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Local adaptation and the evolution of female choice

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Luke Holman and Hanna Kokko

luke.holman@anu.edu.au
hanna.kokko@anu.edu.au

Centre of Excellence in Biological Interactions,
Division of Ecology, Evolution & Genetics,
Research School of Biology,
Australian National University,
Canberra, ACT 0200, Australia.

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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

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

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

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

The Jekyll and Hyde nature of GEIs

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

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

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

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

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

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

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

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

The exact balance of the negative effect (the breakdown in signal reliability under a GEI scenario) and the positive effect (greater variance in male condition, and hence greater returns for being choosy) determines whether GEIs favour female choice. In the model of Kokko and Heubel (2008), the positive and negative effects of GEIs did not 'cancel out', thus GEIs can either favour or prohibit the evolution of female choice depending on patterns of gene flow and the amount of variation maintained by other factors (in this case, mutation). Also, a breakdown in signal reliability can actually favour mate choice in some situations by reducing the ability of mate choice to erode the very genetic variation it needs to operate.

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

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

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

The model

Overview: We constructed an individual-based simulation of a population of sexual haploids living in continuous space on the surface of a toroid (doughnut-shaped) world. Each point on the world had an environmental value, and was hospitable to individuals whose phenotype matched the local environment well (Figures 1 and 2 show some example worlds). Each individual was either male or female, and had L loci (in our examples we used L = 50) carrying one of two possible alleles (a or A, coded as 0 and 1); the phenotype affecting local adaptation (termed z) was the mean allelic value of these L loci ($0 \leq z \leq 1$). An individual's condition (ζ) was determined by the interaction between its phenotype z and up to two environments: its natal environment and/or its post-dispersal environment (depending on the time at which condition was determined relative to dispersal). Condition determined both the probability of survival and, for surviving males, their attractiveness to choosy females. Males may therefore be thought of as possessing a sexual ornament that honestly reveals their condition.

Individuals carried an additional locus with two possible alleles, B and b. This locus was only expressed in females, and controlled whether a female exhibited a preference for males in good condition (allele B), or mated at random (allele b). In each generation, individuals were born, dispersed, survived with a probability determined by the match between their phenotype and their natal and/or post-dispersal environments, reproduced and then died. Generations were thus non-overlapping.

Initialisation phase: At the start of each simulation run, we constructed a toroid world with circumferences of length 1. The world was divided into $s \times s$ squares, each with its own environmental value E_i (our examples below use s = 100). We used an algorithm that allowed us to vary the scale of the environmental grain by adjusting the spatial autocorrelation (i.e. the similarity in E between neighbouring squares) of the environment. The algorithm first generated an $s \times s$ grid of random values, then picked a random square and updated its environmental value E_i using the formula

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

where the first term is the mean environmental value of the eight neighbouring squares multiplied by β (a constant determining the magnitude of the spatial autocorrelation), and x is a pseudorandom number between 0 and 1. This updating procedure was repeated $100s^2$ times, causing neighbouring squares to have similar values when β was high (coarse-grained environment: top of Figure 1 is produced with $\beta = 0.999$) and vary widely when β was low (fine-grained environment: lower right in Figure 1 is produced with β = 0.05). Note that in the toroid world, the neighbour of a 'corner' cell can reside in the opposite corner of the grid, which removes any edge effects: a patch of low (or high) environmental values can extend across apparent edges. The resulting grid was rescaled so that the mean of all E_i values was 0.5, with standard deviation 0.2. We also ran simulations in a completely spatially homogeneous world in which all squares had an environmental value of 0.5, ensuring that the fitness of each genotype was constant in all localities (Figure 1, lower left).

We then initialised a population of 10,000 individuals with random genotypes and sexes, and natal coordinates [x_n, y_n] as real numbers between 0 and 1.

Dispersal: Next, males and females dispersed with probabilities m_m and m_f respectively (in the figures below we use $m_m = m_f = 0.5$). Migrants of both sexes dispersed a random distance drawn from an exponential 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 (β = 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 (β = 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.

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

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

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

Can we generalise?

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

However, as stated above, GEIs are a double-edged sword. Choosy females only benefit significantly from mating with better-adapted males if the present condition of these males reflects the likely viability and attractiveness of the offspring; on the other hand, if this relationship is too tight, variance in male quality is more strongly depleted by female choice. This suggests that the parameter p, which reflects the importance of the natal site (as opposed to the environmental conditions experienced as an adult) as a determinant of condition, could have complex effects (see also Chapter 4). Figure 1 assumes $p = 1$, i.e. natal condition fully determines the subsequent viability and appearance of adults; it also only shows single examples of each case (there is repeatability, but with relatively large variation across runs; not shown).

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

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

GEIs often maintain costly choice — in a suitably variable world

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

One might expect the case $p = 1$ to provide smaller benefits of female choice, because it affords maladapted migrant males greater attractiveness and survival, and indeed there was some evidence of this (open circle in world 4; Figure 2a). However, the presence of many maladapted but attractive migrants also favours female choice, because these migrants leave maladapted, unattractive sons that choosy females 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 females make equally good (or even better) mating decisions than females who select males in good condition.

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

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

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

Prospects for Empirical Work

How should these ideas be incorporated into empirical work? A number of studies have found evidence that GEIs affect the expression of both sexually-selected signals and measures of fitness and condition, although for sexual signals the evidence is skewed towards insects and birds (reviewed in Bussière et al., 2008, Ingleby et al., 2010). For example, quantitative genetic studies of the ultrasonic song of the male lesser waxmoth *Achroia grisella* have revealed GEIs for condition and the male song: the genotype that produces the best song in one rearing environment may not do so in another (Jia et al., 2000, Danielson-François et al., 2006, Greenfield et al., 2012). In bank voles *Clethrionomys glareolus*, socially dominant males sired dominant sons only when the sons were reared in a similar habitat to their father, suggesting that GEIs affect the olfactory dominance signal and/or condition, and that GEIs might compromise the evolution of costly female preferences for dominance (Mills et al., 2007).

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

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

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

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

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

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

Conclusions

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

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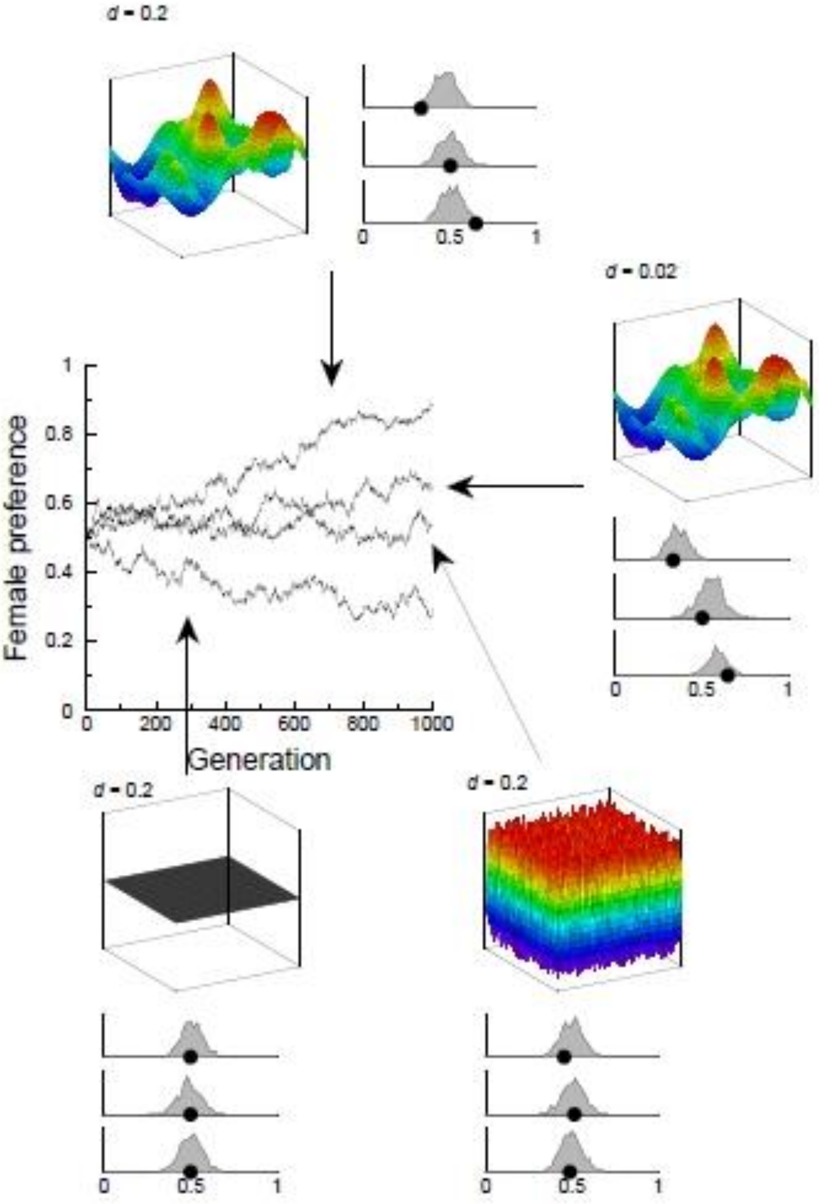
Figure legends

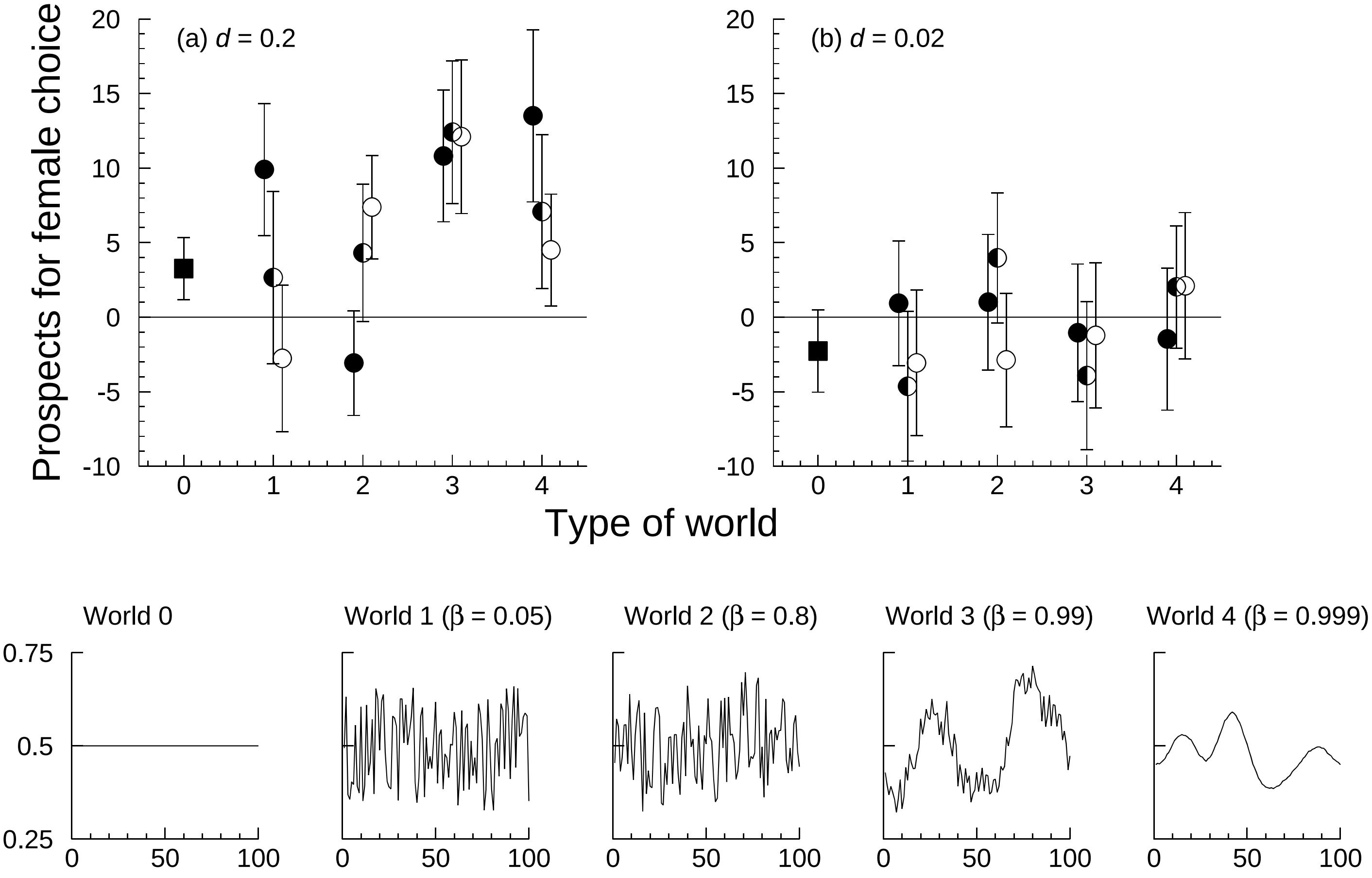
Figure 1: Evolution of female mate choice under gene-by-environment interactions (GEIs).

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

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

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


d = 0.2
0
0.5
1
d = 0.02
Female preference
1
0.8
0.6
0.4
0.2
0
0
200
400
600
800
1000
Generation
d = 0.2
d = 0.2


Prospects for female choice
(a) d = 0.2
(b) d = 0.02
20
15
10
5
0
-5
-10
0
1
2
3
4
Type of world
World 0
World 1 (β = 0.05)
World 2 (β = 0.8)
World 3 (β = 0.99)
World 4 (β = 0.999)
0.75
0.5
0.25
0
50
100