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Local adaptation and the evolution of female choice

5 *Running head: Local adaptation and female choice*

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Introduction

The evolution of mate choice remains controversial, particularly when the choosy sex (typically females) receives nothing but genes ('indirect benefits') from their mates. Indirect benefits are predicted to be meagre because persistent female choice depletes genetic variation in the male traits under sexual selection (the lek paradox; e.g. Borgia, 1979, Rowe and Houle, 1996). The lek paradox is especially important when females choose males based on a trait that is also the target of natural selection (e.g. overall condition), because natural and sexual selection will work together to reduce variation. Low variance in male quality diminishes the benefits of choosing the best available mate relative to cost-minimising mating behaviour, which often can be equated with random mating. Mate choice might be inexpensive in some species (Friedl and Klump, 2005), in which case the lek paradox loses some of its mystery. However, early mathematical models predicted that even very low costs of mate choice can prevent its evolution (e.g. Kirkpatrick, 1985). Therefore, general evolutionary explanations for mate choice must be robust to the presence of choice costs.

At first sight, the evolution of female choice seems unlikely. In addition to the lek paradox, there is the additional problem of signal noise and mate choice errors. Male sexual signals do not always accurately signal male quality, and females may sometimes fail to identify or mate with the best male (e.g. Johnstone and Grafen, 1992, Getty, 1995, Kokko, 1997, Candolin, 2000, Wollerman and Wiley, 2002, Rowell et al., 2006, Nielsen and Holman, 2012). When choice is error-prone, its fitness benefits are expected to be lower because the average genetic quality of the chosen males should be reduced.

However, the astute reader may notice an intriguing interaction between the lek paradox and mate choice errors. If accurate female choice is self-defeating because it erodes variation in male genotypes, then error-prone mate choice may offer a partial solution by maintaining a pool of low-quality males that females must avoid in future generations. This argument implies that imperfect mate choice might be more evolutionarily stable than flawless mate choice under certain conditions (since the latter erodes the variation it depends on). Of course, this depends on the costs of erroneous mate choice decisions relative to the benefits of choosing from among more variable males (as well as the relative costliness of performing sloppy vs efficient mate choice). These costs and benefits are also covered in Chapter 4: erroneous mate choice decisions are there termed "misses" and "false alarms", and choosiness is shown to be more valuable when both high and low quality males are present in significant numbers.

Genotype-by-environment interactions (hereafter GEIs) provide an interesting twist to this argument. GEIs can produce local adaptation when the environment (and therefore selection) is spatially heterogeneous and movement between environments is sufficiently low (e.g. Kirkpatrick and Barton, 1997, Hanski et al., 2011, Blanquart et al., 2012). GEIs thereby contribute to the maintenance of genetic variation at both local and global scales, because migrants continually introduce new alleles, many of which are locally maladapted. GEIs have therefore been proposed to favour the evolution of female choice by providing an important source of variation that can 'fuel' female choice, potentially resolving the lek paradox (e.g. Day, 2000). In this context, it is perhaps surprising that much of sexual selection theory has been developed using the assumption, often left unspoken, that males and females evolve in a single, environmentally-homogeneous deme in which every potential mate is equally easy to reach and evaluate (for exceptions see e.g. Payne and Krakauer, 1997, Day, 2000, Proulx, 2001, Lorch et al., 2003, Reinhold, 2004, Kokko and

70　Heubel, 2008, McGonigle et al., 2012). Below, we discuss a somewhat surprising prediction regarding mate
71　choice for local adaptation: GEIs might boost female choice best when local adaptation is hampered by
72　persistent immigration of maladapted individuals (see also Chapter 4).

73　Local adaptation is a common finding in natural populations (reviewed in Hereford, 2009) and experimental
74　evolution studies (Kassen, 2002, Cuevas et al., 2003), so ignoring GEIs may compromise theoretical
75　predictions regarding the evolution of mate choice. Conversely, mate choice should be considered in
76　studies or models of local adaptation (e.g. Lorch et al., 2003, Dolgin et al., 2006, Fricke and Arnqvist, 2007,
77　Gunnarsson et al., 2012, Long et al., 2012). Theoretical work suggests that the degree of local adaptation is
78　strongly affected by dispersal rates between environments, the extent of local variation in selection and the
79　strength of genetic drift (e.g. Kirkpatrick and Barton, 1997, Hanski et al., 2011, Blanquart et al., 2012), but it
80　is infrequently acknowledged that these parameters interact with mate choice (but see e.g. Arnqvist, 1992).
81　For example, dispersal is often invoked as a constraint on local adaptation, but this is less true if migrant
82　males have low mating or fertilisation success (Reinhold, 2004, Postma and van Noordwijk, 2005).

83　We suggest that the theoretical basis of local adaptation and mate choice has yet to be satisfactorily
84　integrated, but that such integration is highly desirable. Moreover, because local adaptation is central to
85　many important topics including the evolution of dispersal (Billiard and Lenormand, 2005, Gros et al., 2006)
86　and range size (Kirkpatrick and Barton, 1997, Bridle and Vines, 2007), resilience to climate change (Atkins
87　and Travis, 2010) and speciation (Gavrilets, 2003, Nosil et al., 2005), understanding the evolution and
88　genetic consequences of mate choice under GEIs is a priority.

89　The Jekyll and Hyde nature of GEIs

90　Although GEIs can favour the evolution of female choice via their positive effect on levels of genetic
91　variation (Day, 2000), GEIs are a double-edged sword because they potentially reduce the reliability of male
92　sexual traits to signal indirect benefits (e.g. Greenfield and Rodriguez, 2004, Mills et al., 2007; Chapter 4 of
93　this book). Consider the case where there is dispersal between environments and condition is affected by
94　crossover GEIs (i.e. the rank fitness order of genotypes changes between environments). Males in good
95　condition do not sire high-quality offspring in all possible environments, by definition. Therefore, a male
96　who developed in an environment to which he is well-adapted might appear to be in good condition even
97　after migrating to a different environment (or after a temporal change in his environment), weakening the
98　relationship between paternal condition and offspring quality. Even with non-crossover GEIs (i.e. when the
99　relative fitness but not fitness ranks of different genotypes varies among environments), the magnitude of
100　the benefits of choosing an attractive male is environment-dependent.

101　Dishonest signals (i.e. those that offer no information on the quality of interest) are generally predicted to
102　be evolutionarily unstable, because individuals responding to the signal pay a cost for their preference but
103　gain no benefits. Even signalling systems that are 'honest on average' (i.e. strong signals are associated with
104　high quality individuals more often than not, such that the signal provides useful information; Kokko, 1997,
105　Searcy and Nowicki, 2005) are only stable as long as the cost of selecting strong signallers is outweighed by
106　the benefits. Therefore, when there is a lot of residual variation in the relationship between male condition
107　and offspring genetic quality, as when GEIs affect condition and the environment is temporally or spatially
108　heterogeneous, it may not pay females to be choosy.

109 Past studies discussing mate choice and GEIs and/or local adaptation can be largely grouped into three
110 categories:

111 1. Those that focus on the 'Jekyll' effect of GEIs: environmental variation maintains genotypic variation,
112 which favours the evolution of costly female choice (Day, 2000, Jia et al., 2000, Proulx, 2001, Reinhold,
113 2004, Danielson-François et al., 2006, Zhou et al., 2008, Danielson-François et al., 2009, Greenfield et al.,
114 2012).

115 2. Those that focus on the 'Hyde' effect of GEIs: signal reliability may be compromised because a male's
116 current appearance may belie the indirect benefits he provides (Greenfield and Rodriguez, 2004, Higginson
117 and Reader, 2009, Tolle and Wagner, 2011, Vergara et al., 2012).

118 3. Those that acknowledge both effects (Tomkins et al., 2004, Miller and Brooks, 2005, Etges et al., 2007,
119 Mills et al., 2007, Bussière et al., 2008, Cockburn et al., 2008, Kokko and Heubel, 2008, Radwan, 2008, Bro-
120 Jørgensen, 2010, Cornwallis and Uller, 2010, Ingleby et al., 2010, Rodríguez and Al-Wathiqui, 2011).

121 A complete picture of the role of GEIs in female choice cannot be gained by studying either their positive or
122 negative aspects in isolation. Thus a key question is: given that both effects operate together, which one
123 prevails? In other words, do we see the evolution of costly female preferences more often and/or do we
124 see the evolution of *more costly* female preferences when there is a lot of spatial heterogeneity, GEIs and
125 local adaptation, or does spatial complexity in the selective environment instead select against female
126 choice?

127 To date, only one theoretical model has explicitly addressed this balance. Kokko and Heubel (2008) used a
128 population genetic model to evaluate the relative importance of the positive and negative consequences of
129 GEIs for the evolution of female choice. They found that GEIs inhibited the evolution of mate choice when
130 ample genetic variation for condition was maintained by a high mutation rate, because GEIs reduce the
131 reliability of the male signal. However, when mutation rates were lower, such that directional selection
132 from female choice could deplete genetic variation, GEIs coupled with dispersal created additional genetic
133 variation that allowed female choice to persist in parameter spaces where it was otherwise not favoured.
134 Specific details mattered, however. Kokko and Heubel (2008) also allowed some males to migrate between
135 environments after selection but before mating – the assumptions of the model meant that these males
136 were mostly in good condition, but were maladapted to the environment in which their offspring would be
137 born relative to non-migrants. Interestingly, the influx of attractive but maladapted males actually favoured
138 the evolution of female choice in some cases, because these males produced maladapted sons that females
139 needed to avoid in future generations. The model therefore produced the predicted paradoxical result that
140 female choice can provide greater average indirect benefits when it is error-prone.

141 The exact balance of the negative effect (the breakdown in signal reliability under a GEI scenario) and the
142 positive effect (greater variance in male condition, and hence greater returns for being choosy) determines
143 whether GEIs favour female choice. In the model of Kokko and Heubel (2008), the positive and negative
144 effects of GEIs did not 'cancel out', thus GEIs can either favour or prohibit the evolution of female choice
145 depending on patterns of gene flow and the amount of variation maintained by other factors (in this case,

146 mutation). Also, a breakdown in signal reliability can actually favour mate choice in some situations by
147 reducing the ability of mate choice to erode the very genetic variation it needs to operate.

148 However, Kokko and Heubel's model made a number of simplifying assumptions that might compromise its
149 generality. Most importantly, condition was determined by a single locus with two alleles, which were
150 differentially adapted to one of only two possible environments. This locus was intended to symbolise the
151 summed effects of mutations across many loci, and therefore had a potentially high mutation rate.
152 However, a single locus with a high mutation rate does not always behave analogously to a set of loci with
153 individually low mutation rates (Spichtig and Kawecki, 2004), and most traits involved in local adaptation
154 are probably polygenic (e.g. Savolainen et al., 2007, Le Corre and Kremer, 2012). Moreover, polygenic
155 determination of condition is key to the well-known "genic capture" solution to the lek paradox (Rowe and
156 Houle, 1996), in which the high combined mutation rate of large assemblages of loci (potentially the entire
157 genome) maintains substantial genetic variance in condition, potentially favouring mate choice for sexual
158 signals that reveal condition.

159 Kokko and Heubel's model further assumed two types of habitat, each containing a very large (effectively
160 infinite) deme in which choosy females were always able to identify and mate with a male in good
161 condition. The model therefore negates genetic drift, and excludes mate choice errors other than mating
162 with a deceptively high-condition migrant male who is actually locally maladapted. Other forms of mate
163 choice errors (e.g. unattractive males gaining some paternity with choosy females) should also affect the
164 standing genetic variance for condition, and therefore the value of being choosy. Given the simplifying
165 assumptions in Kokko & Heubel (2008), it is not clear how GEIs are expected to behave in reality. It appears
166 particularly important to reconcile their findings with a central result of population genetics: that even low
167 amounts of gene flow can prevent local adaptation (e.g. Mayr, 1963, Kirkpatrick and Barton, 1997).

168 Here, we analyse a genetically explicit individual-based simulation that relaxes many of the assumptions of
169 Kokko and Heubel's model. In the new model, condition is modelled as a polygenic trait by using a large but
170 finite number of loci that interact additively to determine local adaptation, and individuals inhabit
171 continuous space on the surface of a world with locally varying phenotypic optima. Habitat in the world can
172 be coarse-grained, fine-grained or invariant over space. Dispersal consequently does not occur between
173 discrete habitat types; instead, dispersing individuals experience weaker correspondence between
174 environmental conditions at their natal and their breeding sites the further they disperse, particularly in a
175 fine-grained world. It follows that asking whether there is crossover or non-crossover GEI is less important
176 than asking how spatial variation creates differences in local adaptation, and whether female choice can
177 persist when females encounter males from diverse backgrounds (natal environments). We feel that the
178 distinction between crossover and non-crossover GEIs is more useful when there is a small number of
179 possible genotypes and environments. Our model examines the evolutionary relationships between local
180 adaptation and mate choice, and evaluates how dispersal, signal reliability and spatial variation affect the
181 evolution of mate choice for locally adapted genes.

The model

182

183 **Overview**: We constructed an individual-based simulation of a population of sexual haploids living in
184 continuous space on the surface of a toroid (doughnut-shaped) world. Each point on the world had an

185   environmental value, and was hospitable to individuals whose phenotype matched the local environment

186   well (Figures 1 and 2 show some example worlds). Each individual was either male or female, and had L loci

187   (in our examples we used L = 50) carrying one of two possible alleles (a or A, coded as 0 and 1); the

188   phenotype affecting local adaptation (termed z) was the mean allelic value of these L loci ($0 \leq z \leq 1$). An

189   individual's condition (ζ) was determined by the interaction between its phenotype z and up to two

190   environments: its natal environment and/or its post-dispersal environment (depending on the time at

191   which condition was determined relative to dispersal). Condition determined both the probability of

192   survival and, for surviving males, their attractiveness to choosy females. Males may therefore be thought of

193   as possessing a sexual ornament that honestly reveals their condition.

194   Individuals carried an additional locus with two possible alleles, B and b. This locus was only expressed in

195   females, and controlled whether a female exhibited a preference for males in good condition (allele B), or

196   mated at random (allele b). In each generation, individuals were born, dispersed, survived with a

197   probability determined by the match between their phenotype and their natal and/or post-dispersal

198   environments, reproduced and then died. Generations were thus non-overlapping.

199   **Initialisation phase**: At the start of each simulation run, we constructed a toroid world with circumferences

200   of length 1. The world was divided into $s \times s$ squares, each with its own environmental value E_i (our

201   examples below use s = 100). We used an algorithm that allowed us to vary the scale of the environmental

202   grain by adjusting the spatial autocorrelation (i.e. the similarity in E between neighbouring squares) of the

203   environment. The algorithm first generated an $s \times s$ grid of random values, then picked a random square

204   and updated its environmental value E_i using the formula

205
$$E_i = \beta \sum_{j=1}^{8} E_j / 8 + (1 - \beta)x \tag{1}$$

206   where the first term is the mean environmental value of the eight neighbouring squares multiplied by β (a

207   constant determining the magnitude of the spatial autocorrelation), and x is a pseudorandom number

208   between 0 and 1. This updating procedure was repeated $100s^2$ times, causing neighbouring squares to have

209   similar values when β was high (coarse-grained environment: top of Figure 1 is produced with $\beta = 0.999$)

210   and vary widely when β was low (fine-grained environment: lower right in Figure 1 is produced with $\beta =$

211   0.05). Note that in the toroid world, the neighbour of a 'corner' cell can reside in the opposite corner of the

212   grid, which removes any edge effects: a patch of low (or high) environmental values can extend across

213   apparent edges. The resulting grid was rescaled so that the mean of all E_i values was 0.5, with standard

214   deviation 0.2. We also ran simulations in a completely spatially homogeneous world in which all squares

215   had an environmental value of 0.5, ensuring that the fitness of each genotype was constant in all localities

216   (Figure 1, lower left).

217   We then initialised a population of 10,000 individuals with random genotypes and sexes, and natal

218   coordinates [x_n, y_n] as real numbers between 0 and 1.

219   **Dispersal:** Next, males and females dispersed with probabilities m_m and m_f respectively (in the figures below

220   we use m_m = m_f = 0.5). Migrants of both sexes dispersed a random distance drawn from an exponential

221   distribution with mean d in a random direction. The position of each migrant was then updated to yield its

breeding coordinates [x_b, y_b]; because the world was toroid, an individual who migrated further than an apparent edge (e.g. x_b = 1.1) simply re-emerged from the other end of the world (x_b updated to 0.1).

For all individuals, we then calculated the z phenotype controlled by the L loci. We assumed that each of the L loci contributed equally to the phenotype, such that z was the proportion of alleles with value '1'.

Determination of condition and viability selection: We next determined the condition of all males and females and applied viability selection. The interaction between the z phenotype and each individual's natal and breeding environments together determined condition (ζ) via the following formula

$$\zeta_i = p(1 - |z_i - E_i|) + (1 - p)(1 - |z_i - E'_i|) \tag{2}$$

where z_i is the phenotype of the focal individual, E_i is its natal environment (the environmental value of the world at [x_n, y_n]), E'_i is its breeding environment (the environmental value of the world at [x_b, y_b]; note that $E_i = E'_i$ for non-migrants), and p is a constant determining the relative effects of these two environments on condition ($0 \leq p \leq 1$). Individuals survived viability selection with a probability equal to their condition ζ_i.

Breeding: Mating interactions were local, but because each of the $s \times s$ squares only contained an expected number of 0.5 males (assuming a population size of 10000 and s = 100), we defined a set of larger squares defining the locality within which mate-searching occurred. We thus redivided the world into $M \times M$ squares (in the examples below, M = 20, leading to an average of 12.5 males per square). Each of the $M \times M$ 'mating squares' produced $10000/M^2$ offspring assuming that at least one male and one female was present; otherwise, no offspring were produced. Randomly mating mothers enjoyed a fecundity benefit in this context, modelled as a cost of choice, c. Each offspring was randomly assigned a mother, such that the probability of a given female being picked was

$$\frac{1 - g_i c}{\sum_{j=1}^{N} 1 - g_j c} \tag{3}$$

where g_i is the genotypic value of the focal female at the choosy B/b locus (B = 1 and b = 0), c is the fecundity cost of being choosy and N is the number of females in the territory. Competition between non-choosy and choosy females was thus modelled on a local scale (soft selection), with non-choosy females more likely to contribute offspring to the next generation than their choosy neighbours when $c > 0$.

Each offspring was then assigned a father among the locally available males. The sire was chosen randomly for mothers carrying the b allele, or based on male condition (i.e. attractiveness) for those offspring whose mother had the B allele. In the latter case, each male's probability of becoming the sire was equal to

$$\frac{\zeta_i^k}{\sum_{j=1}^{n} \zeta_j^k} \tag{4}$$

where ζ_i is the condition of the focal male, k determines how efficiently females are able to discriminate among males based on their current condition ($k \geq 0$) and n is the number of males. As k tends to infinity, the probability that females choose a male with the locally best condition value tends to one. When k is zero, low condition males have an equal chance of being chosen as high condition males. This method of assigning mothers and sires allows for both female and male multiple mating.

When the mother and father of each offspring had been determined, offspring inherited a randomly chosen parental allele at each locus (i.e. we assume negligible genetic linkage), were randomly assigned a sex, and were born such that their natal coordinates were equal to their mother's breeding coordinates. Afterwards, all adults were removed from the population.

Mutation: Each of the L loci controlling the z phenotype in every offspring had an independent probability μ of mutating. Mutations converted a 0 to 1 or vice versa. In order to reduce stochasticity in the results, we assumed no mutation at the B/b locus.

After the new generation was formed, the population was again run from the dispersal step onwards. The simulation proceeded either for a set number of generations or until the b allele reached 90% frequency (see below).

Less local adaptation, *more* female choice!

It is instructive to begin the analysis of our model with some individual simulation runs. In populations initiated with equally many b and B alleles (i.e. 50% of females are choosy in generation 0), a fecundity cost of 0.1% ($c = 0.001$) was sufficient to select against female choice in some spatial settings but not others. Figure 1 shows four representative simulation runs, each lasting 1000 generations. The density plots in Figure 1 show the distribution of male phenotypic values (z) sampled for the last 50 generations at the end of each of the four runs, exemplified by three different arbitrarily chosen mating squares: one that contains the location [0.75, 0.25], another that contains [0.5, 0.5], and finally [0.25, 0.75]. These distributions illustrate the range of male phenotypes available for female choice. We also show the mean environmental value of all locations within these mating squares, which approximates the phenotype that maximises survival and attractiveness for individuals inhabiting that location (shown by the dots in the density plots in Figure 1). The spatial covariance between the actual distribution of phenotypes and the locally optimal phenotype provides a simple and general measure of the degree of local adaptation that the population has been able to achieve in the face of dispersal and mutation (Blanquart et al., 2012).

The only case in which the choosy B allele clearly increased towards fixation is a coarse-grained environment ($\beta = 0.999$) in which dispersal distances are quite long (Figure 1, top left). This is associated with poor local adaptation, which is visible when comparing local optima and male phenotypic distributions at the three sample points in the world: males have similar (mostly intermediate) genotypic values at all locations, irrespective of whether the local environment selects for low, medium or high z phenotype values. This reflects a swamping of local adaptation by high dispersal rates (50% of individuals migrated per generation) and distances ($d = 0.2$).

By contrast, when dispersal distance was shorter (the upper-right figure; $d = 0.02$) substantial local adaptation was observed within the same world structure ($\beta = 0.999$). Female choice was still not selected against, but its spread was less clearly able to withstand the 0.1% fecundity cost, causing the B allele to barely rise above its starting frequency. The difference between these two scenarios illustrates a key finding of our model: **female choice is more valuable when dispersal prevents strong local adaptation and keeps populations away from their naturally-selected local optima.** This reflects the "Jekyll" effect of GEIs.

293 The third and fourth scenarios also produced negligible benefits of female choice that were not enough to
294 compensate for the 0.1% fecundity cost. In a fine-grained world (lower right), dispersing offspring arrive in
295 an environment type that correlates only weakly with their natal environment**, meaning that it may not be**
296 **beneficial to select a locally-adapted male when many offspring disperse to unpredictable environments**.
297 Also, natural selection in this capricious world is predicted to strongly favour the jack-of-all trades z = 0.5
298 phenotype, meaning that even non-choosy females will predominantly encounter z = 0.5 males (as shown
299 by the density plots). The flat world lacking GEI (lower left) likewise disfavoured female choice, in spite of
300 the presence of some genetic variation for fitness. This is likely explained by the fact that randomly-mating
301 females picked a male with close to the optimal phenotype of z = 0.5 in the majority of cases, weakening
302 the benefit of being choosy.

303 The last three scenarios all share the same problem: the mean of the distribution of potential mates is close
304 to the optimal phenotype for a female to choose (approximated by the dots in Figure 1). This can happen
305 when dispersal is weak enough to enable strong local adaptation (top right example), or when the
306 environment is so fine-grained that the best option is to choose an intermediate phenotype that is close to
307 the population average (lower right example), or when many males are well-adapted because there is no
308 spatial variation at all (lower left example). In each of these three cases, the high correspondence between
309 what male type is 'best' and what is most common means that it is hard for choosy females to produce
310 sufficiently better offspring than the benchmark set by randomly mating females. Any marginal cost of
311 choice is then sufficient to select against female preferences.

312 The positive, 'Jekyll' effect of GEIs (the maintenance of genetic variation in male quality) is therefore highly
313 pronounced in only one of the examples of Figure 1. In the top left figure, dispersal among environments is
314 pervasive, and the environmental grain is of a suitable scale that a female will produce fitter offspring if she
315 finds a locally adapted male (and such males are rare, meaning that non-choosy females tend to miss
316 them). **In sum, the presence of GEIs is not enough: the patterns and rates of dispersal are important.**

Can we generalise?

318 The results above offer exciting food for thought. Intuition might suggest that the more a process (e.g.
319 spatial or temporal variation) is able to create local adaptation, the better the prospects for female choice.
320 The above results, however, show that scenarios in which local adaptation ought to be beneficial but fails
321 (due to 'too much' dispersal) might instead offer the best prospects for significant female choice for locally
322 adapted genes. In hindsight, this is almost obvious. Female choice for indirect benefits can only pay off if
323 females, for whatever reason, continually face the task of distinguishing between genetically 'good' and
324 'bad' males — in the current context, males varying in local adaptedness. When locally adapted males are
325 desirable but rare, females can be selected to distinguish males according to their ability to survive and
326 produce sexual signals in the local environment, even when mate choice is costly.

327 However, as stated above, GEIs are a double-edged sword. Choosy females only benefit significantly from
328 mating with better-adapted males if the present condition of these males reflects the likely viability and
329 attractiveness of the offspring; on the other hand, if this relationship is too tight, variance in male quality is
330 more strongly depleted by female choice. This suggests that the parameter p, which reflects the
331 importance of the natal site (as opposed to the environmental conditions experienced as an adult) as a

332 determinant of condition, could have complex effects (see also Chapter 4). Figure 1 assumes $p = 1$, i.e. natal
333 condition fully determines the subsequent viability and appearance of adults; it also only shows single
334 examples of each case (there is repeatability, but with relatively large variation across runs; not shown).

335 We therefore next conducted an extensive set of simulations designed to establish the robustness of our
336 predictions regarding the relative benefits of female choice under different spatial scenarios. In order to
337 rapidly measure the relative benefits of female choice in a range of parameter spaces, we set the cost of
338 female choice (c) to zero at the start of the simulation and increased c with each successive generation,
339 such that the cost in generation t was $c(t) = 10^{-9} \times t^3$. This means that the fecundity cost of female choice
340 reached 0.1% by generation 100, 1% by generation 215, 5% by generation 369 and 100% by generation
341 1000. The female choice allele was therefore doomed to extinction in all runs because its costs eventually
342 became too much to bear. The time to extinction can then be used as an indicator of the ability of female
343 choice to persist in the face of mounting costs (i.e. it is a measure of the fitness benefits of female choice).

344 To determine whether female choice provides a benefit, we contrasted the time it took the B allele to
345 decline from 50% to 10% frequency (to minimise the impact of stochasticity inherent in the final decline to
346 zero) with the null extinction time in the absence of benefits. The null extinction time was calculated by
347 setting $k = 0$ (i.e. by preventing the choice allele from having any effect on mate choice). The mean number
348 of additional generations the B allele persisted beyond the mean of 40 runs of the null model was then
349 used as a robust measure of the benefits of female choice (N = 40 simulation runs and 40 null runs per
350 parameter space). We call this overall measure 'prospects for female choice' as it measures the overall
351 potential to persist under a range of costs. Note that it is possible for the B allele to decline faster when it
352 affects mating behaviour than when $k = 0$. This produces a negative value of 'prospects for female choice',
353 and indicates that choosing males in good condition produces less fit offspring than choosing males at
354 random.

GEIs often maintain costly choice — in a suitably variable world

356 The results confirmed previous predictions that GEIs can sometimes favour the evolution of female choice
357 by maintaining variance in male fitness (e.g. Day, 2000, Kokko and Heubel, 2008). However, as predicted
358 from the single runs in Figure 1, **GEIs only favoured the evolution of choosy females when dispersal**
359 **distance was sufficiently high, because weak dispersal allows depletion of genetic variation at local scales**
360 **(compare Figures 2a and 2b)**. The structure of the world therefore only had a noticeable effect on the
361 evolution of choice when dispersal distance was high (Figure 2a). With long-range dispersal, the spatially
362 ordered worlds 3 and 4 favoured female choice for most values of p (the parameter controlling the extent
363 to which condition is determined by the natal vs post-dispersal environment), because dispersal maintained
364 genetic variation and the high spatial autocorrelation ensured that well-adapted parents tended to produce
365 well-adapted offspring.

366 One might expect the case $p = 1$ to provide smaller benefits of female choice, because it affords
367 maladapted migrant males greater attractiveness and survival, and indeed there was some evidence of this
368 (open circle in world 4; Figure 2a). However, the presence of many maladapted but attractive migrants also
369 favours female choice, because these migrants leave maladapted, unattractive sons that choosy females
370 can avoid in subsequent generations. Also, in ordered worlds like 3 and 4, migrants will tend to come from

similar environments, and mating with a migrant will not necessarily produce strongly locally maladapted offspring.

The degree to which condition is determined in the natal environment (parameter p) had surprisingly unpredictable effects on the potential for female choice that depended on the grain of the environment (Figure 2a). For example, in the small-grained world 1, female choice was most beneficial when condition was determined after dispersal (allowing females to accurately gauge a male's adaptedness to his current environment). Conversely, in the smoother world 2 the prediction was opposite, despite the superficial similarity of these worlds (the spatial autocorrelation of world 2 is actually substantially higher than world 1, although this is not obvious in the figure). The parameter p also had dissimilar effects in worlds 3 and 4, in spite of the apparent similarity between these worlds. These complex results highlight the difficulty of making concrete predictions about when GEIs should favour the evolution of female choice. **Our models clearly show that the amount of dispersal between environments (and hence local adaptation) is key, but they also suggest that the relative effects of pre- and post-dispersal conditions on survival and attractiveness are important (a result echoed in Chapter 4)**.

We additionally ran simulations (not shown) that suggested that the ratio of dispersal that is performed by males and females (while holding constant the overall mean number of individuals dispersing, i.e. $m_m + m_f = 1$) does not have a clear effect on the evolution of female choice. This result is somewhat unexpected, because the benefits of mate choice should depend on the range of male types encountered by females, which is influenced by male dispersal. A possible explanation is that other factors overrode any effect of sex-biased dispersal. To illustrate, consider the scenario at the top of Figure 1, in which strong spatial autocorrelation of environment types and relatively high dispersal rate colluded to favour female choice by keeping the population off local adaptive peaks. Even if females performed most of the dispersal, some of the maladapted females would survive and produce sons, which would then need to be screened out in mate choice. So long as dispersal is common and long-ranged relative to the environmental grain, dispersal will provide a constant influx of poorly-adapted males that can be screened out in female choice.

We also ran comparable simulations with 6 loci, which produced results highly similar to those presented here. This suggests that our results, and those of Kokko and Heubel (2008), are robust to different assumptions regarding the genetic architecture of condition. The fact that female choice was not noticeably more valuable when condition was determined by 50 rather than 6 loci also provides some evidence that 'genic capture' played a limited role in our simulations. That is, variation in condition introduced by mutation across many loci was small relative to variation introduced by dispersal.

Insights from the model

Our new analysis reaffirms that GEIs have both positive and negative effects on the evolution of female choice. Our models also suggest that the literature on GEIs and sexual selection may have overestimated the importance of GEIs featuring a crossover. In our new polygenic model, which tracks local adaptation in a continuous trait in a continuously variable environment, it hardly makes sense to distinguish between crossover and non-crossover GEIs. In both cases, females face the choice of males with different genetic and environmental backgrounds. Also, both cases can produce situations in which randomly-mating

409 females make equally good (or even better) mating decisions than females who select males in good
410 condition.

411 Because situations in which randomly-mating females tend to pick the right male represent unfavourable
412 conditions for costly female choice, it is desirable to know when these situations arise. An important
413 variable is the degree of gene flow between habitats. Restricted gene flow sets the stage for strong local
414 adaptation. As a naïve first thought, one might be tempted to argue that strong local adaptation will
415 increase selection for female choice, because one cause of strong local adaptation is strong differences in
416 selection across space, meaning that females would have more to gain by producing locally-adapted
417 offspring. However, on closer inspection the flaw in the argument is clear: strong local adaptation also
418 implies low gene flow between environments, and low genetic variation at local scales. Females in highly
419 locally adapted populations therefore predominantly encounter well-adapted males, so that cheap, non-
420 choosy female strategies should often be favoured, even if the benefits of the correct choice are substantial
421 (see also Chapter 4). As discussed below, this insight has important implications for empiricists studying
422 local adaptation and mate choice.

423 In hindsight, our argument that the rate of dispersal among environment types determines the potential
424 for GEIs to favour female choice should be clear. At the extreme, one can consider female choice for locally
425 adapted genes within a number of isolated populations. Evolution then proceeds independently within
426 sites, and the lek paradox repeats itself within each local population. Substantial rates of dispersal between
427 sites are required to keep each population from locally adapting. Genetic drift is also more important in
428 poorly connected populations, increasing the rate at which genetic variation is lost stochastically. Although
429 mutation across many loci could produce a non-trivial amount of standing genetic variation in male quality
430 (Rowe and Houle, 1996), this may not be enough if the costs of choice are substantial. The amount of
431 variance maintained at mutation-selection-drift balance also depends on population structure and dispersal
432 regimes (e.g. Burger and Lande, 1994, Blanquart et al., 2012).

433 By contrast, when dispersal pressure is suitably strong and the selective environment varies across space,
434 local adaptation will remain weak (Blanquart et al., 2012). Weak local adaptation ensures that many sites
435 will contain many potential mates that are maladapted to current conditions to varying degrees. Of course,
436 some of a female's offspring under those conditions will again disperse to somewhere else. Selection on
437 these offspring is difficult to predict, which weakens the benefits of paying attention to the condition of
438 potential mates in the mating environment. Nevertheless, females can gain significantly choosing locally
439 adapted males if the dispersal ecology of a species combines a suitable amount of philopatry (which
440 ensures benefits of screening males for local adaptedness) with suitably many dispersal events that reach a
441 somewhat different selective environment (which creates the situation where not all males are locally
442 adapted). Our model therefore reaffirms that the Jekyll and Hyde effects of GEIs do not cancel out.

Prospects for Empirical Work

443

444 How should these ideas be incorporated into empirical work? A number of studies have found evidence
445 that GEIs affect the expression of both sexually-selected signals and measures of fitness and condition,
446 although for sexual signals the evidence is skewed towards insects and birds (reviewed in Bussière et al.,
447 2008, Ingleby et al., 2010). For example, quantitative genetic studies of the ultrasonic song of the male

448 lesser waxmoth *Achroia grisella* have revealed GEIs for condition and the male song: the genotype that
449 produces the best song in one rearing environment may not do so in another (Jia et al., 2000, Danielson-
450 François et al., 2006, Greenfield et al., 2012). In bank voles *Clethrionomys glareolus*, socially dominant
451 males sired dominant sons only when the sons were reared in a similar habitat to their father, suggesting
452 that GEIs affect the olfactory dominance signal and/or condition, and that GEIs might compromise the
453 evolution of costly female preferences for dominance (Mills et al., 2007).

454 As well as gathering further evidence on the relative importance of GEIs to among-male variance in
455 attractiveness, we suggest several avenues for empirical work that have yet to be explored. Though
456 previous studies have found GEIs for sexual signals, it is much less clear how frequently parents and
457 offspring experience a difference in the environmental dimensions under study in natural populations (e.g.
458 because of dispersal or a temporal change in the environment). As shown by our model and many others
459 (e.g. Hanski et al., 2011, Blanquart et al., 2012), the amount of dispersal between dissimilar environments
460 affects the amount of genetic variation maintained at equilibrium. For pragmatic reasons of experimental
461 design, many studies have emphasized discrete variation in environments (and correspondingly large
462 fitness differences with clear crossover), but the real world might more often feature subtler variation of a
463 relatively continuous nature. Fortunately, this is not necessarily bad news for the prospects for GEIs to
464 favour female choice. In the model presented here, the cases of choice that were found to resist costs best
465 were found in relatively gently varying worlds (Figure 2). Ecologically oriented field studies of GxE and/or
466 local adaptation of course exist (Postma and van Noordwijk, 2005, Hanski et al., 2011, Evans et al., 2012,
467 Gunnarsson et al., 2012, Kelly et al., 2012), but they are surprisingly rarely linked to sexual selection (but
468 see e.g. Klappert and Reinhold, 2005).

469 The present model also shows that the timing of dispersal and the development of sexual signals are
470 important. If females are able to accurately gauge how well-adapted males are to the environment that
471 their offspring will experience (e.g. because males' signals reflect adaptedness to the current environment
472 more than the natal environment), costly female choice can evolve more easily in some cases. However,
473 this is hardly a rule of thumb because of the 'Jekyll and Hyde' nature of the GEI: overly accurate assessment
474 will again destroy variation. However, this might be less of a problem in empirical studies than it first
475 appears. When studying a population at equilibrium, we expect overly accurate assessment to already have
476 depleted variation, and extant cases of female choice that is 'too accurate for its own good' might not exist.
477 In experimental studies on the other hand, one could conceivably see if this process works as expected by
478 manipulating the degree to which females can express their preferences.

479 A strong test of our predictions could be achieved using experimental evolution studies. After identifying a
480 male sexual trait subject to a GEI, one could examine the evolution of female preferences for that trait
481 under various spatial regimes. For example, the control group could use two parallel populations, each in
482 one environment type, that were genetically isolated from one another. Other treatments could
483 experimentally add varying rates and types (e.g. male-biased or female-biased) of dispersal between the
484 populations each generation. We might then predict that populations without migrants would evolve
485 weaker female preferences, because only mutation would introduce new maladapted males that would
486 need to be avoided by females. The dispersal treatments might evolve relatively strong female preferences
487 (because dispersal stymies local adaptation, boosting genetic variation for fitness), or weaker preferences
488 (if the migrant males bear misleadingly high-quality signals developed in the other environment).

489

Prospects for Theoretical Work

There is also plenty of room for further theoretical work. We have focused on spatial heterogeneity and dispersal, but temporal fluctuations in selection are common and potentially important (Siepielski et al., 2009). For most purposes, we expect spatial and temporal heterogeneity to have similar consequences for the evolution of mate choice under GEIs; for example, temporal variability in selection should increase standing genetic variation (Bussière et al., 2008, Siepielski et al., 2009, Greenfield et al., 2012), and may cause females to erroneously select males that are well-adapted to past but not future conditions. Future studies could establish the similarities and differences between spatial and temporal variation in their effects on mate choice and local adaptation.

We also kept dispersal rates and distances fixed in each simulation run, although it is clear that the evolution of dispersal itself is expected to respond to local adaptation and spatially varying population dynamics (Billiard and Lenormand, 2005, Gros et al., 2006). In a somewhat different context from the present one (inbreeding avoidance), male dispersal was found to evolve in response to spatial variation in mating prospects (Lehmann and Perrin, 2003). In the present context of mate choice for local adaptation, one might predict that male dispersal would be more strongly selected if male ornaments are highly dependent on the male's natal environment. Therefore, males well-adapted to their natal site could carry their high attractiveness with them when dispersing. By contrast, if male attractiveness were heavily influenced by the post-dispersal environment and migrants tend to be less locally adapted, male dispersal might evolve to a lower level. However, the complexity of interactions between the degree of female choosiness and the relative timing of dispersal and the determination of attractiveness (Figure 2) suggest that feedback between the evolution of mate choice and dispersal is probably more complicated than this simplistic prediction suggests.

There is also an interesting parallel between GEIs and interactions among genes. Gene-by-gene interactions (epistasis or GxG) might sometimes increase the amount of standing genetic variation, because alleles experience fluctuating selection as they recombine through different genetic backgrounds. More variance in fitness would seem to favour the evolution of female choice. However, females often cannot be expected to know how their genes will interact with those of their mate prior to mating (but see e.g. Fromhage et al., 2009), such that choosiness might become less worthwhile when GxG is a major component of fitness. Interesting effects may occur when females are partially or fully able to screen out poorly genetically compatible mates. One might initially expect that female choice for compatible mates would evolve and be maintained most easily when it is very effective, yet mate choice errors might help maintain a pool of males carrying alleles that are incompatible with the majority of females. As in our GEI model, the value of mate choice for compatible genes might depend on a great deal of interacting factors, including dispersal, the efficacy of choice and the relative contribution of GxG to fitness.

Similarly, the fitness of an individual can depend on interactions between its own genes and those of its social partners. For example, the effect of a particular allele on attractiveness or condition may depend on the genotypes of competing individuals (Danielson-François et al., 2009). The biotic environment experienced by an allele therefore changes over evolutionary time as the population evolves; the

528   consequences for mate choice of an evolving social environment are far from clear, and the subject
529   deserves a thorough treatment elsewhere.

530   Our model implemented sexual selection in a very general way: males in good condition simply fathered
531   more offspring, on average. We did not differentiate between pre- and post-copulatory sexual selection;
532   the model is equally consistent with biological scenarios in which females actively select males in good
533   condition, and/or mate multiply and then ensure that their eggs are predominantly fertilised by sperm from
534   high quality males. However, modelling these processes separately might produce interesting insights. For
535   example, we expect that the parameter p might often differ for male traits affecting pre- and post-
536   copulatory sexual selection. In stalk-eyed flies *Cyrtodiopsis dalmanni*, the length of males' eyestalks (which
537   affects their attractiveness) is affected by pre-imaginal conditions but is fixed throughout adulthood
538   (Cotton et al., 2004). Male eyespan therefore only indicates adaptedness to the environment experienced
539   as a juvenile, prior to dispersal ($p = 1$). However, adult male stalk-eyed flies kept under different nutritional
540   regimes developed different sized testes and accessory glands, suggesting that adult nutrition affects
541   competitive fertilisation ability (Baker et al., 2003). Therefore, a male's success in post-copulatory sexual
542   selection may partially reflect his adaptedness to the current locality ($p < 1$). Effects of adult male nutrition
543   on competitive fertilisation ability have also been reported in *Drosophila* (Amitin and Pitnick, 2007, Fricke
544   et al., 2008), as have GEIs for traits affecting mating success whose expression is fixed in the larval phase
545   (Ribó et al., 1989). Therefore, parameters that favour the evolution and maintenance of pre-copulatory
546   female choice might be different to those favouring post-copulatory choice.

547   Whenever sperm competitive ability more accurately reflects local adaptation than male sexual ornaments,
548   females could increase the proportion of their eggs that are fertilised by locally-adapted males by mating
549   with multiple males. Female choice for local adaptation therefore suggests a novel (to our knowledge)
550   benefit of polyandry, which might contribute to the maintenance of polyandry in spite of its direct costs.
551   Future models could explore the magnitude of this putative benefit of polyandry under different scenarios,
552   and assess which parameters (e.g. dispersal regimes) favour elevated polyandry. We note however that
553   greater success of locally-adapted males in post-copulatory sexual selection should increase local
554   adaptation, possibly removing the variation needed to maintain female 'choice' via polyandry.

Conclusions

556   In sum, there is ample scope for further theoretical and empirical progress. Sexual selection studies rarely
557   focus on spatially explicit local adaptation. Our model provides interesting food for thought for students of
558   sexual selection, a field where some systems appear to support female choice based on indirect benefits,
559   and others do not. Our results feature scenarios where immigration provides a constant supply of locally
560   maladapted males, and screening for male quality can be selectively favoured even if females pay a
561   fecundity cost for doing so. However, the same process does not work when there is a less suitable
562   combination of spatial variation, dispersal and the relative timing of dispersal and the determination of
563   condition. Although the number of possible interactions (Figure 2) makes it hard to make simple directional
564   predictions for all of these variables, our model highlights that much of the variation in outcomes is driven
565   by how much females benefit from choosing locally adapted males rather than mating at random, which in
566   turn depends upon the extent to which dispersal is able to prevent local adaptation.

References

AMITIN, E. G. & PITNICK, S. 2007. Influence of developmental environment on male- and female-mediated sperm precedence in *Drosophila melanogaster*. *Journal of Evolutionary Biology,* 20**,** 381-391.

ARNQVIST, G. 1992. Spatial variation in selective regimes: Sexual selection in the water strider, *Gerris odontogaster*. *Evolution,* 46**,** 914-929.

ATKINS, K. E. & TRAVIS, J. M. J. 2010. Local adaptation and the evolution of species' ranges under climate change. *Journal of Theoretical Biology,* 266**,** 449-457.

BAKER, R. H., DENNIFF, M., FUTERMAN, P., FOWLER, K., POMIANKOWSKI, A. & CHAPMAN, T. 2003. Accessory gland size influences time to sexual maturity and mating frequency in the stalk-eyed fly, *Cyrtodiopsis dalmanni*. *Behavioral Ecology,* 14**,** 607-611.

BILLIARD, S. & LENORMAND, T. 2005. Evolution of migration under kin selection and local adaptation. *Evolution,* 59**,** 13-23.

BLANQUART, F., GANDON, S. & NUISMER, S. L. 2012. The effects of migration and drift on local adaptation to a heterogeneous environment. *Journal of Evolutionary Biology,* 25**,** 1351-1363.

BORGIA, G. 1979. Sexual selection and the evolution of mating systems. *In:* BLUM, M. S. & BLUM, N. A. (eds.) *Sexual Selection and Reproductive Competition in Insects.* New York: Academic Press.

BRIDLE, J. R. & VINES, T. H. 2007. Limits to evolution at range margins: when and why does adaptation fail? *Trends in Ecology and Evolution,* 22**,** 140-147.

BRO-JØRGENSEN, J. 2010. Dynamics of multiple signalling systems: animal communication in a world in flux. *Trends in Ecology and Evolution,* 25**,** 292-300.

BURGER, R. & LANDE, R. 1994. On the distribution of the mean and variance of a quantitative trait under mutation-selection-drift balance. *Genetics,* 138**,** 901-912.

BUSSIÈRE, L., HUNT, J., STÖLTING, K., JENNIONS, M. & BROOKS, R. 2008. Mate choice for genetic quality when environments vary: suggestions for empirical progress. *Genetica,* 134**,** 69-78.

CANDOLIN, U. 2000. Changes in expression and honesty of sexual signalling over the reproductive lifetime of sticklebacks. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 267**,** 2425-2430.

COCKBURN, A., OSMOND, H. L. & DOUBLE, M. C. 2008. Swingin' in the rain: condition dependence and sexual selection in a capricious world. *Proceedings of the Royal Society B,* 275**,** 605-612.

CORNWALLIS, C. K. & ULLER, T. 2010. Towards an evolutionary ecology of sexual traits. *Trends in Ecology and Evolution,* 25**,** 145-152.

COTTON, S., FOWLER, K. & POMIANKOWSKI, A. 2004. Condition dependence of sexual ornament size and variation in the stalk-eyed fly *Cyrtodiopsis dalmanni* (Diptera: Diopsidae). *Evolution,* 58**,** 1038-1046.

CUEVAS, J. M., MOYA, A. & ELENA, S. F. 2003. Evolution of RNA virus in spatially structured heterogeneous environments. *Journal of Evolutionary Biology,* 16**,** 456-466.

DANIELSON-FRANÇOIS, A., ZHOU, Y. & GREENFIELD, M. 2009. Indirect genetic effects and the lek paradox: inter-genotypic competition may strengthen genotype × environment interactions and conserve genetic variance. *Genetica,* 136**,** 27-36.

DANIELSON-FRANÇOIS, A. M., KELLY, J. K. & GREENFIELD, M. D. 2006. Genotype × environment interaction for male attractiveness in an acoustic moth: evidence for plasticity and canalization. *Journal of Evolutionary Biology,* 19**,** 532-542.

DAY, T. 2000. Sexual selection and the evolution of costly female preferences: Spatial effects. *Evolution,* 54**,** 715-730.

DOLGIN, E. S., WHITLOCK, M. C. & AGRAWAL, A. F. 2006. Male *Drosophila melanogaster* have higher mating success when adapted to their thermal environment. *Journal of Evolutionary Biology,* 19**,** 1894-1900.

ETGES, W. J., DE OLIVEIRA, C. C., GRAGG, E., ORTÍZ-BARRIENTOS, D., NOOR, M. A. F. & RITCHIE, M. G. 2007. Genetics of incipient speciation in *Drosophila mojavensis*. I. Male courtship song, mating success, and genotype x environment interactions. *Evolution,* 61**,** 1106-1119.

EVANS, K. L., NEWTON, J., GASTON, K. J., SHARP, S. P., MCGOWAN, A. & HATCHWELL, B. J. 2012. Colonisation of urban environments is associated with reduced migratory behaviour, facilitating divergence from ancestral populations. *Oikos,* 121**,** 634-640.

FRICKE, C. & ARNQVIST, G. 2007. Rapid adaptation to a novel host in a seed beetle (Callosobruchus maculatus): The role of sexual selection. *Evolution,* 61**,** 440-454.

FRICKE, C., BRETMAN, A. & CHAPMAN, T. 2008. Adult male nutrition and reproductive success in *Drosophila melanogaster*. *Evolution,* 62**,** 3170-3177.

FRIEDL, T. W. P. & KLUMP, G. M. 2005. Sexual selection in the lek-breeding European treefrog: body size, chorus attendance, random mating and good genes. *Animal Behaviour,* 70**,** 1141-1154.

FROMHAGE, L., KOKKO, H. & REID, J. M. 2009. Evolution of mate choice for genome-wide heterozygosity. *Evolution,* 63**,** 684-694.

GAVRILETS, S. 2003. Models of speciation: What have we learned in 40 years? *Evolution,* 57**,** 2197-2215.

628 GETTY, T. 1995. Search, discrimination, and selection: Mate choice by pied flycatchers. *The American*
629   *Naturalist,* 145**,** 146-154.

630 GREENFIELD, M. D., DANKA, R. G., GLEASON, J. M., HARRIS, B. R. & ZHOU, Y. 2012. Genotype × environment
631   interaction, environmental heterogeneity and the lek paradox. *Journal of Evolutionary Biology,* 25**,**
632   601-613.

633 GREENFIELD, M. D. & RODRIGUEZ, R. L. 2004. Genotype-environment interaction and the reliability of
634   mating signals. *Animal Behaviour,* 68**,** 1461-1468.

635 GROS, A., JOACHIM POETHKE, H. & HOVESTADT, T. 2006. Evolution of local adaptations in dispersal
636   strategies. *Oikos,* 114**,** 544-552.

637 GUNNARSSON, T. G., SUTHERLAND, W. J., ALVES, J. A., POTTS, P. M. & GILL, J. A. 2012. Rapid changes in
638   phenotype distribution during range expansion in a migratory bird. *Proceedings of the Royal Society*
639   *B: Biological Sciences,* 279**,** 411-416.

640 HANSKI, I., MONONEN, T. & OVASKAINEN, O. 2011. Eco-evolutionary metapopulation dynamics and the
641   spatial scale of adaptation. *The American Naturalist,* 177**,** 29-43.

642 HEREFORD, J. 2009. A quantitative survey of local adaptation and fitness trade-offs. *The American*
643   *Naturalist,* 173**,** 579-588.

644 HIGGINSON, A. D. & READER, T. 2009. Environmental heterogeneity, genotype-by-environment interactions
645   and the reliability of sexual traits as indicators of mate quality. *Proceedings of the Royal Society B,*
646   276**,** 1153-1159.

647 INGLEBY, F. C., HUNT, J. & HOSKEN, D. J. 2010. The role of genotype-by-environment interactions in sexual
648   selection. *Journal of Evolutionary Biology,* 23**,** 2031-2045.

649 JIA, F.-Y., GREENFIELD, M. D. & COLLINS, R. D. 2000. Genetic variance of sexually selected traits in
650   waxmoths: Maintenance by genotype x environment interaction. *Evolution,* 54**,** 953-967.

651 JOHNSTONE, R. A. & GRAFEN, A. 1992. Error-Prone Signalling. *Proceedings of the Royal Society of London*
652   *Series B,* 248**,** 229-233.

653 KASSEN, R. 2002. The experimental evolution of specialists, generalists, and the maintenance of diversity.
654   *Journal of Evolutionary Biology,* 15**,** 173-190.

655 KELLY, M. W., SANFORD, E. & GROSBERG, R. K. 2012. Limited potential for adaptation to climate change in a
656   broadly distributed marine crustacean. *Proceedings of the Royal Society B: Biological Sciences,* 279**,**
657   349-356.

658 KIRKPATRICK, M. 1985. Evolution of female choice and male parental investment in polygynous species:
659   The demise of the "sexy son". *The American Naturalist,* 125**,** 788-810.

660   KIRKPATRICK, M. & BARTON, N. H. 1997. Evolution of a species' range. *American Naturalist,* 150**,** 1-23.

661   KLAPPERT, K. & REINHOLD, K. 2005. Local adaptation and sexual selection: a reciprocal transfer experiment
662   with the grasshopper *Chorthippus biguttulus*. *Behavioral Ecology and Sociobiology,* 58**,** 36-43.

663   KOKKO, H. 1997. Evolutionarily stable strategies of age-dependent sexual advertisement. *Behavioral*
664   *Ecology and Sociobiology,* 41**,** 99-107.

665   KOKKO, H. & HEUBEL, K. 2008. Condition-dependence, genotype-by-environment interactions and the lek
666   paradox. *Genetica,* 134**,** 55-62.

667   LE CORRE, V. & KREMER, A. 2012. The genetic differentiation at quantitative trait loci under local
668   adaptation. *Molecular Ecology,* 21**,** 1548-1566.

669   LEHMANN, L. & PERRIN, N. 2003. Inbreeding avoidance through kin recognition: Choosy females boost
670   male dispersal. *American Naturalist,* 162**,** 638-652.

671   LONG, T. A. F., AGRAWAL, A. F. & ROWE, L. 2012. The effect of sexual selection on offspring fitness depends
672   on the nature of genetic variation. *Current Biology,* 22**,** 204-208.

673   LORCH, P. D., PROULX, S., ROWE, L. & DAY, T. 2003. Condition-dependent sexual selection can accelerate
674   adaptation. *Evolutionary Ecology Research,* 5**,** 867-881.

675   MAYR, E. 1963. *Animal Species and Evolution,* Cambridge, MA, Harvard University Press.

676   MCGONIGLE, L. K., MAZZUCCO, R., OTTO, S. P. & DIECKMANN, U. 2012. Sexual selection enables long-term
677   coexistence despite ecological equivalence. *Nature,* 484**,** 506-509.

678   MILLER, L. K. & BROOKS, R. 2005. The effects of genotype, age, and social environment on male
679   ornamentation, mating behavior, and attractiveness. *Evolution,* 59**,** 2414-2425.

680   MILLS, S. C., ALATALO, R. V., KOSKELA, E., MAPPES, J., MAPPES, T. & OKSANEN, T. A. 2007. Signal reliability
681   compromised by genotype-by-environment interaction and potential mechanisms for its
682   preservation. *Evolution,* 61**,** 1748-1757.

683   NIELSEN, M. L. & HOLMAN, L. 2012. Terminal investment in multiple sexual signals: Immune-challenged
684   males produce more attractive pheromones. *Functional Ecology,* 26**,** 20-28.

685   NOSIL, P., VINES, T. H. & FUNK, D. J. 2005. Reproductive isolation caused by natural selection against
686   immigrants from divergent habitats. *Evolution,* 59**,** 705-719.

687   PAYNE, R. J. H. & KRAKAUER, D. C. 1997. Sexual selection, space, and speciation. *Evolution,* 51**,** 1-9.

688 POSTMA, E. & VAN NOORDWIJK, A. J. 2005. Gene flow maintains a large genetic difference in clutch size at
689   a small spatial scale. *Nature,* 433**,** 65-68.

690 PROULX, S. R. 2001. Female choice via indicator traits easily evolves in the face of recombination and
691   migration. *Evolution,* 55**,** 2401-2411.

692 RADWAN, J. 2008. Maintenance of genetic variation in sexual ornaments: a review of the mechanisms.
693   *Genetica,* 134**,** 113-127.

694 REINHOLD, K. 2004. Modeling a version of the good-genes hypothesis: female choice of locally adapted
695   males. *Organisms Diversity and Evolution,* 4**,** 157-163.

696 RIBÓ, G., OCAÑA, J. & PREVOSTI, A. 1989. Effect of larval crowding on adult mating behaviour in *Drosophila
697   melanogaster*. *Heredity,* 63**,** 195-202.

698 RODRÍGUEZ, R. & AL-WATHIQUI, N. 2011. Genotype × environment interaction is weaker in genitalia than in
699   mating signals and body traits in *Enchenopa* treehoppers (Hemiptera: Membracidae). *Genetica,*
700   139**,** 871-884.

701 ROWE, L. & HOULE, D. 1996. The lek paradox and the capture of genetic variance by condition dependent
702   traits. *Proceedings of the Royal Society of London Series B: Biological Sciences,* 263**,** 1415-1421.

703 ROWELL, JONATHAN T., ELLNER, STEPHEN P. & REEVE, H. K. 2006. Why animals lie: How dishonesty and
704   belief can coexist in a signaling system. *The American Naturalist,* 168**,** E180-E204.

705 SAVOLAINEN, O., PYHAJARVI, T. & KNURR, T. 2007. Gene flow and local adaptation in trees. *Annual Review
706   of Ecology, Evolution and Systematics,* 38**,** 595-619.

707 SEARCY, W. A. & NOWICKI, S. 2005. *The Evolution of Animal Communication: Reliability and Deception in
708   Signaling Systems,* Princeton, Princeton University Press.

709 SIEPIELSKI, A. M., DIBATTISTA, J. D. & CARLSON, S. M. 2009. It's about time: the temporal dynamics of
710   phenotypic selection in the wild. *Ecology Letters,* 12**,** 1261-1276.

711 SPICHTIG, M. & KAWECKI, TADEUSZ J. 2004. The maintenance (or not) of polygenic variation by soft
712   selection in heterogeneous environments. *The American Naturalist,* 164**,** 70-84.

713 TOLLE, A. E. & WAGNER, W. E. 2011. Costly signals in a field cricket can indicate high- or low-quality direct
714   benefits depending upon the environment. *Evolution,* 65**,** 283-294.

715 TOMKINS, J. L., RADWAN, J., KOTIAHO, J. S. & TREGENZA, T. 2004. Genic capture and resolving the lek
716   paradox. *Trends in Ecology & Evolution,* 19**,** 323-328.

717 VERGARA, P., MOUGEOT, F., MARTÍNEZ-PADILLA, J., LECKIE, F. & REDPATH, S. M. 2012. The condition
718   dependence of a secondary sexual trait is stronger under high parasite infection level. *Behavioral*
719   *Ecology,* 23**,** 502-511.

720 WOLLERMAN, L. & WILEY, R. H. 2002. Background noise from a natural chorus alters female discrimination
721   of male calls in a Neotropical frog. *Animal Behaviour,* 63**,** 15-22.

722 ZHOU, Y., KUSTER, H. K., PETTIS, J. S., DANKA, R. G., GLEASON, J. M. & GREENFIELD, M. D. 2008. Reaction
723   norm variants for male calling song in populations of *Achroia grisella* (Lepidoptera: Pyralidae):
724   Towards a resolution of the lek paradox. *Evolution,* 62**,** 1317-1334.

725

Figure legends

727

728 *Figure 1*: Evolution of female mate choice under gene-by-environment interactions (GEIs).

729 Each line in the centre plot shows the change in frequency over successive generations of the female choice
730 allele for four different spatial scenarios. The four insets show a 3D plot of the worlds used in the
731 simulations (where elevation describes the environment type E and the other dimensions are [x, y]
732 positions on the map), and the density plots show the distribution of phenotypic values at each of three
733 arbitrarily chosen locations. The dots on the density plots show the mean environmental value at that
734 location, and thus the genotypic value that maximises fitness. Shown (clockwise from top) are the results
735 for a highly spatially-autocorrelated world with high dispersal (note absence of local adaptation in the
736 density plot), a highly spatially-autocorrelated world with low dispersal (note local adaptation), a world
737 with largely randomly-distributed environmental types, and a world with only one environmental type.

738

739 *Figure 2*: The prospects for the evolution of costly female choice (calculated as described in the text) for
740 different types of world, dispersal distances (d; left and right panels) and values of p.

741 The insets show a cross-section of each world, sliced through the middle site along one of the axes of the
742 toroid. Black circles represent $p = 0$ (i.e. condition is determined in the natal environment), white circles are
743 $p = 1$ (condition is determined in the post-dispersal environment) and bicoloured circles are $p = 0.5$ (both
744 environments equally affect determination of condition).

745