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

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23 **Abstract**

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

39

40 *Key words:* condition dependence; environmental heterogeneity; female preference;  
41 fluctuating selection; good-genes; indirect benefits; lek paradox; resource acquisition;  
42 resource allocation; sexual selection

43

44 *Abbreviations:* GEI: genotype-by-environment interaction

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47

47 **Introduction**

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

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

71           The “genetic 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           Genetic 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; Bric-  
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

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; Bonduriansky 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

297 2) *How important are GEIs for maintaining additive genetic variance in*  
298 *condition?*

299 GEIs present an exciting avenue for exploring Rowe and Houle's (1996)  
300 model of sexual selection because its key insight is that condition dependence allows  
301 females to evaluate male performance regardless of the source of the variation in male  
302 condition. Although many laboratory manipulations of environment have revealed the  
303 near ubiquity of GEIs, in most studies the number of simultaneously presented  
304 environments has been low for logistical reasons (i.e. generally only two  
305 environments are tested in the laboratory). Even when several environments are  
306 presented, they tend to differ along a single environmental dimension, such as food  
307 quality or temperature (but see Table 1 for exceptions). As a result, these studies may  
308 overestimate the extent to which some genetic variants are consistently the best  
309 performing across treatments (e.g., animals with superior foraging ability regardless  
310 of the resource level), because the same genetic variants may be inferior when  
311 exposed to other stressors. Species in which there is no evidence for GEI or rank-  
312 order changes in the expression of sexually selected traits (Merila 1996; David et al.  
313 2000) may therefore still exhibit appreciable genetic variance as a result of GEI.  
314 Moreover, environmental heterogeneity may sustain even more genetic variation than  
315 our best empirical studies suggest if much of the genetic variation arising from GEI is  
316 cryptic, and only observable once specific environmental perturbations arise (Gibson  
317 and Dworkin 2004). This is because the penetrance of some mutations depends on  
318 environmental conditions and genetic background; for example, alleles that are  
319 effectively neutral in benign situations may play a role in promoting survival under  
320 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

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).

434

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