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Mate choice for genetic quality when environments vary: suggestions for

empirical progress

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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 preferences (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?

Key words: condition dependence; environmental heterogeneity; female preference;

fluctuating selection; good-genes; indirect benefits; lek paradox; resource acquisition;

resource allocation; sexual selection

Abbreviations: GEI: genotype-by-environment interaction

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 matechoice 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).

71   The "genic capture" model is currently the most popular resolution to the lek

72   paradox (Andersson 1982; Rowe and Houle 1996), and rests on the observation that

73   many sexually selected traits are condition dependent (Tomkins et al. 2004); that is,

74   their degree of expression covaries with the ability of a male to acquire resources and

75   convert them into structures, behaviours, or metabolic fuel. If females base their

76   choice on condition-dependent sexual traits, rather than choosing males with genes for

77   more elaborate sexual traits *per se*, they are choosing males on the basis of their

78   ability to acquire resources. Because general performance in acquiring resources

79   depends on many traits expressed by an individual, condition is likely to be encoded

80   by many genes. Additive genetic variation for condition should therefore be eroded

81   more slowly by directional selection, and should be supplemented more rapidly by

82   mutation than additive variance for traits whose expression depends on fewer loci

83   (Rowe and Houle 1996; Tomkins et al. 2004).

84

85   **What maintains genetic variation in the face of strong selection?**

86   Genic capture notwithstanding, persistent selection will eventually deplete

87   additive genetic variation for condition unless there are mechanisms to sustain it.

88   These fall into four main categories: overdominance, frequency dependent selection,

89   mutation, and fluctuating selection. By definition, neither overdominance nor

90   frequency dependent selection generate persistent directional selection for specific

91   alleles, and therefore we do not discuss them further in this article. The role of

92   mutation in maintaining genetic variation has been the subject of several important

93   reviews and many influential models (Houle 1989; Zeng and Cockerham 1993; Brcic-

94   Kostic 2005; Zhang and Hill 2005). Rather than repeat this earlier work, we direct

95   readers to these sources. Here we focus on fluctuating selection for two main reasons.

96   First, the genic capture model relies on condition dependent sexual traits, which

97   allows females to assess male condition regardless of the particular genes that

98   increase it. In other words, genic capture enables remarkable plasticity in mate choice,

99   because females favour whichever genes were most suitable for the environment in

100   which the sire developed. The environmental heterogeneity that is often associated

101   with fluctuating selection is therefore particularly relevant to the maintenance of

102   additive genetic variance for sexually selected traits. Second, the empirical assessment

103   of how GEIs influence sexual selection is a relatively recent preoccupation, and the

104   field is thus ripe for an assessment of progress so far. We hope this will indicate

105   fruitful directions for future work.

106

107   **Fluctuating selection and GEIs**

108   Fluctuating selection involves changes in selection over time and/or space.

109   This phenomenon therefore includes subcategories such as sexually antagonistic

110   selection (Candolin 2004; Pischedda and Chippindale 2006) and balancing selection

111   across different episodes of a life cycle or different social contexts (Moore and Moore

112   1999; Andersson et al. 2002; Bonduriansky and Rowe 2003; Candolin 2004). We will

113   focus on influences of temporal and spatial environmental heterogeneity on sexual

114   selection, because these have been the subject of the most empirical research across

115   the widest diversity of animal systems.

116   Variation in condition could be maintained in spite of strong mate choice for

117   high condition if the conditions under which males develop sexual traits do not covary

118   perfectly with the conditions in which their offspring will develop (Greenfield and

119   Rodriguez 2004). Although selection on condition itself is consistently positive, the

120   direction of selection on specific alleles can change depending on environmental

121   conditions. Consequently, females will sometimes choose the 'wrong' male thereby

122   reducing the rate at which mate choice erodes additive variation.

123   Both temporal and spatial fluctuations in selection may be important for

124   maintaining genetic variation, but the conditions under which temporal variation can

125   sustain variation in isolation appear to be more restricted than those for spatial

126   heterogeneity (Roff 1997). Specifically, in the same way that migration across

127   spatially heterogeneous patches promotes variance, some form of overlapping

128   generations appears to be required to sustain variation in the face of temporally

129   fluctuating selection (Ellner and Hairston 1994). This is because long-lived

130   individuals that span different developmental environments are shielded from

131   selection during the development of subsequent generations. Even if selection during

132   the developmental period of a focal generation is quite severe, the older generations

133   can contribute genes that are suboptimal for such conditions, but better suited to

134   alternate environmental conditions. In contrast, severe selection in the absence of

135   overlapping generations can lead to the fixation of alleles that are optimal in only the

136   current context.

137   Both spatial and temporal fluctuations in selection can result in two forms of

138   GEI: those involving changes in only the strength of selection or changes in the net

139   direction of selection. The former might occur, for example, if under benign

140   conditions the intensity of selection is depressed because all animals have access to

141   ample resources and most males surpass a female mating criterion threshold. This will

142   slow the depletion of additive variance relative to the case in a harsh environment

143   where selection is much stronger, although the response to selection is difficult to

144   predict because additive genetic variances can also change with the harshness of the

145   environment (Gebhardt-Henrich and van Noordwijk 1991; Charmantier and Garant

146   2005). However, if the rank order of genotypic fitness stays constant across

147   environments, this kind of fluctuating selection is unlikely to maintain additive

148   variance in the face of persistent directional selection.

149   By contrast, reversals of the direction of selection on specific genotypes across

150   environments or time have substantial potential to sustain genetic variation and have

151   consequently received considerable theoretic attention (Haldane and Jayakar 1963;

152   Felsenstein 1976; Hedrick et al. 1976; Takahata 1981; Hedrick 1986; Frank and

153   Slatkin 1990; Bürger and Gimelfarb 2002), although less so than studies of mutation,

154   perhaps on account of the relative difficulties in realistically modelling GEI (Byers

155   2005). Nevertheless, both one-locus (Kirzhner et al. 1995) and multi-locus or

156   quantitative models (Kirzhner et al. 1994; Kondrashov and Yampolsky 1996) support

157   a role for fluctuating selection in maintaining additive genetic variation. Bürger and

158   Gimelfarb (2002) have recently shown in a mutation-selection model that under

159   fluctuating selection, there is a positive relationship between the numbers of loci

160   affecting a trait and the amount of genetic variation underlying it that can be

161   maintained. This finding has clear relevance for selection on condition given the large

162   number of loci that are likely to be involved (Rowe and Houle 1996).

163   In the current issue of *Genetica*, Kokko and Heubel (2007), have modelled

164   how spatial heterogeneity affects the benefits of choice for condition-dependent

165   signals of genetic quality. Their model demonstrates that GEI can either enhance or

166   diminish genetic benefits to mate choice, depending on the degree to which GEI

167   maintains variation (and therefore sustains genetic benefits to choice) and the extent

168   to which it obscures signal quality (by diminishing the correlation between sire trait

169   expression and the performance of offspring who might develop in a different

170   environment). Crucial components affecting the outcome of their model include the

171 mutation rate (the other source of genetic variation that is required if costly choice is

172 to persist) and the timing of dispersal across environments (i.e. the extent to which

173 females choose sires whose developmental environment differs from the likely

174 environment in which their offspring will develop).

175   We surveyed recent empirical studies of GEI and sexual selection by

176 searching the Web of Science for the last 10 years (1998-2007) using the following

177 terms: ("sexual selection" OR "ornament" OR "mate choice" OR "female choice")

178 AND ("GxE" OR "GEI" OR "genotype by environment" OR "genotype-environment

179 interaction" OR "context dependen*"). This search yielded 49 studies. Fifteen of these

180 are featured in Table 1, which summarizes their findings. Of the remaining papers,

181 another five were relevant but did not provide results that could be summarized in

182 Table 1. We omitted papers on GEI and sexual reproduction in plants (n=6), where

183 the theoretical expectations of mate choice evolution are sufficiently distinct to

184 warrant separate treatment. The remaining studies were either theoretical and review

185 papers (n=8), or used the term "context-dependence" to refer to phenomena other than

186 GEI (n=15).

187   The studies in Table 1 were conducted on a range of taxa (insects, fish, frogs,

188 mammals, and birds), using a variety of approaches, with laboratory and field studies

189 on a number of environmental dimensions, some experimentally induced, and others

190 estimated by observation. They suggest that GEIs for sexually selected traits are

191 relatively common, at least in the systems that are amenable to this type of research.

192 Unsurprisingly, GEIs for sexually selected traits frequently accompany GEIs for other

193 performance indices. We note that many studies relied on full-sib analyses and so

194 cannot distinguish maternal effects from additive genetic variance, and that

195 performance is rarely assessed in a way that approximates total fitness (e.g., number

196   of grandchildren). Although GEIs could be statistically detected or inferred in many

197   studies, in 5 of the 11 studies commenting on the consistency of performance ranks

198   there was little evidence that the environmental background determined which

199   genotypes outperformed others (i.e., there was no evidence of rank-order changes in

200   genotype performance across environments). This could be a problem of statistical

201   power or reflect practical limitations in exposing populations to sufficient naturally

202   relevant environmental heterogeneity. Alternatively, it might suggest that GEIs often

203   reduce the efficiency of directional selection, but only sometimes change its sign. We

204   focus the remainder of this article on exploring how this question and others might be

205   resolved in future studies.

206

207   **Suggested directions for empirical progress in studying mate choice for genetic**

208   **quality**

209   *1)   How is condition-dependence affected by environmental variation?*

210   We still know very little about the mechanics underlying the acquisition of

211   resources and allocation to life history traits in a single environment, let alone in

212   multiple environments. Are sexually selected traits particularly sensitive to

213   environmental influences on condition because small deviations from the optimal

214   level of expression for male in a given condition can have large fitness costs, while,

215   costs aside, increased expression is always favoured due to directional female choice

216   (Glazier 2002; Bonduriansky and Rowe 2005)? To what extent is the condition-

217   dependence of traits sex-specific, with males showing much steeper condition-

218   dependence due to sexual selection for increased trait expression, and concomitant

219   selection on females for condition-independence (Bonduriansky and Rowe 2005)?

220   Does allocation to different condition-dependent traits vary across environmental

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221 conditions, and does it respond to selection in a similar way to other allocation trade-

222 offs; in other words is there something special about allometric investment in

223 condition-dependent traits (Emlen 1996; Frankino et al. 2005; Bondurianksy 2007)?

224 To what extent is variation across populations in allocation to condition-dependent

225 sexual traits determined by the strength of sexual selection imposed by choosy

226 females, as opposed to environmental variation, such as the mean level of acquisition

227 (Roff and Fairbairn 2007)?

228   The answers to these questions require the estimation of two notoriously

229 elusive parameters: condition (i.e. resource acquisition ability) and the allocation

230 strategy of individuals. Many problems with condition indices have been ably

231 discussed elsewhere (Tomkins et al. 2004; Cotton et al. 2006; Lailvaux and Irschick

232 2006), and do not need to be repeated. However, there are special problems associated

233 with simple condition indices that focus on a single trait; for example, body mass

234 (Brandt and Greenfield 2004) or the residuals of a regression of body mass on body

235 size (Kotiaho et al. 2001). Condition indices are invariably life-history traits, so they

236 are expected to trade-off against other life-history traits, including sexual signals

237 (Hunt et al. 2004b). For example, there is a long history of assuming that longevity is

238 a correlate of condition because, all else being equal, individuals with more resources

239 should live longer (Kokko 1998). However, all else is rarely equal. The marginal

240 payoffs to investment in life history traits are expected to change across environments

241 and across different levels of resource acquisition. While long-lived animals may have

242 higher fitness in some situations, in others it is better to reproduce early in life at the

243 expense of longevity (Brooks 2000; Kokko et al. 2002; Hunt et al. 2004b). Longevity

244 has been shown to covary negatively with resource availability and early-life

245 reproductive success in several recent studies (Charmantier et al. 2006; Hunt et al.

246   2006; Robinson et al. 2006). Hunt et al. (2004a) showed that the sign of the

247   correlation between longevity and condition can change depending on resource

248   availability, demonstrating that traits that reliably signal quality under some

249   conditions do not do so under others. While this work is especially relevant to the

250   usefulness of longevity as a condition index, it also advocates caution in interpreting

251   the signal value of any other single condition-dependent life-history trait.

252   Ultimately, we need to know more about the relationship between condition

253   indices, acquisition, and the conversion of resources to phenotypic traits (Tomkins et

254   al. 2004). Just as multivariate analyses of selection have the potential to reveal

255   otherwise cryptic patterns in selection for complex phenotypes (Blows 2007), it would

256   be useful to know how multivariate approaches to condition improve one's estimate

257   of performance. One approach is to replace one-dimensional estimates of size, for

258   example, with geometric morphometric estimates (Klingenberg 2003). These analyses

259   separately estimate the size and shape of morphological structures as distinct

260   parameters, so they should be less likely to mistake changes in total allocation with

261   changes in body form. In addition, one could adopt data reduction techniques to find

262   the axes of variance across both morphological and life-history traits that is most

263   likely to reflect condition (in contrast to size alone, which is sometimes a weak index

264   of performance, Tomkins et al. 2004). It is well-established that the sign of

265   phenotypic covariance between life-history traits tends to be positive when most of

266   the variation in performance is due to differences in acquisition, and negative when

267   most of the variation is due to differences in allocation (van Noordwijk and de Jong

268   1986; Glazier 1999; Roff and Fairbairn 2007). Consequently, a strong index of

269   condition may be expected to covary positively with a range of life history traits.

270   Canonical analyses (e.g., principal component analysis) could provide the best

271 condition indices by revealing the major axis of positive phenotypic covariance across

272 life-history traits and morphology. One limitation is that in the absence of prior

273 knowledge of their relative cost (in terms of raw resources), the relative weighting of

274 different life history components will be rather arbitrary. Nevertheless, multivariate

275 approaches cannot provide worse information than individual condition indices, and

276 may help considerably when comparing animals whose allocation strategies to

277 different traits differ, e.g., in species with status-dependent investment in sexual traits

278 such as dung beetles, (Hunt and Simmons 2001), earwigs (Forslund 2003) and mites

279 (Radwan et al. 2002).

280   Quantifying differences in allocation strategies across individuals represents

281 another central challenge in the study of condition-dependence. In many instances it is

282 nearly impossible to partition the relative importance of acquisition and allocation to

283 the expression of a given condition-dependent sexual trait (Hunt et al. 2004b). In

284 some systems where adults do not feed, this problem can be partly circumvented

285 because acquisition can be estimated before adults allocate resources to different life-

286 history components (Brandt and Greenfield 2004). Laboratory studies that

287 experimentally manipulate resource availability have also proven useful in studying

288 allocation patterns across different genotypes (Hunt et al. 2004a; Bonduriansky and

289 Rowe 2005). A complementary approach is to manipulate allocation for a given level

290 of acquisition. Simmons and Emlen (2006) artificially prevented investment in

291 sexually selected beetle horns by cauterizing larval cells that are the precursors to

292 horns in adults, and thereby demonstrated how allocation to horns came at a net cost

293 to investment in testes. Adopting such techniques for traits that are the primary target

294 of mate choice could reveal more about how the allocation of resources to such traits

295 trades against other life history traits.

296

2)   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 its key insight 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

321   which many environmental variables are simultaneously manipulated can address this

322   question.

323   A complementary approach to laboratory manipulations of the environment

324   involves estimating GEIs in pedigreed natural populations using an animal model

325   (Kruuk 2004). In principle, this statistical approach to partitioning phenotypic

326   variation into its causal components has considerable power to detect the influence of

327   environmental covariates on genetic variance, particularly in conjunction with

328   "random regression" models that estimate random effects variance components such

329   as environmental conditions (Henderson 1982). Although random regression has been

330   extensively used in the animal breeding literature (Schaeffer 2004), it has only

331   recently been adopted for evolutionary studies of GEI's (Wilson et al. 2006; Nussey et

332   al. 2007). In a pioneering study, Wilson et al., (2006) have illustrated its potential by

333   demonstrating the influence of environmental quality, estimated using lamb survival

334   rates, on selection and genetic variance in Soay sheep. Since the theoretical basis for

335   these analyses is firmly rooted in quantitative genetics, their estimated parameters

336   such as breeding values scale directly with the presumed indirect benefits of mate

337   choice for genetic quality. More importantly, however, using animal models in natural

338   populations enables one to assess the consequences of mate choice under biologically

339   realistic levels of natural and sexual selection.

340

341   *3)*   *How much do GEIs reduce the signalling value of male condition?*

342   GEIs can both rescue additive genetic variance for condition and also weaken

343   selection for female preferences (Greenfield and Rodriguez 2004; Kokko and Heubel

344   2007; Mills et al. 2007). This occurs because environmental fluctuations disrupt the

345   predictive relationship between a sire's phenotype and the performance of his

346   offspring. In other words, whenever GEIs affect condition, the signal quality of a

347   sire's condition-dependent trait depends on the similarity between the environment

348   that the sire has experienced during his development and that of his offspring. More

349   generally, mate choice for indirect benefits that is based on condition dependent

350   characters is only adaptive if the phenotypic value of a signal trait has a considerable

351   genetic component (Rowe and Houle 1996). Even without GEI, environmental

352   variances could disrupt the signal to a significant degree, and therefore decrease

353   selection on females for exerting choice on the basis of genetic quality (Hunt et al.

354   2004b). Studies that manipulate both the environment of sires and of their offspring

355   may reveal the extent to which the signal value of sexual traits depends on the

356   congruence of sire and offspring environments.

357   Whether GEIs substantially reduce genetic benefits is a question well suited

358   for testing in wild populations (where environmental differences can be well

359   characterised) using the animal model. One important caveat is that when testing

360   hypotheses about how male phenotype predicts genetic quality, the breeding values

361   for individual sires should be estimated from the dataset while iteratively omitting the

362   sire's own phenotype (but including the phenotypes of all other sires) (Postma 2006).

363   The reasons for this precaution are two-fold. First, because one important component

364   of the sire's breeding value is his own level of sexual advertisement, a test of the

365   correlation between advertisement and the sire's breeding value for fitness (which

366   includes advertisement) would amount to autocorrelation. Second, if one wishes to

367   study the relationship between sexual advertisement and offspring fitness in several

368   environments, the sire phenotype is only useful for the environment that the sire

369   experienced. By omitting the sire from this estimate, one can fairly compare the

370   breeding value across environments because the breeding values in all environments

371   are estimated from a similar group of related individuals (i.e., not including the sire

372   himself). Consequently, just as the animal model allows one to estimate breeding

373   values for male traits in a female that never expresses them, one could similarly

374   estimate the environment-specific breeding values for the condition of animals that

375   have never themselves experienced the particular environment in question.

376

377   *4)*   *How does GEI affect the multivariate version of the lek paradox?*

378   Although there is mounting evidence of ample additive genetic variation in

379   sexual signals and life-history traits, and that the requirements for the genic capture

380   model may often be satisfied (Kotiaho et al. 2001; Tomkins et al. 2004), several

381   recent studies suggest that the lek paradox may persist in a multivariate form. These

382   studies show that there is often relatively little multivariate genetic variation in the

383   main direction of multivariate selection (the direction in which selection is pushing

384   the population mean; (Hall et al. 2004; Hine et al. 2004; Blows and Hoffmann 2005;

385   Van Homrigh et al. 2007). Similarly, the main axes of multivariate stabilizing sexual

386   selection (Brooks et al. 2005) can also be associated with depleted genetic variance,

387   with most genetic variation in cricket call structure occurring in multivariate

388   directions under very weak selection (Hunt et al. 2007). Thus, even if there is

389   substantial genetic variation for individual traits there may remain little potential to

390   gain genetic benefits from choice because of the associations between genes for

391   different traits. Two manipulative tests in different species of Australian *Drosophila*

392   indicate that variation in resource acquisition is unlikely to resolve the lack of relevant

393   multivariate genetic variation (Hine et al. 2004; Van Homrigh et al. 2007).

394   The importance of using multivariate methods when studying sexual selection

395   and evolution is only now receiving the attention it deserves (see Blows 2007, and

396   subsequent commentary in the same issue). To the extent that GEI is an important

397   element underlying the evolution and maintenance of female choice for indirect

398   benefits, it complicates the study of multivariate phenotypic selection because the

399   genetic architecture that defines constraints on evolutionary change can itself change

400   with different environmental conditions (Sgrò and Hoffmann 2004). Much more work

401   is needed to clarify the concordance of multivariate axes of selection and genetic

402   variation in natural populations, both within and across meaningful dimensions of

403   environmental heterogeneity, and to determine whether this constitutes a full

404   multivariate resurrection of the lek paradox.

405

406   *5)   Have mating biases for high-condition males evolved because of indirect*

407   *benefits?*

408   Ultimately, determining whether mating biases evolved in the context of mate

409   choice for good-genes requires a concerted effort to study the fitness consequences of

410   genetic variation in female choice. We suggest that researchers focus on the details of

411   variation in mating biases within and across different environments (see Rodriguez

412   and Greenfield 2003). Whether the model of mate choice for genetic benefits accounts

413   for much of the observed diversity in sexual traits depends on whether female

414   preferences actually increase female fitness via indirect effects. Our field has been

415   justifiably preoccupied with the difficult challenge of demonstrating that indirect

416   benefits of mating with high condition males exist. In fact, the evidence favouring

417   substantial genetic benefits is still sparse (but see e.g., Welch et al. 1998; Tallamy et

418   al. 2003; Head et al. 2005). Some authors have recently argued that there has been too

419   much emphasis on adaptive female choice to the exclusion of alternative explanations

420   for mating biases, such as male manipulation (Arnqvist and Kirkpatrick 2005; but see

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421 Griffith 2007). We agree that selection on males could play an important (and in some

422 cases underappreciated) role in determining mating biases, but wish to emphasize that

423 the fitness consequences of variation in female choice have received too little

424 attention because it is simpler to assume that all females have a similar mate choice

425 strategy. The solution to this dilemma requires more information on selection on

426 choice in females in conjunction with a thorough study of potentially conflicting male

427 interests. Selection analysis of male traits has proved useful in exploring how sexual

428 selection operates on male sexual traits (e.g., Hine et al. 2004; LeBas et al. 2004;

429 Brooks et al. 2005; Bentsen et al. 2006). The potential for applying these techniques

430 to the study of female mating preferences is similarly strong, particularly in

431 conjunction with tests of the reliability of male signals and female mating preferences

432 across heterogeneous environments, and will help test the assumption that variation in

433 mating decisions represents adaptive plasticity by females (Shuster and Wade 2003).

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