# Mate choice for genetic quality when environments vary: suggestions for empirical progress

**Luc F. Bussière · John Hunt · Kai N. Stölting · Michael D. Jennions · Robert Brooks**

**Abstract** Mate choice for good-genes remains one of the most controversial evolutionary processes ever proposed. This is partly because strong directional choice should theoretically deplete the genetic variation that explains the evolution of this type of female mating preference (the so-called lek paradox). Moreover, good-genes benefits are generally assumed to be too small to outweigh opposing direct selection on females. Here, we review recent progress in the study of mate choice for genetic quality, focussing particularly on the potential for genotype by environment interactions (GEIs) to rescue additive genetic variation for quality, and thereby resolve the lek paradox. We raise five questions that we think will stimulate empirical progress in this field, and suggest directions for research in each area: (1) How is condition-dependence affected by environmental variation? (2) How important are GEIs for maintaining additive genetic variance in condition? (3) How much do GEIs reduce the signalling value of male condition? (4) How does GEI affect the multivariate version of the lek paradox? (5) Have mating biases for high-condition males evolved because of indirect benefits?

**Abbreviations**
GEI  Genotype-by-environment interaction

L. F. Bussière · K. N. Stölting
Zoologisches Museum der Universität Zürich,
Winterthurerstrasse 190, CH 8057 Zürich, Switzerland

L. F. Bussière (✉)
School of Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA, UK
e-mail: luc.bussiere@stir.ac.uk

K. N. Stölting
e-mail: kai.stoelting@access.uzh.ch

J. Hunt
Centre for Ecology and Conservation, School of Biosciences, The University of Exeter in Cornwall, Penryn TR10 9EZ, UK
e-mail: J.Hunt@exeter.ac.uk

M. D. Jennions
School of Botany and Zoology, Australian National University, Canberra, ACT 0200, Australia
e-mail: michael.jennions@anu.edu.au

R. Brooks
Evolution & Ecology Research Centre and School of Biological, Earth and Environmental Sciences, The University of New South Wales, Sydney, NSW 2052, Australia
e-mail: rob.brooks@unsw.edu.au

## Introduction

The empirical demonstration of indirect benefits to mate choice remains challenging despite a quarter of a century of intense investigation (Kokko et al. 2003; Andersson and Simmons 2006). In this article, we briefly review how temporal and spatial environmental variation can contribute to the maintenance of additive genetic variation for fitness in spite of strong directional mate choice by females. We focus on the additive component of genetic variation because it is the most relevant to the lek paradox, although it is worth noting that selection on non-additive components of fitness can also affect the amount of non-additive genetic variation. We subsequently propose five

questions we think may stimulate progress in the empirical study of mate choice for good genes.

Since the controversy surrounding the evolution of female preferences for indirect benefits has been covered in detail elsewhere (Kirkpatrick and Ryan 1991; Andersson 1994; Kokko et al. 2003; Arnqvist and Rowe 2005), we treat the issue only briefly to provide the context for our discussion of future research directions. Consider a hypothetical species in which female preferences evolve solely to locate a mate of high genetic quality. The female fitness benefits of choice are therefore purely indirect, and their magnitude will covary with the amount of variation in genetic quality across males. The stronger the female preference, the greater the fitness benefit, but the sooner the variation in genetic quality that underpins this benefit will be eroded. This, in turn, will erode any indirect benefits of choosiness. This negative feedback cycle is the basis for the lek paradox: the genetic variation that favours female preferences is depleted by these very preferences (Rowe and Houle 1996; Tomkins et al. 2004).

The "genic capture" model is currently the most popular resolution to the lek paradox (Andersson 1982; Rowe and Houle 1996), and rests on the observation that many sexually selected traits are condition dependent (Tomkins et al. 2004), meaning that their degree of expression covaries with the ability of a male to acquire resources and convert them into structures, behaviours, or metabolic fuel. If females base their choice on condition-dependent sexual traits, rather than choosing males with genes for more elaborate sexual traits per se, they are choosing males on the basis of their ability to acquire resources. Because general performance in acquiring resources depends on many traits expressed by an individual, condition is likely to be encoded by many genes. Additive genetic variation for condition should therefore be eroded more slowly by directional selection, and should be supplemented more rapidly by mutation than additive variance for traits whose expression depends on fewer loci (Rowe and Houle 1996; Tomkins et al. 2004).

## What maintains genetic variation in the face of strong selection?

Genic capture notwithstanding, persistent selection will eventually deplete additive genetic variation for condition unless there are mechanisms to sustain it. These fall into four main categories: overdominance, frequency dependent selection, mutation, and fluctuating selection; see Radwan (2007) in the current issue for a review of mechanisms that maintain genetic variation in sexual traits in general. By definition, neither overdominance nor frequency dependent selection generate persistent directional selection for

specific alleles, and therefore we do not discuss them further in this article. The role of mutation in maintaining genetic variation has been the subject of several important reviews and many influential models (Houle 1989; Zeng and Cockerham 1993; Brcic-Kostic 2005; Zhang and Hill 2005). Rather than repeat this earlier work, we direct readers to these sources. Here we focus on fluctuating selection for two main reasons. First, the genic capture model relies on condition dependent sexual traits, which allows females to assess male condition regardless of the particular genes that increase it. In other words, genic capture enables remarkable plasticity in mate choice, because females favour whichever genes were most suitable for the environment in which the sire developed. The environmental heterogeneity that is often associated with fluctuating selection is therefore particularly relevant to the maintenance of additive genetic variance for sexually selected traits. Second, the empirical assessment of how GEIs influence sexual selection is a relatively recent preoccupation, and the field is thus ripe for an assessment of progress so far. We hope this will indicate fruitful directions for future work.

## Fluctuating selection and GEIs

Fluctuating selection involves changes in selection over time and/or space. This phenomenon therefore includes subcategories such as sexually antagonistic selection (Candolin 2004; Pischedda and Chippindale 2006) and balancing selection across different episodes of a life cycle or different social contexts (Moore and Moore 1999; Andersson et al. 2002; Bonduriansky and Rowe 2003; Candolin 2004). We will focus on influences of temporal and spatial environmental heterogeneity on sexual selection, because these have been the subject of the most empirical research across the widest diversity of animal systems.

Variation in condition could be maintained in spite of strong mate choice for high condition if the conditions under which males develop sexual traits do not covary perfectly with the conditions in which their offspring will develop (Greenfield and Rodriguez 2004). Although selection on condition itself is consistently positive, the direction of selection on specific alleles can change depending on environmental conditions. Consequently, females will sometimes choose the 'wrong' male thereby reducing the rate at which mate choice erodes additive variation.

Both temporal and spatial fluctuations in selection may be important for maintaining genetic variation, but the conditions under which temporal variation can sustain variation in isolation appear to be more restricted than those for spatial heterogeneity (Roff 1997). Specifically, in the same way that migration across spatially heterogeneous

patches promotes variance, some form of overlapping generations appears to be required to sustain variation in the face of temporally fluctuating selection (Ellner and Hairston 1994). This is because long-lived individuals that span different developmental environments are shielded from selection during the development of subsequent generations. Even if selection during the developmental period of a focal generation is quite severe, the older generations can contribute genes that are suboptimal for such conditions, but better suited to alternate environmental conditions. In contrast, severe selection in the absence of overlapping generations can lead to the fixation of alleles that are optimal in only the current context.

Both spatial and temporal fluctuations in selection can result in two forms of GEI: those involving changes in only the strength of selection or changes in the net direction of selection. The former might occur, for example, if under benign conditions the intensity of selection is depressed because all animals have access to ample resources and most males surpass a female mating criterion threshold. This will slow the depletion of additive variance relative to the case in a harsh environment where selection is much stronger, although the response to selection is difficult to predict because additive genetic variances can also change with the harshness of the environment (Gebhardt-Henrich and van Noordwijk 1991; Charmantier and Garant 2005). However, if the rank order of genotypic fitness stays constant across environments, this kind of fluctuating selection is unlikely to maintain additive variance in the face of persistent directional selection.

By contrast, reversals of the direction of selection on specific genotypes across environments or time have substantial potential to sustain genetic variation and have consequently received considerable theoretic attention (Haldane and Jayakar 1963; Felsenstein 1976; Hedrick et al. 1976; Takahata 1981; Hedrick 1986; Frank and Slatkin 1990; Bürger and Gimelfarb 2002), although less so than studies of mutation, perhaps on account of the relative difficulties in realistically modelling GEI (Byers 2005). Nevertheless, both one-locus (Kirzhner et al. 1995) and multi-locus or quantitative models (Kirzhner et al. 1994; Kondrashov and Yampolsky 1996) support a role for fluctuating selection in maintaining additive genetic variation. Bürger and Gimelfarb (2002) have recently shown in a mutation-selection model that under fluctuating selection, there is a positive relationship between the numbers of loci affecting a trait and the amount of genetic variation underlying it that can be maintained. This finding has clear relevance for selection on condition given the large number of loci that are likely to be involved (Rowe and Houle 1996).

In the current issue of *Genetica*, Kokko and Heubel (2007), have modelled how spatial heterogeneity affects the benefits of choice for condition-dependent signals of genetic quality. Their model demonstrates that GEI can either enhance or diminish genetic benefits to mate choice, depending on the degree to which GEI maintains variation (and therefore sustains genetic benefits to choice) and the extent to which it obscures signal quality (by diminishing the correlation between sire trait expression and the performance of offspring who might develop in a different environment). Crucial components affecting the outcome of their model include the mutation rate (the other source of genetic variation that is required if costly choice is to persist) and the timing of dispersal across environments (i.e. the extent to which females choose sires whose developmental environment differs from the likely environment in which their offspring will develop).

We surveyed recent empirical studies of GEI and sexual selection by searching the Web of Science for the last 10 years (1998–2007) using the following terms: ("sexual selection" OR "ornament" OR "mate choice" OR "female choice") AND ("GxE" OR "GEI" OR "genotype by environment" OR "genotype-environment interaction" OR "context dependen*"). This search yielded 49 studies. Fifteen of these are featured in Table 1, which summarizes their findings. Of the remaining papers, another five were relevant but did not provide results that could be summarized in Table 1. We omitted papers on GEI and sexual reproduction in plants ($n = 6$), where the theoretical expectations of mate choice evolution are sufficiently distinct to warrant separate treatment. The remaining studies were either theoretical and review papers ($n = 8$), or used the term "context-dependence" to refer to phenomena other than GEI ($n = 15$).

The studies in Table 1 were conducted on a range of taxa (insects, fish, frogs, mammals, and birds), using a variety of approaches, with laboratory and field studies on a number of environmental dimensions, some experimentally induced, and others estimated by observation. They suggest that GEIs for sexually selected traits are relatively common, at least in the systems that are amenable to this type of research. Unsurprisingly, GEIs for sexually selected traits frequently accompany GEIs for other performance indices. We note that many studies relied on full-sib analyses and so cannot distinguish maternal effects from additive genetic variance, and that performance is rarely assessed in a way that approximates total fitness (e.g., number of grandchildren). Although GEIs could be statistically detected or inferred in many studies, in 5 of the 11 studies commenting on the consistency of performance ranks there was little evidence that the environmental background determined which genotypes outperformed others (i.e., there was no evidence of rank-order changes in genotype performance across environments). This could be a problem of statistical power or reflect practical

**Table 1** A summary of selected studies featuring investigations of GEI and sexually selected traits in the last decade (1998–2007). See the text for a detailed description of how the survey was conducted

| Taxon | Environmental dimension(s) | GEI for sexually selected male trait | GEI for performance index | Rank-order change in performance or mating success across environments | Environmental dependence of mate choice benefits | Reference |
|---|---|---|---|---|---|---|
| Bank vole (*Clethrionomys glareolus*) | Litter size | Yes (dominance) | No (condition: residuals of body mass on head width) | Yes | Yes (dominant males sire more dominant sons only when reared in similar environments) | (Mills et al. 2007) |
| Blue tit (*Parus caeruleus*) | Experimentally manipulated brood size | | No?[a] (tarsal length) | No | | (Merila et al. 1999) |
| Coal tit (*Parus ater*) | Early versus late in the season | | Yes (recruitment & no. of grandchildren) | Yes | Yes (extrapair young have higher fitness if born late in the season) | (Schmoll et al. 2005) |
| Collared flycatcher (*Ficedula albicollis*) | Year of study | | | | Yes (benefits of mating older male not apparent in some years) | (Hegyi et al. 2006) |
| Collared flycatcher (*Ficedula albicollis*) | Year of study & experimentally manipulated brood size | | | | Yes (sons resembled fathers only during favourable conditions) | (Qvarnstrom 1999) |
| *Drosophila mojavensis* | Host cactus species | Yes (song traits) | | Yes | | (Etges et al. 2007) |
| Gray tree frog (*Hyla versicolor*) | Larval density | | Yes (developmental period & size at metamorphosis) | Yes | Yes (choice adaptive in only one environment) | (Welch 2003) |
| Guppy (*Poecilia reticulata*) | Social environment (opportunity to expend energy mating and courting) | No (male colour, display rate & attractiveness) | No (male size) | No | | (Miller and Brooks 2005) |
| Lesser waxmoth (*Achroia grisella*) | Food quantity, temperature, & photoperiod | Yes (male signal rate) | Yes (developmental period) | Yes | | (Jia et al. 2000) |
| Lesser waxmoth (*Achroia grisella*) | Larval density | Yes (song attractiveness) | Yes (body mass & development rate) | Yes | | (Danielson-Francois et al. 2006) |
| Lesser waxmoth (*Achroia grisella*) | Temperature | Yes (song attractiveness) | | | Yes? (significant GEI for threshold of female choice) | (Rodriguez and Greenfield 2003) |

**Table 1** continued

| Taxon | Environmental dimension(s) | GEI for sexually selected male trait | GEI for performance index | Rank-order change in performance or mating success across environments | Environmental dependence of mate choice benefits | Reference |
|---|---|---|---|---|---|---|
| Moor frog (*Rana arvalis*) | Predator size | | Yes (survival) | | Yes (higher survival for offspring of blue males only when predator is large) | (Sheldon et al. 2003) |
| Orange sulphur butterfly (*Colias eurytheme*) | Food quality & presence of thermal stress | No[b] (wing colouration) | | No[b] | | (Kemp and Rutowski 2007) |
| Stalk-eyed fly (*Cyrtodiopsis dalmanni*) | Food quality | Yes (eye span) | | No | | (David et al. 2000) |
| Tree swallow (*Tachycineta bicolor*) | Nest temperature & parasite abundance | | Yes (longer flight feathers) | No | Yes (genetic benefits significant only in favourable environment) | (O'Brien and Dawson 2007) |

[a] Merila et al. (1999) report a marginally non-significant GEI during the harshest year, but no GEI in other years

[b] Kemp and Rutowski (2007) do report some significant GEI, but not in the pattern expected if GEI is a large factor in signal evolution

limitations in exposing populations to sufficient naturally relevant environmental heterogeneity. Alternatively, it might suggest that GEIs often reduce the efficiency of directional selection, but only sometimes change its sign. We focus the remainder of this article on exploring how this question and others might be resolved in future studies.

## Suggested directions for empirical progress in studying mate choice for genetic quality

### How is condition-dependence affected by environmental variation?

We still know very little about the mechanics underlying the acquisition of resources and allocation to life history traits in a single environment, let alone in multiple environments. Are sexually selected traits particularly sensitive to environmental influences on condition because small deviations from the optimal level of expression for male in a given condition can have large fitness costs, while, costs aside, increased expression is always favoured due to directional female choice (Glazier 2002; Bonduriansky and Rowe 2005)? To what extent is the condition-dependence of traits sex-specific, with males showing much steeper condition-dependence due to sexual selection for increased trait expression, and concomitant selection on females for condition-independence (Bonduriansky and Rowe 2005)? Does allocation to different condition-dependent traits vary across environmental conditions, and does it respond to selection in a similar way to other allocation trade-offs; in other words is there something special about allometric investment in condition-dependent traits (Emlen 1996; Frankino et al. 2005; Bonduriansky 2007)? To what extent is variation across populations in allocation to condition-dependent sexual traits determined by the strength of sexual selection imposed by choosy females, as opposed to environmental variation, such as the mean level of acquisition (Roff and Fairbairn 2007)?

The answers to these questions require the estimation of two notoriously elusive parameters: condition (i.e., resource acquisition ability) and the allocation strategy of individuals. Many problems with condition indices have been ably discussed elsewhere (Tomkins et al. 2004; Cotton et al. 2006; Lailvaux and Irschick 2006), and do not need to be repeated. However, there are special problems associated with simple condition indices that focus on a single trait; for example, body mass (Brandt and Greenfield 2004) or the residuals of a regression of body mass on body size (Kotiaho et al. 2001). Condition indices are invariably life-history traits, so they are

expected to trade-off against other life-history traits, including sexual signals (Hunt et al. 2004b). For example, there is a long history of assuming that longevity is a correlate of condition because, all else being equal, individuals with more resources should live longer (Kokko 1998). However, all else is rarely equal. The marginal payoffs to investment in life history traits are expected to change across environments and across different levels of resource acquisition. While long-lived animals may have higher fitness in some situations, in others it is better to reproduce early in life at the expense of longevity (Brooks 2000; Kokko et al. 2002; Hunt et al. 2004b). Longevity has been shown to covary negatively with resource availability and early-life reproductive success in several recent studies (Charmantier et al. 2006; Hunt et al. 2006; Robinson et al. 2006). Hunt et al. (2004a) showed that the sign of the correlation between longevity and condition can change depending on resource availability, demonstrating that traits that reliably signal quality under some conditions do not do so under others. While this work is especially relevant to the usefulness of longevity as a condition index, it also advocates caution in interpreting the signal value of any other single condition-dependent life-history trait.

Ultimately, we need to know more about the relationship between condition indices, acquisition, and the conversion of resources to phenotypic traits (Tomkins et al. 2004). Just as multivariate analyses of selection have the potential to reveal otherwise cryptic patterns in selection for complex phenotypes (Blows 2007), it would be useful to know how multivariate approaches to condition improve one's estimate of performance. One approach is to replace one-dimensional estimates of size, for example, with geometric morphometric estimates (Klingenberg 2003). These analyses separately estimate the size and shape of morphological structures as distinct parameters, so they should be less likely to mistake changes in total allocation with changes in body form. In addition, one could adopt data reduction techniques to find the axes of variance across both morphological and life-history traits that is most likely to reflect condition (in contrast to size alone, which is sometimes a weak index of performance, Tomkins et al. 2004). It is well-established that the sign of phenotypic covariance between life-history traits tends to be positive when most of the variation in performance is due to differences in acquisition, and negative when most of the variation is due to differences in allocation (van Noordwijk and de Jong 1986; Glazier 1999; Roff and Fairbairn 2007). Consequently, a strong index of condition may be expected to covary positively with a range of life history traits. Canonical analyses (e.g., principal components analysis) could provide the best condition indices by revealing the major axis of positive phenotypic covariance across life-history traits and morphology. One limitation is that in the

absence of prior knowledge of their relative cost (in terms of raw resources), the relative weighting of different life history components will be rather arbitrary. Nevertheless, multivariate approaches cannot provide worse information than individual condition indices, and may help considerably when comparing animals whose allocation strategies to different traits differ, e.g., in species with status-dependent investment in sexual traits such as dung beetles, (Hunt and Simmons 2001), earwigs (Forslund 2003) and mites (Radwan et al. 2002).

Quantifying differences in allocation strategies across individuals represents another central challenge in the study of condition-dependence. In many instances it is nearly impossible to partition the relative importance of acquisition and allocation to the expression of a given condition-dependent sexual trait (Hunt et al. 2004b). In some systems where adults do not feed, this problem can be partly circumvented because acquisition can be estimated before adults allocate resources to different life-history components (Brandt and Greenfield 2004). Laboratory studies that experimentally manipulate resource availability have also proven useful in studying allocation patterns across different genotypes (Hunt et al. 2004a; Bondurian-sky and Rowe 2005). A complementary approach is to manipulate allocation for a given level of acquisition. Simmons and Emlen (2006) artificially prevented investment in sexually selected beetle horns by cauterizing larval cells that are the precursors to horns in adults, and thereby demonstrated how allocation to horns came at a net cost to investment in testes. Adopting such techniques for traits that are the primary target of mate choice could reveal more about how the allocation of resources to such traits trades off with other life history traits.

## How important are GEIs for maintaining additive genetic variance in condition?

GEIs present an exciting avenue for exploring Rowe and Houle's (1996) model of sexual selection because a key insight of genic capture is that condition dependence allows females to evaluate male performance regardless of the source of the variation in male condition. Although many laboratory manipulations of environment have revealed the near ubiquity of GEIs, in most studies the number of simultaneously presented environments has been low for logistical reasons (i.e.. generally only two environments are tested in the laboratory). Even when several environments are presented, they tend to differ along a single environmental dimension, such as food quality or temperature (but see Table 1 for exceptions). As a result, these studies may overestimate the extent to which some genetic variants are consistently the best performing

across treatments (e.g., animals with superior foraging ability regardless of the resource level), because the same genetic variants may be inferior when exposed to other stressors. Species in which there is no evidence for GEI or rank-order changes in the expression of sexually selected traits (Merila 1996; David et al. 2000) may therefore still exhibit appreciable genetic variance as a result of GEI. Moreover, environmental heterogeneity may sustain even more genetic variation than our best empirical studies suggest if much of the genetic variation arising from GEI is cryptic, and only observable once specific environmental perturbations arise (Gibson and Dworkin 2004). This is because the penetrance of some mutations depends on environmental conditions and genetic background; for example, alleles that are effectively neutral in benign situations may play a role in promoting survival under certain kinds of stress (Dykhuizen and Hartl 1980). Only large-scale genetic studies in which many environmental variables are simultaneously manipulated can address this question.

A complementary approach to laboratory manipulations of the environment involves estimating GEIs in pedigreed natural populations using an animal model (Kruuk 2004). In principle, this statistical approach to partitioning phenotypic variation into its causal components has considerable power to detect the influence of environmental covariates on genetic variance, particularly in conjunction with "random regression" models that estimate random effects variance components such as environmental conditions (Henderson 1982). Although random regression has been extensively used in the animal breeding literature (Schaeffer 2004), it has only recently been adopted for evolutionary studies of GEIs (Wilson et al. 2006; Nussey et al. 2007). In a pioneering study, Wilson et al. (2006) have illustrated its potential by demonstrating the influence of environmental quality, estimated using lamb survival rates, on selection and genetic variance in Soay sheep. Since the theoretical basis for these analyses is firmly rooted in quantitative genetics, their estimated parameters such as breeding values scale directly with the presumed indirect benefits of mate choice for genetic quality. More importantly, however, using animal models in natural populations enables one to assess the consequences of mate choice under biologically realistic levels of natural and sexual selection.

### How much do GEIs reduce the signalling value of male condition?

GEIs can both rescue additive genetic variance for condition and also weaken selection for female preferences (Greenfield and Rodriguez 2004; Kokko and Heubel 2007; Mills et al. 2007). This occurs because environmental

fluctuations disrupt the predictive relationship between a sire's phenotype and the performance of his offspring. In other words, whenever GEIs affect condition, the signal quality of a sire's condition-dependent trait depends on the similarity between the environment that the sire has experienced during his development and that of his offspring. More generally, mate choice for indirect benefits that is based on condition dependent characters is only adaptive if the phenotypic value of a signal trait has a considerable genetic component (Rowe and Houle 1996). Even without GEI, environmental variances could disrupt the signal to a significant degree, and therefore decrease selection on females for exerting choice on the basis of genetic quality (Hunt et al. 2004b). Studies that manipulate both the environment of sires and of their offspring may reveal the extent to which the signal value of sexual traits depends on the congruence of sire and offspring environments.

Whether GEIs substantially reduce genetic benefits is a question well suited for testing in wild populations (where environmental differences can be well characterised) using the animal model. One important caveat is that when testing hypotheses about how male phenotype predicts genetic quality, the breeding values for individual sires should be estimated from the dataset while iteratively omitting the sire's own phenotype (but including the phenotypes of all other sires) (Postma 2006). The reasons for this precaution are two-fold. First, because one important component of the sire's breeding value is his own level of sexual advertisement, a test of the correlation between advertisement and the sire's breeding value for fitness (which includes advertisement) would amount to autocorrelation. Second, if one wishes to study the relationship between sexual advertisement and offspring fitness in several environments, the sire phenotype is only useful for the environment that the sire experienced. By omitting the sire from this estimate, one can fairly compare the breeding value across environments because the breeding values in all environments are estimated from a similar group of related individuals (i.e., not including the sire himself). Consequently, just as the animal model allows one to estimate breeding values for male traits in a female that never expresses them, one could similarly estimate the environment-specific breeding values for the condition of animals that have never themselves experienced the environment in question.

### How does GEI affect the multivariate version of the lek paradox?

Although there is mounting evidence of ample additive genetic variation in sexual signals and life-history traits,

and that the requirements for the genic capture model may often be satisfied (Kotiaho et al. 2001; Tomkins et al. 2004), several recent studies suggest that the lek paradox may persist in a multivariate form. These studies show that there is often relatively little multivariate genetic variation in the main direction of multivariate selection (the direction in which selection is pushing the population mean; (Hall et al. 2004; Hine et al. 2004; Blows and Hoffmann 2005; Van Homrigh et al. 2007). Similarly, the main axes of multivariate stabilizing sexual selection (Brooks et al. 2005) can also be associated with depleted genetic variance, with most genetic variation in cricket call structure occurring in multivariate directions under very weak selection (Hunt et al. 2007). Thus, even if there is substantial genetic variation for individual traits there may remain little potential to gain genetic benefits from choice because of the associations between genes for different traits. Two manipulative tests in different species of Australian *Drosophila* indicate that variation in resource acquisition is unlikely to resolve the lack of relevant multivariate genetic variation (Hine et al. 2004; Van Homrigh et al. 2007).

The importance of using multivariate methods when studying sexual selection and evolution is only now receiving the attention it deserves (see Blows 2007, and subsequent commentary in the same issue). To the extent that GEI is an important element underlying the evolution and maintenance of female choice for indirect benefits, it complicates the study of multivariate phenotypic selection because the genetic architecture that defines constraints on evolutionary change can itself change with different environmental conditions (Sgrò and Hoffmann 2004). Much more work is needed to clarify the concordance of multivariate axes of selection and genetic variation in natural populations, both within and across meaningful dimensions of environmental heterogeneity, and to determine whether this constitutes a full multivariate resurrection of the lek paradox.

### Have mating biases for high-condition males evolved because of indirect benefits?

Ultimately, determining whether mating biases evolved in the context of mate choice for good-genes requires a concerted effort to study the fitness consequences of genetic variation in female choice. We suggest that researchers focus on the details of variation in mating biases within and across different environments (see Rodriguez and Greenfield 2003). Whether the model of mate choice for genetic benefits accounts for much of the observed diversity in sexual traits depends on whether female preferences actually increase female fitness via indirect effects. Our field

has been justifiably preoccupied with the difficult challenge of demonstrating that indirect benefits of mating with high condition males exist. In fact, the evidence favouring substantial genetic benefits is still sparse (but see e.g., Welch et al. 1998; Tallamy et al. 2003; Head et al. 2005). Some authors have recently argued that there has been too much emphasis on adaptive female choice to the exclusion of alternative explanations for mating biases, such as male manipulation (Arnqvist and Kirkpatrick 2005; but see Griffith 2007). We agree that selection on males could play an important (and in some cases underappreciated) role in determining mating biases, but wish to emphasize that the fitness consequences of variation in female choice have received too little attention because it is simpler to assume that all females have a similar mate choice strategy. The solution to this dilemma requires more information on selection on choice in females in conjunction with a thorough study of potentially conflicting male interests. Selection analysis of male traits has proved useful in exploring how sexual selection operates on male sexual traits (e.g., Hine et al. 2004; LeBas et al. 2004; Brooks et al. 2005; Bentsen et al. 2006). The potential for applying these techniques to the study of female mating preferences is similarly strong, particularly in conjunction with tests of the reliability of male signals and female mating preferences across heterogeneous environments, and will help test the assumption that variation in mating decisions represents adaptive plasticity by females (Shuster and Wade 2003).

### References

Andersson M (1982) Sexual selection, natural selection and quality advertisement. Biol J Linn Soc 17:375–393

Andersson M (1994) Sexual selection. Princeton University Press, Princeton, NJ

Andersson M, Simmons LW (2006) Sexual selection and mate choice. Trends Ecol Evol 21:296–302

Andersson S, Pryke SR, Ornborg J, Lawes MJ, Andersson M (2002) Multiple receivers, multiple ornaments, and a trade-off between agonistic and epigamic signaling in a widowbird. Am Nat 160:683–691

Arnqvist G, Kirkpatrick M (2005) The evolution of infidelity in socially monogamous passerines: the strength of direct and indirect selection on extrapair copulation behavior in females. Am Nat 165:S27–S36

Arnqvist G, Rowe L (2005) Sexual conflict. Princeton University Press, Princeton

Bentsen CL, Hunt J, Jennions MD, Brooks R (2006) Complex multivariate sexual selection on male acoustic signaling in a wild population of *Teleogryllus commodus*. Am Nat 167:E102–E116

Blows MW (2007) A tale of two matrices: multivariate approaches in evolutionary biology. J Evol Biol 20:1–8

Blows MW, Hoffmann AA (2005) A reassessment of genetic limits to evolutionary change. Ecology 86:1371–1384

Bonduriansky R (2007) The evolution of condition-dependent sexual dimorphism. Am Nat 169:9–19

Bonduriansky R, Rowe L (2003) Interactions among mechanisms of sexual selection on male body size and head shape in a sexually dimorphic fly. Evolution 57:2046–2053

Bonduriansky R, Rowe L (2005) Sexual selection, genetic architecture, and the condition dependence of body shape in the sexually dimorphic fly *Prochyliza xanthostoma* (Piophilidae). Evolution 59:138–151

Brandt LSE, Greenfield MD (2004) Condition-dependent traits and the capture of genetic variance in male advertisement song. J Evol Biol 17:821–828

Brcic-Kostic K (2005) Neutral mutation as the source of genetic variation in life history traits. Genet Res 86:53–63

Brooks R (2000) Negative genetic correlation between male sexual attractiveness and survival. Nature 406:67–70

Brooks R, Hunt J, Blows MW, Smith MJ, Bussière LF, Jennions MD (2005) Experimental evidence for multivariate stabilizing sexual selection. Evolution 59:871–880

Bürger R, Gimelfarb A (2002) Fluctuating environments and the role of mutation in maintaining quantitative genetic variation. Genet Res 80:31–46

Byers DL (2005) Evolution in heterogeneous environments and the potential of maintenance of genetic variation in traits of adaptive significance. Genetica 123:107–124

Candolin U (2004) Opposing selection on a sexually dimorphic trait through female choice and male competition in a water boatman. Evolution 58:1861–1864

Charmantier A, Garant D (2005) Environmental quality and evolutionary potential: lessons from wild populations. Proc R Soc Lond B 272:1415–1425

Charmantier A, Perrins C, McCleery RH, Sheldon BC (2006) Quantitative genetics of age at reproduction in wild swans: support for antagonistic pleiotropy models of senescence. Proc Natl Acad Sci USA 103:6587–6592

Cotton S, Small J, Pomiankowski A (2006) Sexual selection and condition-dependent mate preferences. Curr Biol 16:R755–R765

Danielson-Francois AM, Kelly JK, Greenfield MD (2006) Genotype x environment interaction for male attractiveness in an acoustic moth: evidence for plasticity and canalization. J Evol Biol 19:532–542

David P, Bjorksten T, Fowler K, Pomiankowski A (2000) Condition-dependent signalling of genetic variation in stalk-eyes flies. Nature 406:186–188

Dykhuizen D, Hartl DL (1980) Selective neutrality of 6PGD allozymes in *Escherichia coli* and the effects of genetic background. Genetics 96:801–817

Ellner S, Hairston NG (1994) Role of overlapping generations in maintaining genetic variation in a fluctuating environment. Am Nat 143:403–417

Emlen DJ (1996) Artificial selection on horn length body-size allometry in the horned beetle *Onthophagus acuminatus* (Coleoptera, Scarabaeidae). Evolution 50:1219–1230

Etges WJ, de Oliveira CC, Gragg E, Ortiz-Barrientos D, Noor MAF, Ritchie MG (2007) Genetics of incipient speciation in *Drosophila mojavensis*. I. Male courtship song, mating success, and genotype x environment interactions. Evolution 61:1106–1119

Felsenstein J (1976) The theoretical population genetics of variable selection and migration. Ann Rev Genet 10:253–280

Forslund P (2003) An experimental investigation into status dependent male dimorphism in the European earwig, *Forficula auricularia*. Anim Behav 65:309–316

Frank SA, Slatkin M (1990) Evolution in a variable environment. Am Nat 136:244–260

Frankino WA, Zwaan BJ, Stern DL, Brakefield PM (2005) Natural selection and developmental constraints in the evolution of allometries. Science 307:718–720

Gebhardt-Henrich SG, van Noordwijk AJ (1991) Nestling growth in the Great Tit. I. Heritability estimates under different environmental conditions. J Evol Biol 3:341–362

Gibson G, Dworkin I (2004) Uncovering cryptic genetic variation Nature Reviews. Genetics 5:681–U11

Glazier DS (1999) Trade-offs between reproductive and somatic (storage) investments in animals: a comparative test of the van Noordwijk and de Jong model. Evol Ecol 13:539–555

Glazier DS (2002) Resource-allocation rules and the heritability of traits. Evolution 56:1696–1700

Greenfield MD, Rodriguez RL (2004) Genotype-environment interactions and the reliability of mating signals. Anim Behav 68:1461–1468

Griffith SC (2007) The evolution of infidelity in socially monogamous passerines: neglected components of direct and indirect selection. Am Nat 169:274–281

Haldane JBS, Jayakar SD (1963) Polymorphism due to selection of varying direction. Heredity 58:237–242

Hall M, Lindholm AK, Brooks R (2004) Direct selection on male attractiveness and female preference fails to produce a response. BMC Evol Biol 4:1

Head ML, Hunt J, Jennions MD, Brooks R (2005) The indirect benefits of mating with attractive males outweigh the direct costs. PLoS Biol 3:289–294

Hedrick PW (1986) Genetic polymorphism in heterogeneous environments: a decade later. Ann Rev Ecol Syst 17:535–566

Hedrick PW, Ginevan ME, Ewing EP (1976) Genetic polymorphism in heterogeneous environments. Ann Rev Ecol Syst 7:1–32

Hegyi G, Rosivall B, Torok J (2006) Paternal age and offspring growth: separating the intrinsic quality of young from rearing effects. Behav Ecol Sociobiol 60:672–682

Henderson CR (1982) Analysis of covariance in the mixed model: higher-level, non-homogeneous, and random regressions. Biometrics 38:623–640

Hine E, Chenoweth SF, Blows MW (2004) Multivariate quantitative genetics and the lek paradox: genetic variance in male sexually selected traits of *Drosophila serrata* under field conditions. Evolution 58:2754–2762

Houle D (1989) The maintenance of polygenic variation in finite populations. Evolution 43:1767–1780

Hunt J, Blows MW, Zajitschek F, Jennions MD, Brooks R (2007) Reconciling strong stabilizing selection with the maintenance of genetic variation in a natural population of black field crickets (*Teleogryllus commodus*). Genetics 177:875–880

Hunt J, Brooks R, Jennions MD, Smith MJ, Bentsen CL, Bussière LF (2004a) High-quality male field crickets invest heavily in sexual display but die young. Nature 432:1024–1027

Hunt J, Bussière LF, Jennions MD, Brooks R (2004b) What is genetic quality? Trends Ecol Evol. 19:329–333

Hunt J, Jennions MD, Spyrou N, Brooks R (2006) Artificial selection on male longevity influences age-dependent reproductive effort in the black field cricket *Teleogryllus commodus*. Am Nat 168:E72–E86

Hunt J, Simmons LW (2001) Status-dependent selection in the dimorphic beetle *Onthophagus taurus*. Proc R Soc Lond B 268: 2409–2414

Jia FY, Greenfield MD, Collins RD (2000) Genetic variance of sexually selected traits in waxmoths: maintenance by genotype x environment interaction. Evolution 54:953–967

Kemp DJ, Rutowski RL (2007) Condition dependence, quantitative genetics, and the potential signal content of iridescent ultraviolet butterfly coloration. Evolution 61:168–183

Kirkpatrick M, Ryan M (1991) The evolution of mating preferences and the paradox of the lek. Nature 350:33–38

Kirzhner VM, Korol AB, Ronin YI, Nevo E (1994) Cyclical behavior of genotype frequencies in a 2–locus population under fluctuating haploid selection. Proc Natl Acad Sci USA 91:11432–11436

Kirzhner VM, Korol AB, Ronin YI, Nevo E (1995) Genetic supercycles caused by cyclical selection. Proc Natl Acad Sci USA 92: 7130–7133

Klingenberg CP (2003) Quantitative genetics of geometric shape: heritability and the pitfalls of the univariate approach. Evolution 57:191–195

Kokko H (1998) Good genes, old age and life-history trade-offs. Evol Ecol 12:739–750

Kokko H, Brooks R, Jennions MD, Morley J (2003) The evolution of mate choice and mating biases. Proc R Soc Lond B 270:653–664

Kokko H, Brooks R, McNamara JM, Houston AI (2002) The sexual selection continuum. Proc R Soc Lond B 269:1331–1340

Kokko H, Heubel K (2007) Condition-dependence, genotype-by-environment interactions, and the lek paradox. Genetica. doi: 10.1007/s10709-007-9166-1

Kondrashov AS, Yampolsky LY (1996) High genetic variability under the balance between symmetric mutation and fluctuating stabilizing selection. Genet Res 68:157–164

Kotiaho JS, Simmons LW, Tomkins JL (2001) Towards a resolution of the lek paradox. Nature 410:684–686

Kruuk LEB (2004) Estimating genetic parameters in natural populations using the 'animal model'. Phil Trans R Soc Lond B 359:873–890

Lailvaux SP, Irschick DJ (2006) A functional perspective on sexual selection: insights and future prospects. Anim Behav 72:263–273

LeBas NR, Hockham LR, Ritchie MG (2004) Sexual selection in the gift-giving dance fly, *Rhamphomyia sulcata*, favors small males carrying small gifts. Evolution 58:1763–1772

Merila J (1996) Genetic variation in offspring condition: an experiment. Funct Ecol 10:465–474

Merila J, Przybylo R, Sheldon BC (1999) Genetic variation and natural selection on blue tit body condition in different environments. Genet Res 73:165–176

Miller LK, Brooks R (2005) The effects of genotype, age, and social environment on male ornamentation, mating behavior, and attractiveness. Evolution 59:2414–2425

Mills SC, Alatalo RV, Koskela E, Mappes J, Mappes T, Oksanen TA (2007) Signal reliability compromised by genotype-by-environment interactions and potential mechanisms for its preservation. Evolution 61:1748–1757

Moore AJ, Moore PJ (1999) Balancing sexual selection through opposing mate choice and male competition. Proc R Soc Lond B 266:711–716

Nussey DH, Wilson AJ, Brommer JE (2007) The evolutionary ecology of individual phenotypic plasticity in wild populations. J Evol Biol 20:831–844

O'Brien EL, Dawson RD (2007) Context-dependent genetic benefits of extra-pair mate choice in a socially monogamous passerine. Behav Ecol Sociobiol 61:775–782

Pischedda A, Chippindale AK (2006) Intralocus sexual conflict diminishes the benefits of sexual selection. PLoS Biol 4:2099–2103

Postma E (2006) Implications of the difference between true and predicted breeding values for the study of natural selection and micro-evolution. J Evol Biol 19:309–320

Qvarnstrom A (1999) Genotype-by-environment interactions in the determination of the size of a secondary sexual character in the collared flycatcher (*Ficedula albicollis*). Evolution 53:1564–1572

Radwan J (2007) Maintenance of genetic variation in sexual ornaments: a review of the mechanisms. Genetica. doi:10.1007/s10709-007-9203-0

Radwan J, Unrug J, Tomkins JL (2002) Status-dependence and morphological trade-offs in the expression of a sexually selected character in the mite, *Sancassania berlesei*. J Evol Biol 15:744–752

Robinson MR, Pilkington JG, Clutton-Brock TH, Pemberton JM, Kruuk LEB (2006) Live fast, die young: trade-offs between fitness components and sexually antagonistic selection on weaponry in Soay sheep. Evolution 60:2168–2181

Rodriguez RL, Greenfield MD (2003) Genetic variance and phenotypic plasticity in a component of female mate choice in an ultrasonic moth. Evolution 57:1304–1313

Roff DA (1997) Evolutionary quantitative genetics. Chapman & Hall, New York

Roff DA, Fairbairn DJ (2007) The evolution of trade-offs: where are we? J Evol Biol 20:433–447

Rowe L, Houle D (1996) The lek paradox and the capture of genetic variance by condition dependent traits. Proc R Soc Lond B 263:1415–1421

Schaeffer LR (2004) Application of random regression models in animal breeding. Livest Prod Sci 86:35–45

Schmoll T, Dietrich V, Winkel W, Epplen JT, Schurr F, Lubjuhn T (2005) Paternal genetic effects on offspring fitness are context dependent within the extrapair mating system of a socially monogamous passerine. Evolution 59:645–657

Sgrò CM, Hoffmann AA (2004) Genetic correlations, tradeoffs and environmental variation. Heredity 93:241–248

Sheldon BC, Arponen H, Laurila A, Crochet PA, Merila J (2003) Sire coloration influences offspring survival under predation risk in the moorfrog. J Evol Biol 16:1288–1295

Shuster SM, Wade MJ (2003) Mating systems and strategies. Princeton University Press, Princeton

Simmons LW, Emlen DJ (2006) Evolutionary trade-off between weapons and testes. Proc Natl Acad Sci USA 103:16346–16351

Takahata N (1981) Genetic variability and rate of gene substitution in a finite population under mutation and fluctuating selection. Genetics 98:427–440

Tallamy DW, Darlington MB, Pesek JD, Powell BE (2003) Copulatory courtship signals male genetic quality in cucumber beetles. Proc R Soc Lond B 270:77–82

Tomkins JL, Radwan J, Kotiaho JS, Tregenza T (2004) Genic capture and resolving the lek paradox. Trends Ecol Evol 19:323–328

Van Homrigh A, Higgie M, McGuigan K, Blows MW (2007) The depletion of genetic variance by sexual selection. Curr Biol 17:528–532

van Noordwijk AJ, de Jong G (1986) Acquisition and allocation of resources: their influence on variation in life-history tactics. Am Nat 128:137–142

Welch AM (2003) Genetic benefits of a female mating preference in gray tree frogs are context-dependent. Evolution 57:883–893

Welch AM, Semlitsch RD, Gerhardt HC (1998) Call duration as an indicator of genetic quality in male gray tree frogs. Science 280:1928–1930

Wilson AJ, Pemberton JM, Pilkington JG, Coltman DW, Mifsud DV, Clutton-Brock TH, Kruuk LEB (2006) Environmental coupling of selection and heritability limits evolution. PLoS Biol 4:1270–1275

Zeng ZB, Cockerham CC (1993) Mutation models and quantitative genetic-variation. Genetics 133:729–736

Zhang XS, Hill WG (2005) Genetic variability under mutation selection balance. Trends Ecol Evol 20:468–470