to present the latest on the evolutionary ecology of genetic quality in the context of sexual selection. The work comes from different fields of study including behavioral ecology, quantitative genetics and molecular genetics on a diversity of organisms using different approaches from comparative studies, mathematical modeling, field studies and laboratory experiments. The papers presented in this special issue primarily focus on genetic quality in relation to (1) sources of genetic variation, (2) polyandry, (3) new theoretical developments and (4) comprehensive reviews.

Keywords Good genes · Compatible genes · Genetic quality · Mate choice · Sexual selection · Polyandry

Introduction

At the most basic level, evolution can be thought of in terms of gene frequency changes over generations. Fundamental to understanding evolution therefore is the notion that, in terms of evolutionary fitness, some individuals in the population are genetically of higher quality than others. While this notion of genetic quality is central to any understanding of biological evolution there is considerable

work remaining to both better define genetic quality in terms of theory and to better measure variation in genetic quality. For instance, good genes models of sexual selection rely on the idea that fitness is heritable, which contrasts sharply with the non-additive form of genetic quality associated with compatible gene models of sexual selection, which is not generally considered heritable (but see Neff and Pitcher 2008). Understanding genetic quality is relevant in studies of multiple mating, cryptic female choice, exaggerated male sexual ornaments, and conservation genetics, to name a few. Several recent reviews have focused on additive, good genes genetic quality (e.g. Hunt et al. 2004; Tomkins et al. 2004) and many have focused on non-additive forms of genetic quality, namely genetic compatibility (Mays and Hill 2004) or both (Neff and Pitcher 2005). In efforts to highlight the latest developments we organized a symposium on the evolutionary ecology of genetic quality as part of the 11th Congress of the International Society of Behavioral Ecology in Tours, France on July 29, 2006. The papers presented in this special issue of *Genetica* arose from this symposium and primarily focus on genetic quality in relation to (1) sources of genetic variation, (2) polyandry, and (3) theoretical developments and reviews.

Sources of genetic variation

To measure genetic quality and genetic benefits related to mate choice, variation in both genes and fitness must be assessed. Genetic quality can be partitioned into the independent effects of parental genotypes (additive genetic effects) and the interaction between parental genotypes (non-additive genetic effects) (Neff and Pitcher 2005). Several contributions to this special issue focus on the use

T. E. Pitcher (✉)
Department of Biological Sciences, University of Windsor,
Windsor, ON, Canada N9B 3P4
e-mail: tpitcher@uwindsor.ca

H. L. Mays Jr.
Cincinnati Museum Center, 1301 Western Ave., Cincinnati
OH 45203, USA

of quantitative genetic breeding designs to assign variance in fitness related traits to the different currencies of genetic quality. First, Wedekind et al. (2008) used full-factorial breeding designs to examine the genetic architecture of fitness related traits in Apline whitefish (*Coregonus* sp.). Wedekind and colleagues found that offspring mortality was influenced by male and female genetic effects, and that this pattern of mortality was associated with a secondary sexual trait. These results suggest that males do differ in terms of genetic quality and that females could in theory choose amongst males to increase their offspring's genetic quality. Second, Petrie et al. (2008) examined the heritability of a secondary sexual character (from a model system in sexual selection), the peacock's train (i.e. tail). Petrie and colleagues used two breeding experiments to demonstrate that contrary to theory, there are significant levels of heritability in the peacock's train length while other morphological traits not related to mate choice were not heritable. Third, Rodriguez-Munoz et al. (2008) used a half-sib breeding design to assay additive genetic variance and dam effects in a suite of reproductive and non-reproductive traits in the field cricket (*Gryllus bimaculatus*). Overall, Rodriguez-Munoz and colleagues found that additive genetic effects were weak but non-additive genetic effects were strong with respect to metrics related to fitness in this mating system. These findings suggest that female mate choice in this mating system may be driven by differences in genetic compatibility between mates rather than by differences in good genes.

Polyandry

In many mating systems, females mate with more than one male during a single reproductive event (see Birkhead and Moller 1998). In the absence of direct benefits from males, it has been posited that female multiple mating evolved as a mechanism to promote the genetic quality of the offspring (reviewed by Jennions and Petrie 2000; Simmons 2005). Presumably, a female could obtain sperm from multiple males and fertilize her egg with the sperm that would produce an offspring of the highest possible genetic quality. In order to calculate the fitness effects of genetic quality investigators have taken advantage of mating systems in which females multiply mate and employed experiments that randomly allocate females to either a single mating group, in which females are given one male with which to mate, or a multiple mating group, in which females are given multiple males with which to mate. Females in the multiple mating group are predicted to produce offspring of higher fitness than females in the single mating group, and the magnitude of the genetic benefits can be calculated from the difference in the fitness

of offspring from the two groups. Several contributions in this issue reflect this interest in multiple mating (i.e. polyandry) and the potential acquisition of genetic benefits for offspring. Pitcher et al. (2008) examined whether female guppies (*Poecilia reticulata*) can offset the costs of genetic incompatibility (as measured by inbreeding depression) by multiply mating and biasing paternity towards more compatible (i.e. unrelated) males. Pitcher and colleagues provide some data suggesting that female guppies may be able to multiply mate and discriminate against closely related males or their sperm. Female ability to bias paternity towards certain males over others is not unique to vertebrate mating systems (see Simmons 2005). Ward et al. (2008) examine the issue of why female yellow dung flies (*Scathophaga stercoraria*) with four spermathecae are better able to influence paternity than are those with three spermathecae. Ward and colleagues specifically examine the costs associated with having more or less spermathecae; their findings suggest that there is a substantial cost to having more spermathecae which helps explain why not all individuals have the same number of spermathecae.

Much of the work on multiple mating by females has been done in birds. Like many other species, birds have stubbornly resisted many of the explanations for the adaptive significance of polyandry. Mays et al. (2008) look at the evidence for a recent hypothesis that potentially can explain female mate preferences and polyandry in birds, namely the genetic complementarity or compatibility hypothesis. Genetic complementarity has been used as an explanation for extra-pair mating systems in birds where females obtain fertilizations from males other than their social mate. The support for this hypothesis is mixed at best and while a few studies have found evidence for complementary-based choice in birds many others have not. Potential explanations for the relative paucity of evidence for complementary-based choice in birds include sensory constraints in making fine distinctions among males and the antagonistic interaction between choice for complementary males versus males with good genes (i.e. good genes in the sense of additive genetic variance in male quality).

Theoretical developments

Theoretical developments have played a critical part in understanding the role of genetic quality in sexual selection by providing new hypotheses and predictions for empiricists to test. Several works in this issue explore new theoretical avenues with respect to genetic quality. Among these Kokko and Heubel (2008) explores a theoretical approach that combines condition dependence and genotype-by-environment interactions in a single population

genetic model to explain how genetic diversity is maintained in traits under sexual selection. Using this model the authors found that the introduction of genotype-by-environment interactions can increase the spread of costly female preferences, but, only under certain life-history and mutational parameters. Kokko and Heubel emphasize the need for theory to consider the context-specific associations between male attractiveness and offspring fitness in any solution to the lek paradox. Wolf et al. (2008) focus on competition dependence as a source of genetic quality and as a mechanism which maintains heritable variation in the face of selection. Wolf and colleagues present two models which show how social competition can contribute to competition dependent traits that have very different evolutionary dynamics compared to sources of variation in genetic quality.

Reviews of the literature related to genetic quality

Many of the papers in this issue present a synthesis of our current knowledge of some area of genetic quality. Explaining the evolution of polyandry and offering potential solutions to the lek paradox are again common themes in these reviews. First, Evans and Simmons (2008) examined the evidence for sperm competition's role in polyandry. Good-sperm and sexy-sperm hypotheses generally predict that polyandry can drive sexual selection for additive genetic variance in male traits related to success in sperm competition. If sperm related traits are heritable (as is the case in some species, Birkhead et al. 2005) females may benefit from multiple mating via their son's increased fertilization success. In an extensive review of the available literature Evans and Simmons conclude that there is little in the way of conclusive support for either the good-sperm or sexy-sperm hypotheses and that future work should examine genetic constraints, antagonistic selection and possible correlated responses to selection between female mating frequency and traits influencing male fertilization success. Second, Zeh and Zeh (2008) explore two non-Mendelian mechanisms (maternal inheritance of mitochondria and epigenetic regulation of gene expression) that may help explain variation in male fitness traits that are important in post-copulatory sexual selection arising from selection due to polyandry. Third, Price and Wedell (2008) tackle the problem of polyandry by looking at selfish genetic elements. Selfish genetic elements are a growing area of research (see Burt and Trivers 2006) with the potential to present new explanations to several problems in evolutionary ecology. Selfish genetic elements are those genes that are disproportionately represented in the next generation often imposing a relative fitness cost to the organism. Males carrying selfish genetic elements often

exhibit a lower competitive ability relative to other males without selfish genetic elements and this reduction may be as much as a 97% reduction in fertility (Price and Wedell, this issue). Price and Wedell make the argument that females promote sperm competition through multiple mating in part to avoid the fitness costs associated with fertilizations from males carrying selfish genetic elements.

In addition to polyandry, another overarching theme in the study of genetic quality has been the lek paradox and other papers in this issue deal specifically with this challenge (Kokko and Heubel 2008; Wolf et al. 2008). Radwan (2008) provides an exhaustive survey of the various hypotheses that have been presented as solutions to the lek paradox. Radwan reviews the mechanisms that can contribute to the maintenance of variation in additive genetic variation in sexual ornamentation (that female preference selects upon). Bussiere et al. (2008) review the issue of genotype by environment interaction (GEI) effects on mate choice for genetic quality. Bussiere and colleagues examine a suite of questions that will undoubtedly stimulate empirical research in the field of sexual selection as it relates to genetic quality, these questions included (among others) how important are GEIs at maintaining additive genetic variance and whether mating biases for high condition males evolved because of variation in genetic quality.

Roberts and Little (2008) reviewed the current literature regarding genetic quality and mate choice in humans. Humans are equally subject to the evolutionary processes governing the competition for mates and recent years have seen considerable work on elucidating the selective pressures that have shaped human mate preferences. Indeed, pioneering work on MHC based mate preferences in humans led the way for similar studies in other animals. Roberts and Little provide a review of how both good genes and compatible genes models of sexual selection relate to human mate preferences. Several studies have shown that humans utilize often subtle trait variation such as facial masculinity, digit length ratios, and skin condition as indicators of the genetic quality of a potential mate. Also, humans have been shown to pay attention to self-referential genetic dissimilarity-based characters such as the olfactory cues indicative of particular MHC haplotypes. Understanding how organisms integrate these two conflicting criteria for mate preferences into a single mate choice strategy remains a challenge and humans may prove ideal model organisms for tackling some aspects of this problem.

Conclusions and future challenges

As evident from this special issue, research into the relationship between genetic quality and sexual selection

appears to be vibrant and growing. Several recent reviews and this symposium have summarized previous work in the field and have pointed to new avenues of research. Future breakthroughs in the study of genetic quality appears to lie in the increased use of quantitative genetic approaches to assess the magnitude of additive and non-additive genetic effects on survival and reproductive success (e.g. Birkhead et al. 2005; Pitcher and Neff 2007), identify the genes that underlie genetic quality and mate choice (see Fitzpatrick et al. 2005 for a review of the candidate gene approach), partitioning of genetic quality variation to specific alleles and combinations of alleles (see Pitcher and Neff 2006 for a novel genetic algorithm), and examine gene by environment interactions (e.g. Welch 2003).

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