

Liking the good guys: amplifying local adaptation via the evolution of condition-dependent mate choice

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Abstract

Local adaptation can be strengthened through a diversity of mechanisms that reduce gene flow between contrasting environments. Recent work revealed that mate choice could enhance local adaptation when females preferentially mate with locally adapted males and that such female preferences readily evolve, but the opposing effects of recombination, migration and costs of female preferences remain relatively unexplored. To investigate these effects, we develop a two-patch model with two genes, one influencing an ecological trait and one influencing female preferences, where both male signals and female preferences are allowed to depend on the match between an individual's ecological trait and the local environment (condition). Because trait variation is limited when migration is rare and the benefits of preferential mating are short-lived when migration is frequent, we find that female preferences for males in high condition spread most rapidly with intermediate levels of migration. Surprisingly, we find that preferences for locally adapted males spread fastest with higher recombination rates, which contrasts with earlier studies. This is because a stronger preference allele for locally adapted males can only get uncoupled from maladapted ecological alleles following migration through recombination. The effects of migration and recombination depend strongly on the condition of the males being chosen by females, but only weakly on the condition of the females doing the choosing, except when it comes to the costs of preference. Although costs always impede the spread of female preferences for locally adapted males, the impact is substantially lessened if costs are borne primarily by females in poor condition. The abundance of empirical examples of condition-dependent mate choice combined with our theoretical results suggests that the evolution of mate choice could commonly facilitate local adaptation in nature.

Introduction

Adaptation to local ecological conditions can be facilitated or hampered by evolutionary processes such as migration, recombination and sexual selection. Migration, here defined as the permanent movement of individuals from the site of birth to the site of reproduction (i.e. used here as a synonym for 'dispersal'), can

facilitate adaptation by increasing genetic variation through gene flow. On the other hand, migration decreases the consistency of the ecological environments encountered by offspring, weakening selection for local adaptation. Similarly, recombination can generate novel genotypes, creating variation for selection to act upon, but it also disrupts well-adapted genotypes. How these counteracting forces impact observed patterns of local adaptation has long interested evolutionary biologists (Maynard Smith, 1966; Lenormand, 2002; Kawecki & Ebert, 2004). These forces can in turn generate indirect selection to alter the evolutionary processes themselves,

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with selection for reduced migration (Wiener & Feldman, 1993) and reduced recombination (Pylkov *et al.*, 1998; Lenormand & Otto, 2000) to improve the match between genotypes and their environments.

Similarly, nonrandom mating may facilitate or hamper local adaptation, depending on whether locally adapted males have a higher or lower mating success. Sexual selection is particularly likely to impact local adaptation if male sexual signals are condition dependent and reflect the level of ecological adaptation (Proulx, 1999, 2001a, 2002; van Doorn *et al.*, 2009; Schindler *et al.*, 2013). Earlier work has demonstrated that the evolution of sexual preferences can have a strong impact on the degree of local adaptation (see Background section). Here, we build upon this earlier work by analysing an explicit two-locus, two-patch model that explores how migration, recombination and preference costs influence the evolution of female preferences when the direction of selection differs among patches. The current work adds to our understanding of the interplay between sexual selection and local adaptation by explicitly determining when alleles modifying female preferences invade when rare, allowing for linkage disequilibria among loci and including potential costs of these preferences. In addition to allowing a male's trait to reflect his fitness in the current environment, we also explore the impact of allowing a female's condition to affect her preferences. For example, locally adapted females may have more resources to invest in mate choice and/or may experience lower costs of choice. In this study, we use the term condition-dependent mate choice for scenarios where male signal expression, the strength of female preference and/or the costs of choosiness depend on the male's or female's condition.

Within each patch, the match of an individual to local conditions depends on an ecologically relevant trait locus with two alleles, each allele being better adapted to one of two patches. A second locus determines the strength of female preferences, which alters their ability to discriminate between ecologically well-adapted and poorly adapted males. Although stronger mating preferences improve local adaptation, we show that the evolution of such preferences is critically dependent on the cost of preferences as well as the rate of migration between the two patches and recombination between the trait and female preference loci. Before describing these results, we next situate the current study with respect to previous work on the evolution of sexual preferences.

Background

Our model focuses on the evolution of condition-dependent sexual preferences within spatially heterogeneous environments. With the exception of the models described below in greater detail, the majority of studies

exploring the evolution of sexual preferences assume that the phenotype of a male depends solely on his genotype within a single environment (Fisher, 1915; O'Donald, 1980; Lande, 1981; Kirkpatrick, 1982; Pomiankowski *et al.*, 1991; Pomiankowski & Iwasa, 1998). More recent models have expanded these results to account for spatial structure explicitly (Servedio & Kirkpatrick, 1997; Kirkpatrick & Servedio, 1999; Proulx, 1999, 2001a, 2002; Servedio, 2001; Lorch *et al.*, 2003; van Doorn *et al.*, 2009; Proulx & Servedio, 2009; Schindler *et al.*, 2013; Thibert-Plante & Gavrillets, 2013). An important recent insight is that with different traits favoured in each of two patches, sexual preferences for a trait that is not condition dependent typically reduce the degree of local adaptation, rather than enhance it (Servedio & Bürger, 2014). This surprising phenomenon occurs because indirectly selected preference alleles spread between patches more readily than directly selected trait alleles, enhancing the mating success of locally nonadapted alleles.

When male traits contain information about their fitness in the local environment, however, sexual preferences for males that match their environment ('high condition') can strongly promote local adaptation (Proulx, 1999, 2002; Lorch *et al.*, 2003; Proulx & Servedio, 2009). For example, Proulx (1999) examined the degree of local adaptation to a new habitat ('island') in populations with migration from a mainland population with different ecological conditions. Whether locally adapted mutant alleles could invade the island was calculated for three different mating strategies: random mating, positive assortative mating (females prefer males with the same allele at the ecological locus) and 'locally adapted male mating advantage' (LAMMA), where females choose the most fit partner from a subset of n males ('best-of- n ' strategy). Alleles that were locally adapted to the island were able to spread under a broader range of parameters with LAMMA than with either assortative or random mating. LAMMA even allowed the spread of very weakly selected alleles on the island, which was not otherwise observed. Qualitatively similar results were obtained when this framework was extended to include perceptual errors and two-way migration (Proulx, 2002).

Whether LAMMA is likely to evolve in the face of costs of choice, migration and recombination is the focus of the current study and has been investigated in some previous studies. Proulx (2001b) explored a 'best-of- n ' model of female preference for locally adapted males in a two-patch model with ecologically heterogeneous selection. In the 'best-of- n ' model, females are presented with a subset of n males drawn randomly from the population and choose the male closest to their preference from among this subset; mating probabilities thus explicitly depend on the frequencies of different male genotypes. To allow for a stochastic component of mate choice, Proulx incorporated a

distribution of perceptual errors. He also allowed female survival to decline with search effort. Proulx then numerically identified the evolutionarily stable strategy (ESS) for both the degree of local adaptation and the extent of female preferences. Females evolved to choose high-quality males as long as ecological selection was sufficiently strong, and they evolved to be choosier when assessments of males were more accurate. Relative to that study, our work provides simpler explicit conditions for the evolution of female preferences using a fixed relative preference scheme (Kirkpatrick, 1982) and modelling fixed preference costs, plus we explicitly account for linkage disequilibrium within patches and the impact of recombination. Specifically, with a fixed relative preference scheme, the chance that a female mates with a particular male type is proportional to that type's attractiveness times its frequency, normalized such that each female is guaranteed a mate. Thus, a female is more likely to mate with a more common type of mate, as well as a more attractive type of mate (see the model outline below), providing a simple but biologically relevant mate-choice model.

In another two-patch model with ecological selection, van Doorn *et al.* (2009) examined how female preferences for a male condition-dependent signal (revealing a male's level of ecological adaptation) affects reproductive isolation between populations. The three traits (ecological character, female preference and male signal) were modelled as polygenic traits with free recombination. The model was analysed using individual-based simulations as well as numerical analyses of the degree of disruptive selection. Sexual selection based on condition-dependent male signals and ecological adaptation increased the level of ecological adaptation. These results were placed in a speciation context by defining speciation to have occurred once the ecological characters diverged beyond a certain threshold.

Recently, Schindler *et al.* (2013) analysed a two-locus two-patch model that is structurally very similar to the model considered here. One locus governed ecological adaptation (a/A), and the other locus determined the absence/presence of a preference for locally adapted males (m/M , respectively). Again, the two loci were assumed to recombine freely. Females with a preference mate with a locally well-adapted male with probability μ and mate randomly with probability $(1 - \mu)$, regardless of the frequency of the male genotypes. In this 'absolute preference scheme' (Maynard Smith, 1985), well-adapted males may receive an unrealistically high mating success when extremely rare. By contrast, with the fixed relative preference scheme of Kirkpatrick (1982) used here, the probability of a female choosing a high-quality male is dependent on the frequency of high-quality males. This previous study identified the evolutionary optimum by

calculating mean fitness as a function of μ and also determined the effect of a female becoming choosier on the average fitness of her offspring. Using these metrics, the authors showed that stronger LAMMA (higher μ) is selectively advantageous; they also showed that local adaptation is stronger with LAMMA than with assortative mating. Our approach differs by (a) explicitly accounting for recombination, (b) allowing both wild type and newly introduced preference alleles to influence preferences, (c) allowing female preferences to depend on her condition as well as male condition, (d) incorporating costs of preferences and (e) calculating invasion fitness to determine the spread or loss of introduced alleles. On this latter point, we used the leading eigenvalue (λ) of the local stability matrix describing the dynamics of a new preference allele introduced into a population at migration-selection balance to assess whether new preference alleles would invade ($\lambda > 1$) or not ($\lambda < 1$).

The model

In our two-locus, two-patch model, the first locus, E , underlies an ecological character with two alleles; e_1 which is fitter in patch 1 and e_2 which is fitter in patch 2 in both males and females. A *Mathematica* package providing details of the analysis is available as Supporting Information. We make no specific assumption about the male trait other than it reflects the state of the ecological character; condition may thus affect the same or different traits in the two patches (e.g. song versus colouration). The second locus, P with alleles p_1 and p_2 , affects the preference of a female, allowing her to discriminate between locally well-adapted and maladapted males as reflected by their ecological trait. For simplicity, the population is assumed to be haploid with nonoverlapping generations. Each generation starts with migration followed by viability selection, mate choice and ends with reproduction. Very similar results are obtained if viability selection occurs first, followed by migration (see Supporting Information *Mathematica* file). In the following section, we describe each of the stages in more detail and derive the recursion equations. An overview of all the variables and parameters is presented in Table 1.

Within each patch, we keep track of the frequencies of each allele combination at the E and P loci in the two patches (f_{ij}) where i is patch type ($i = 1, 2$) and j is the haploid genotype ($j = 1, 2, 3, 4$ for haplotypes $e_1 p_1, e_2 p_1, e_1 p_2, e_2 p_2$, respectively).

Migration

Each generation starts with migration into a patch, which changes the local allele frequencies after migration to:

$$f_{ij}^m = (1 - m_i)f_{ij} + m_i f_{ij} \quad (1)$$

Table 1 Model variables and parameters.

Term	Symbol	Notes
Ecological trait locus	E	e_1 locally adapted allele in patch 1 e_2 locally adapted allele in patch 2
Preference locus	P	p_1 wild-type preference allele p_2 novel preference allele
Ecological selection	s_i^k	strength of natural selection in patch i for individuals of sex $k = \{\text{♀}, \text{♂}\}$
Preference cost	c_i	cost of the novel preference allele p_2
Migration	m_i	proportion of immigrants in patch i
Recombination	r	recombination rate between P and E
Attractiveness	α_{ij}	preference for locally adapted males relative to maladapted males among females of genotype j in patch i
	$\alpha_L; \alpha_H$	preference among females who are in low (L) or high (H) condition and who carry the wild-type allele p_1 (assumes patch symmetry)
	$\delta\alpha_L; \delta\alpha_H$	change in preference among females who are in low (L) or high (H) condition and who carry the new allele p_2 (assumes patch symmetry)

Here, we let m_i measure the immigration rate, which is the proportion of the post-migration population in patch i that originated from the other patch \bar{i} .

Viability selection

Individuals whose **E** locus differs from the locally favoured allele have their viability reduced by s_i^k , which may differ between the sexes ($k = \text{♀}$ or ♂). Letting the fitness of genotype j in sex k in patch i be W_{ij}^k , we thus have $W_{ij}^{\text{♂}} = 1$ for males carrying the locally adapted allele (e_i in patch i), but $W_{ij}^{\text{♂}} = 1 - s_i^{\text{♂}}$ for maladapted males. The same applies for females, except that there is an additional cost to females bearing a stronger preference allele, p_2 , which reduces fitness by $(1 - c_{ij})$, where we allow the cost to depend on the patch i and on the female's trait genotype ($j = 3$ or 4 for bearers of e_1 or e_2 , respectively). Although we generally consider a newly introduced p_2 to confer stronger and more costly preferences than the wild-type p_1 allele, a weaker and less costly preference can also be considered by allowing $c_{ij} < 0$. This cost is assumed to be fixed regardless of the composition of males in the population, reflecting the physical and energetic costs of being able to exert a preference. The ecological and preference costs are assumed to affect fitness multiplicatively; for example, females of genotype e_2p_2 in patch 1 have fitness $(1 - s_1^{\text{♀}})(1 - c_{12})$.

After selection, the frequency of genotype j in sex k within patch i is then:

$$f_{ij}^{sk} = \frac{f_{ij}^m W_{ij}^k}{\sum_{j=1}^4 f_{ij}^m W_{ij}^k} \quad (2)$$

where the denominator represents the mean fitness in the sex of interest in patch i .

Mate choice and reproduction

In patch i , females of genotype j prefer locally adapted males by a factor α_{ij} over males carrying the less adapted allele at the **E** locus.

The average attractiveness (\bar{P}_{ij}) of the males in patch i encountered by a female of genotype j is assumed to be proportional to the frequency of males in the patch:

$$\bar{P}_{ij} = \sum_{\tilde{j}=1}^4 (1 + \delta_{\tilde{j}} \alpha_{ij}) f_{ij}^{s\tilde{j}} \quad (3)$$

where $\delta_{\tilde{j}}$ is one if the male's genotype, \tilde{j} , bears allele e_i in patch i and is zero otherwise.

The probability that a female of genotype j in patch i mates with a male of genotype \tilde{j} is then given by his attractiveness relative to this average:

$$p_{ij\tilde{j}} = \frac{1 + \delta_{\tilde{j}} \alpha_{ij}}{\bar{P}_{ij}}. \quad (4)$$

Finally, the frequency of offspring with genotype j' in patch i is given by

$$f_{ij'}^o = \sum_j \sum_{\tilde{j}} f_{ij}^{s\tilde{j}} \frac{1 + \delta_{\tilde{j}} \alpha_{ij}}{\bar{P}_{ij}} f_{ij}^{s\tilde{j}} T_{\tilde{j}j'}^{s\tilde{j}}, \quad (5)$$

where $T_{\tilde{j}j'}^{s\tilde{j}}$ describes Mendelian transmission from parental ($\tilde{j}\tilde{j}$) to offspring (j') genotypes. For example, a female e_1p_1 and male e_2p_2 have an offspring e_1p_2 with probability $T_{14 \rightarrow 3} = \frac{r}{2}$, where r is the recombination rate between the two loci. At this stage, we have returned to the beginning of the life cycle, with f_{ij}^o in eqn (5) representing the starting frequencies for the next generation.

To recap, the condition of a male influences his attractiveness, with locally adapted males being $1 + \alpha_{ij}$ times more attractive than maladapted males to females of genotype j in patch i . Similarly, a female's condition is allowed to influence both her preferences (through α_{ij}) and the cost of being choosy (through c_{ij}). Finally, the strength of a female's preference can affect whether the female remains unmated (through c_{ij}), but this is assumed to be independent of the array of males in the population.

Although the above assumes that females identify males accurately, one can redefine the preference terms α_{ij} to incorporate perceptual errors. That is, if ρ_i is the probability of correctly identifying a male in patch i , then we can average female preferences over those instances in which she correctly and incorrectly identifies males as locally adapted or maladapted, which results in the same recursion equations but with α_{ij} now describing this average (see details in Supporting Information *Mathematica* package). Thus, we interpret α_{ij} to be the effective preference of a female in patch i for the locally adapted males, accounting for such errors.

Invasion of a new preference allele

As we are interested in the effects of migration, recombination and costs on the evolution of female preferences, we focus on finding the conditions under which a rare p_2 allele can invade a population fixed for p_1 . To obtain a tractable expression for the invasion conditions, we restricted the parameters by making the model symmetric ($s_i^{\delta} \rightarrow s; s_i^{\circ} \rightarrow s; m_i \rightarrow m$). In the Appendix, we find similar results when we relax the symmetry between the patches but assume weak migration. Costs were also assumed equal across patches but can be different for females that are locally adapted, c_H (*High* condition), versus maladapted, c_L (*Low* condition). Similarly, we assumed that a female bearing the p_1 allele prefers the locally adapted males by α_H when she herself is locally adapted or by α_L when she is maladapted. α_L and α_H can be seen as ‘baseline’ preferences of the wild-type females and if larger than zero lead to (male) condition-dependent mate choice (well-adapted males are preferred over poorly adapted males). These preferences become $\alpha_H + \delta\alpha_H$ or $\alpha_L + \delta\alpha_L$ for females bearing the new preference allele p_2 ; $\delta\alpha_H$ and $\delta\alpha_L$ can be positive or negative, but for clarity we focus on preference alleles that increase choosiness ($\delta\alpha_H \geq 0$ and $\delta\alpha_L \geq 0$). Positive $\delta\alpha$ ’s increase the attractiveness of high-condition males to females bearing the p_2 allele; in addition, differences between $\delta\alpha_H$ and $\delta\alpha_L$ alter the effect of a female’s condition on her preferences.

We performed a local stability analysis, assuming that the difference between the two preference alleles is small (e.g. $\delta\alpha_H, \delta\alpha_L, c_H$ and c_L are each on the order of a small term, ϵ). We can then write the leading eigenvalue as one plus two terms favouring the spread of the new preference allele [one involving the strength of preferences among high-condition females (K_H) and one among low-condition females (K_L)] minus a third term measuring the costs of choice (K_c):

$$\lambda = 1 + K_H \frac{\delta\alpha_H}{P_H} + K_L \frac{\delta\alpha_L}{P_L} - K_c + O(\epsilon^2). \tag{6}$$

In eqn (6), K_H and K_L describe the strength of selection for alleles that increase the degree of choosiness among high- and low-condition females, respectively:

$$K_H = mr \frac{(\hat{q}_H^m - \hat{q}_L^m) \hat{q}_H^s \hat{q}_L^s}{2\Psi} \left(\frac{\hat{q}_H^s}{P_H} \right) \tag{7}$$

and

$$K_L = mr \frac{(\hat{q}_H^m - \hat{q}_L^m) \hat{q}_H^s \hat{q}_L^s}{2\Psi} \left(\frac{\hat{q}_L^s}{P_L} \right) \tag{8}$$

where

$$\Psi = m(\hat{q}_H^m \hat{q}_H + \hat{q}_L^m \hat{q}_L) + \left(\frac{1}{2} - m \right) r \hat{q}_H^s \hat{q}_L^s \left(\frac{1}{P_H} + \frac{1 + \alpha_L}{P_L} \right). \tag{9}$$

In these equations, \bar{P}_H and \bar{P}_L are the mean preferences among locally adapted and among maladapted females, \hat{q}_H and \hat{q}_L are the equilibrium frequencies of the locally adapted and maladapted trait allele (with \hat{q}_H^m and \hat{q}_L^m denoting these quantities after migration and \hat{q}_H^s and \hat{q}_L^s denoting these quantities after natural selection), and Ψ is a strictly positive term. Consequently, both K_H and K_L will be positive, selecting for choosier females, as long as there is some migration ($m > 0$), some recombination ($r > 0$) and locally adapted E alleles are more common than poorly adapted alleles ($\hat{q}_H^m > \hat{q}_L^m$). As shown in the Supporting Information *Mathematica* package, if wild-type females strongly prefer maladapted males ($\alpha_j \ll 0$), sexual selection can trump natural selection and cause a reversal in net selection, leading the locally adapted allele with respect to natural selection to be rarer than the maladapted allele ($\hat{q}_H^m < \hat{q}_L^m$). We assume that such strong opposing mating preferences are not present. Consequently, all females, whether locally adapted (K_H) or maladapted (K_L), are selected to evolve stronger preferences for locally adapted males.

Costly mate choice counteracts this selection pressure, however. In the absence of genetic associations, this cost would select against the p_2 allele by an amount $\bar{c}/2$, where

$$\bar{c} = c_H \hat{q}_H^s + c_L \hat{q}_L^s \tag{10}$$

is the cost experienced by a female averaged over the chance that she is in high or low condition (the one-half arising because only females pay the costs of mate choice). Genetic associations do develop, however, between the choosier p_2 allele and trait alleles, altering the impact of costs to:

$$K_c = \frac{\bar{c}}{2} \tag{11a}$$

$$- \frac{\bar{c}}{2} (\hat{q}_H^o - \hat{q}_H^{s\delta}) \frac{\hat{q}_H^m - \hat{q}_L^m}{\Psi} (m(1 - 2r)) \tag{11b}$$

$$- \frac{c_L - c_H}{2} \hat{q}_H^s \frac{\hat{q}_H^m - \hat{q}_L^m}{\Psi} \left(m(1 - 2r) \hat{q}_L^s + \hat{q}_L r m \left(1 + \alpha_H \frac{\hat{q}_H^s}{P_H} \right) \right) \tag{11c}$$

$$+ \frac{c_L - c_H}{2} (\hat{q}_H^o - \hat{q}_H^{s\delta}) \frac{\hat{q}_H^m - \hat{q}_L^m}{\Psi} \left(r m \frac{\hat{q}_H^s}{P_H} \right) \tag{11d}$$

Importantly, these genetic associations are not driven by the preferences of the new p_2 allele ($\delta\alpha_H$ and $\delta\alpha_L$ are not involved). The first association measured by (11b) is driven by sexual preferences of the wild-type females. It is proportional to the term $(\hat{q}_H^o - \hat{q}_H^{s\delta})$, describing the change in equilibrium frequency of the locally adapted trait allele due to sexual selection [i.e. from the stage after natural selection in males (2) to the offspring stage (5)]. If sexual and natural selection act in the same direction, then $\hat{q}_H^o > \hat{q}_H^{s\delta}$, causing term (11b) to be negative and lessening the cost of

preferences. This association develops because males do not bear the cost of the new preference allele and are sexually selected, causing both p_2 and the locally adapted allele to rise in frequency among successful males relative to the population as a whole. As long as there is some linkage ($r < 1/2$), this association with the locally adapted allele is then passed onto the offspring, counteracting the cost of allele p_2 to some extent. The second association measured by (11c) is driven by differential costs between high- and low-condition females. If females in poor condition disproportionately pay the cost of choosiness ($c_L > c_H$), the reduction in female fitness due to costs facilitates local adaptation. This facilitation again generates a genetic association coupling the new preference allele p_2 with the locally adapted allele, lessening the impact of costly preferences. The last association (11d) slightly reduces the above two effects when both are acting.

Altogether, the new preference allele p_2 can invade as long as it increases female preference for males with locally adapted alleles and the costs of the preference are sufficiently small, so that:

$$K_H \frac{\delta\alpha_H}{P_H} + K_L \frac{\delta\alpha_L}{P_L} > K_c \quad (12)$$

Interestingly, as explained below, the left-hand side goes to zero in the absence of either migration or recombination. Thus, for a given cost of preferences (K_c), evolution will only strengthen preferences for locally adapted males when there is sufficient migration and recombination.

The role of migration is illustrated in Fig. 1. For low migration rates, selection for a new preference allele

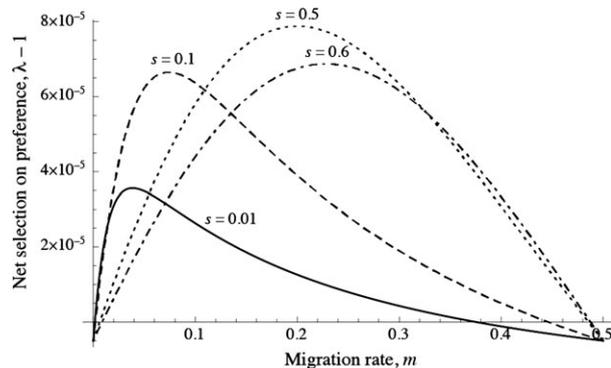


Fig. 1 Effect of migration (m) and strength of natural selection (s) on the invasion of a new female preference allele. Invasion is expected to occur when net selection on the new preference allele is positive ($\lambda - 1 > 0$ from eqn (6)) and is unlikely to occur otherwise. Females bearing the new preference favour locally adapted males by an amount $\delta\alpha_L = \delta\alpha_H = 0.01$ more than wild-type females ($\alpha_L = \alpha_H = 0.1$). Because the new preference allele is costly ($c_L = c_H = 10^{-5}$), net selection becomes negative when migration is too high or too low. Other parameters: $r = 0.25$.

rises with the migration rate. Without migration, genetic variation in the trait would disappear within each patch, removing the benefits of mating preferences and leaving only their costs. When migration is too high ($m \approx 1/2$), however, preferences for locally adapted males have little impact on offspring fitness because the offspring frequently move to the other patch (causing $\hat{q}_H^m \rightarrow \hat{q}_L^m$ and both K_H and K_L to go to zero). Intermediate levels of migration thus maximize selection for condition-dependent preferences. Schindler *et al.* (2013) came to a different conclusion, namely that increasing migration uniformly facilitates the evolution of preferences. This difference is driven by the fact that Schindler *et al.* assess selection on preferences only over a portion of the life cycle (excluding migration). Our analysis based on a stability analysis measures the longer-term fate of a preference allele. When migration rates are very high, the advantage of condition-dependent preferences washes out, because the new preference allele passes back and forth between the patches, alternately favouring and disfavouring the trait allele with which it is found. We confirmed that the discrepancy was not due to our choice of preference scheme by replacing the relative mating preference scheme (4) with the absolute mating preference scheme used by Schindler *et al.* We again found that intermediate migration rates are most favourable to the evolution of condition-dependent preferences (see Supporting Information *Mathematica* file).

Figure 1 also explores the effect of the strength of ecological adaptation, s . When natural selection is very weak, increasing s tends to increase the strength of selection on the preference allele, because the benefits of preferring locally adapted males rise. Once selection becomes strong, however, increasing s further can reduce the net selection on the new preference allele, essentially because natural selection is already highly effective in eliminating maladapted alleles from the population, leaving little opportunity for sexual selection to make a difference.

Interestingly, recombination has a positive effect on the invasion of preferences (Fig. 2), increasing both K_H and K_L . Without recombination, the preference allele in immigrants is irrevocably linked with its ecological allele, favoured in one patch and disfavoured in the other patch, with no net advantage ($K_H = K_L = 0$). Thus, to be positively selected, the p_2 allele must be able to escape from its genetic background after migration, which can only happen through recombination. Free recombination combined with an intermediate rate of migration most favours the spread of preferences (Fig. 2). Observing a positive effect of recombination is unusual in models where indirect selection, acting via genetic associations, favours a feature [e.g. mutation rate, haploid life cycles, sexual reproduction (Otto, 2013)]. Typically, recombination breaks down genetic associations, weakening indirect selection for these

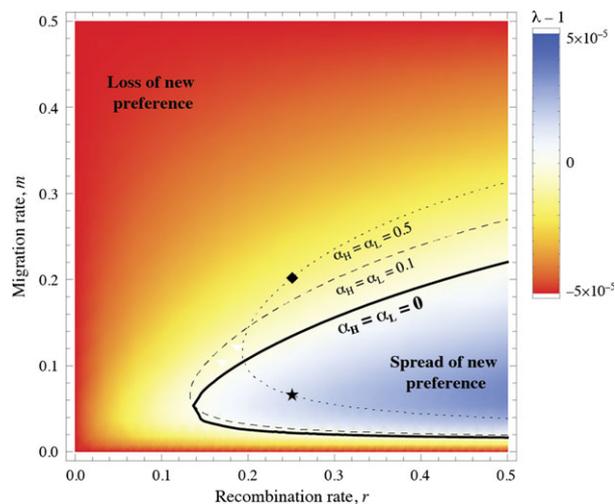


Fig. 2 Selection for increased female preferences as a function of migration and recombination rate. The heat map shows the strength of selection acting on the new preference allele when wild-type preferences are absent, with the neutral isocline shown as a thick curve ($\alpha_L = \alpha_H = 0$). The shift in the neutral isocline is also shown when wild-type females exhibit a slight (long dash: $\alpha_L = \alpha_H = 0.1$) or medium (short dash: $\alpha_L = \alpha_H = 0.5$) preference for locally adapted males. Other parameters: $\delta\alpha_L = \delta\alpha_H = 0.01$, $c_L = c_H = 10^{-4}$, $s = 0.1$.

features. In models where sexual preferences are fixed and not condition dependent, including the one-patch model of Kirkpatrick (1982) and the two-patch model of Servedio & Bürger (2014), recombination has little effect because recombination both builds associations (by placing preference alleles from the mother together on the same chromosome as trait alleles from the father) and breaks them down (through the decay of linkage disequilibrium). With condition-dependent preferences, however, recombination plays a third role, uncoupling alleles as they migrate between patches, generating a net positive impact. This result shows that extending classic sexual selection models into more complex (but biologically realistic) scenarios may yield interesting new insights (Kuijper *et al.*, 2012).

The existence of female preferences within the initial population (α_L, α_H) alters the parameter region in which an increased preference (p_2 allele) can invade (Fig. 2). For the parameters explored, stronger sexual selection in the wild-type population shifts the parameter space favouring the new preference allele towards higher migration rates (up in Fig. 2) and towards higher recombination rates (to the right). This shift can even eliminate the region favouring new preferences when wild-type preferences get too strong ($\alpha_L = \alpha_H > 1.4$ for the parameters considered in Fig. 2).

Figure 2 also provides information about the convergence stability points for the evolution of female preferences (assuming no condition dependence of the

female preference). For example, at the star ($m = 0.0656$, $r = 0.25$), mate choice evolves from random mating to a 50% higher preference for locally adapted males, at which point further evolution of preferences ceases (because the star lies on the $\alpha_L = \alpha_H = 0.5$ isocline). At the diamond ($m = 0.2016$, $r = 0.25$), however, mating preferences will not evolve from random mating, but if females initially prefer locally adapted males to some extent (specifically, $\alpha_L = \alpha_H > 0.25$), then again the system will evolve towards a 50% higher preference for locally adapted males (the diamond also lies on this isocline). The local stability matrix was numerically evaluated at these two points to confirm that these convergence stable points were also evolutionarily stable.

The condition of a female may influence her mate choice and the costs of this choice. For example, females in better condition may be better able to devote time to searching for males and/or may lose fewer resources doing so. In Fig. 3(a), we see that increasing the preference of females in high condition ($\delta\alpha_H$) is more favourable to the evolution of condition-dependent mating preference than increasing the preference of females in low condition ($\delta\alpha_L$). According to eqns (7) and (8) describing the effect of a change in preference, the main difference between K_H and K_L lies in their being proportional to the frequency after selection of the locally adapted (\hat{q}_H^s) and maladapted (\hat{q}_L^s) allele, respectively (assuming wild-type females have similar preferences). Thus, preferences among high-condition females will generally matter more than preferences among low-condition females, as the latter are rarer. In Fig. 3(b), we explore the impact on the evolution of condition-dependent preferences when the costs borne by females are themselves condition dependent. Even when females in low condition pay a very high cost, preferences can still evolve if females in high condition pay a sufficiently low cost, because females are more likely to be locally adapted than maladapted, thus driving down the average cost paid by females. Even if we hold the average cost constant, the same principle holds; it is easier to evolve preferences when the cost is borne by females already in poor condition, because this form of condition-dependent costs facilitates local adaptation (see eqn (11c) and figures in Supporting Information *Mathematica* package).

Although our focus has been on the evolution of condition-dependent preferences, Fig. 4 illustrates the impact that condition-dependent preferences can have on the degree of local adaptation exhibited by a population fixed for a certain preference allele. Preferences have little impact on the degree of local adaptation when migration is rare because natural selection then drives strong local adaptation by itself (left side of Fig. 4), but we have shown that condition-dependent preferences are unlikely to evolve under these circumstances (Figs 1–3). By contrast, preferences are most

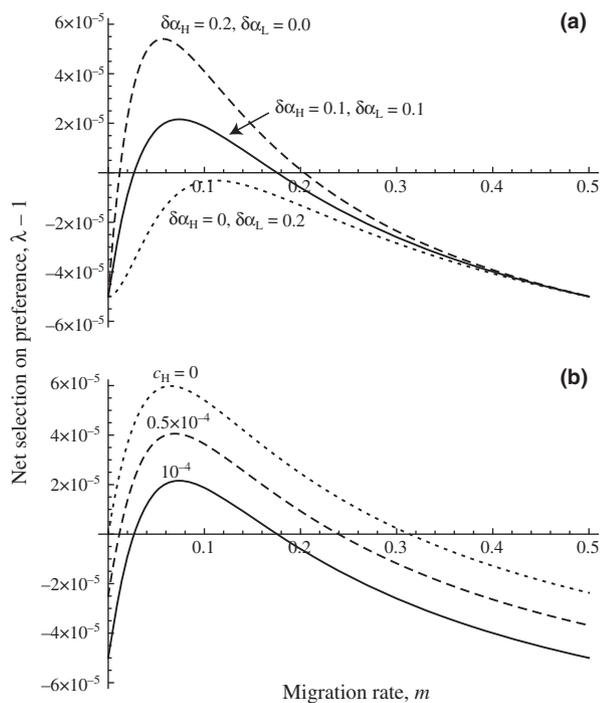


Fig. 3 The effect of condition dependence among females on the evolution of a new preference allele. (a) Net selection for a new preference allele is stronger when it causes females in high condition to become choosier (long dash: $\delta\alpha_H = 0.02$, $\delta\alpha_L = 0$) than when it causes females in low condition to become choosier (short dashed: $\delta\alpha_H = 0$, $\delta\alpha_L = 0.02$). For comparison, the solid curve illustrates net selection on an allele with the same average preference ($\delta\alpha_H = \delta\alpha_L = 0.01$). (b) A new preference allele is more likely to spread when females in high condition can afford to be choosy with little cost, even though females in poor condition must always pay a cost (short dash: $c_H = 0$; long dash: $c_H = 0.5 \times 10^{-4}$; solid: $c_H = 10^{-4}$, all with $c_L = 10^{-4}$). Parameters (unless otherwise mentioned): $\delta\alpha_L = \delta\alpha_H = 0.01$, $\alpha_L = \alpha_H = 0.1$, $c_L = c_H = 10^{-4}$, $s = 0.1$, $r = 0.1$.

likely to evolve when migration rates are intermediate (Figs 1–3), in which case they can strongly augment the degree of local adaptation exhibited (Fig. 4).

Discussion

Our results show that condition dependence of male signals and female preferences facilitates the invasion of mating preferences for locally adapted males, which in turn strengthens the degree of local adaptation. Although migration always hampers the degree of local adaptation (Fig. 4), intermediate levels of migration facilitate the evolution of preferences for locally adapted males (Figs 1–3), essentially because migration is common enough that there is sufficient male trait variation but not so frequent that progeny are likely to move away from the patch of their parents. Surprisingly, we also find that recombination facilitates

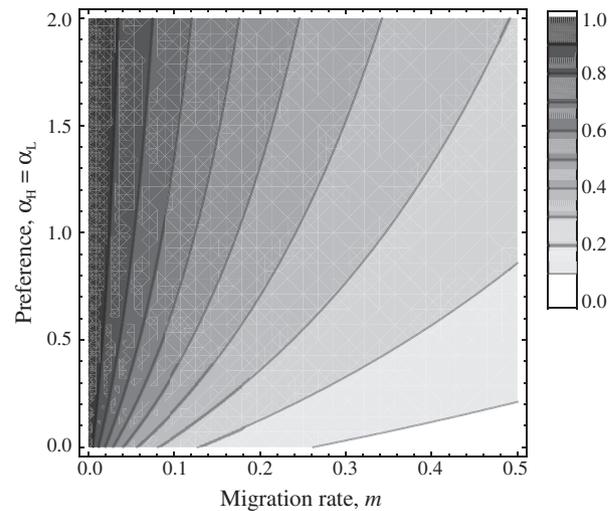


Fig. 4 The effect of condition-dependent mate choice on the degree of local adaptation exhibited within a population. Populations with stronger preferences for locally adapted males (y -axis) exhibit stronger local adaptation, measured here as the difference in frequency between the locally adapted allele and the maladapted allele ($\hat{q}_H - \hat{q}_L$). When migration is much less than the strength of natural selection (here $s = 0.1$), the populations are well adapted even in the absence of preferences (dark shading on left). With frequent migration, however, condition-dependent mate choice can be a potent selective force increasing the match between individuals and their environment. Figure assumes that the population is fixed for a preference allele that causes females to prefer high-condition males by a factor α , regardless of a female's condition ($\alpha_H = \alpha_L = \alpha$).

preference evolution, which is an unusual result in models where a feature (here preferences) evolve in response to indirect selection (Otto, 2013). In this model, stronger female preferences are favoured in each patch, but only if they can move onto locally favoured genetic backgrounds, which explains why recombination is so favourable. Finally, we find that allowing a female's preference to depend on her own condition can facilitate preference evolution, particularly if high-condition females have a stronger preference but pay a reduced cost for expressing this preference.

Models of sexual selection often assume no cost of choice, including earlier work on condition-dependent signalling and local adaptation (Proulx, 1999; Schindler *et al.*, 2013; but see Proulx, 2001b). However, including costs of female preferences has a strong influence on the dynamics of mate-choice models (Kokko *et al.*, 2003), typically inhibiting the evolution of female preferences. Furthermore, there is strong empirical support for the frequent occurrence of cost of choice (Milinski & Bakker, 1992; Rowe, 1994; Jennions & Petrie, 1997). We show that female preferences for condition-dependent male signals can still evolve despite costs of choice, as long as these costs are sufficiently weak. The

negative effect of a preference cost can be further mitigated if it is largely borne by locally maladapted females, in which case it also serves to strengthen local adaptation.

Although we focused our presentation in the text on a highly simplified symmetrical model, with equal migration between the patches and equal selection against locally maladapted alleles, our main results apply even when we relax these assumptions and instead assume weak migration (Appendix). In particular, both approaches confirm the key result that condition-dependent preferences are most likely to evolve when new alleles disproportionately increase the choosiness of high-quality females ($\delta\alpha_H > \delta\alpha_L$), whereas the costs of choosiness are disproportionately borne by low-quality females ($c_L > c_H$). Both approaches also demonstrate that condition-dependent mate choice is most likely to evolve when recombination between preference and trait loci is frequent.

Empirical studies of condition-dependent mate choice have traditionally focused on male signals, which can be indicators for various fitness components, including resistance to parasites and disease (Hamilton & Zuk, 1982) or the ability to acquire a high-quality diet [e.g. the red colouration of male house finches (Hill, 1991)]. These indicator signals are found throughout the animal kingdom, including fish (Nagel & Schluter, 1998; Boughman, 2007), birds (Hill, 1991; McGraw *et al.*, 2002), amphibians (Humfeld, 2013) and insects (Wagner & Hoback, 1999; David *et al.*, 2000; Hedrick, 2005). More recently, the role of condition dependence has been extended to include female preferences. Despite having received less empirical attention, the available studies indicate condition dependence of a female's preference is also taxonomically widespread [found among insects (Hingle *et al.*, 2001; Hunt *et al.*, 2005; Cotton *et al.*, 2006; Judge *et al.*, 2014), fish (T. Bakker *et al.*, 1999; Syriatowicz & Brooks, 2004), amphibians (Jennions *et al.*, 1995) and birds (Rintamaki *et al.*, 1995; Burley & Foster, 2006; Lerch *et al.*, 2013; Dakin & Montgomerie, 2014)]. The positive effect of condition-dependent male signals and female preferences on local adaptation combined with their widespread occurrence in nature suggests that such preferences may be an influential and common evolved pathway towards increasing the degree of local adaptation.

Although we also considered condition-dependent costs of female preferences, conclusive empirical evidence for such condition dependence is lacking, as far as we are aware. Hunt *et al.* (2005) used three diet manipulations to vary female condition in crickets and showed that condition affected the choosiness and preference function of females. They suggest that '...mate choice is costly and that the ratio of benefit to costs of choice is probably lower for females in poorer condition' (p. 87), but they acknowledge the difficulty of measuring these costs precisely. Crickets are a particu-

larly promising group to disentangle these different mechanisms as condition can be manipulated through nutrition (Holzer *et al.*, 2003; Hunt *et al.*, 2005), mate choice assessed in great detail (Hedwig, 2005; Veen *et al.*, 2013) and strength of sexual selection and cost of choice potentially manipulated by controlling access to mates.

Condition-dependent mate choice can have several important evolutionary consequences. Increased strength of local adaptation through condition-dependent male signals can facilitate speciation by reducing the effective amount of gene flow between populations (van Doorn *et al.*, 2009). Our work suggests that in addition condition-dependent mate choice can further enhance reproductive isolation by strengthening the degree of local adaptation, especially if high-condition females have stronger preferences and weaker costs than low-condition females. Such female preferences can also provide a novel explanation for the high frequency of assortative mating found in nature (Jiang *et al.*, 2013), with high-condition males and females pairing up preferentially. Furthermore, by recognizing and preferring male traits that confer high condition, such female preferences can facilitate range expansion into novel environments, both by selecting those few males that can succeed outside of the previous range and by reducing gene swamping from maladapted individuals migrating from the core of the species range. Further empirical and theoretical work promises to improve our understanding of the full nature and implications of condition-dependent sexual selection and how it influences both sexes.

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Appendix (A1) Weak migration approximation

In the text, we have focused on the rate of spread of a new preference allele assuming perfect symmetry between the two patches. Here, instead, we calculate the rate of spread assuming that migration between patches is weak (m_1 and m_2 are of order ϵ), allowing for differences in migration, selection or population size between the two patches. With the wild-type preference allele fixed, the frequency of the maladapted allele in patch i (q_{iL}) reaches a migration-selection balance:

$$\hat{q}_{iL} = \frac{m_i(1 - s_i)}{s_i + \frac{\alpha_{iH}}{2 + \alpha_{iH}}} + O(\epsilon^2), \quad (A1)$$

where α_{iH} is the preference among locally adapted females in patch i for locally adapted males over maladapted males. The fraction in the denominator represents the additional sexual selection favouring local adaptation that occurs whenever wild-type females are choosy.

We then introduce a new allele p_2 with a slight difference in preference ($\delta\alpha_{iH}$ and $\delta\alpha_{iL}$ are on the order of a small term, ϵ). Because most males are locally adapted at migration-selection balance when migration is rare, weak preferences acting on the slight variance among males that exists generates only very weak selection for the new preference allele (on the order of ϵ^2). Thus, if the costs are moderate (of order ϵ), then a new costly preference will never spread [the leading eigenvalue is then given by the first two lines of (A2)]. We thus assume that costs are also very weak (of order ϵ^2), in which case, the spread of allele p_2 is described by:

$$\begin{aligned} \lambda = & 1 - \frac{c_{11}}{2} \left(\frac{m_2(m_1 + r\hat{q}_{1L})\hat{q}_{2L}}{m_1m_2(\hat{q}_{1L} + \hat{q}_{2L}) + (m_1 + m_2)r\hat{q}_{1L}\hat{q}_{2L}} \right) \\ & - \frac{c_{22}}{2} \left(\frac{m_1(m_2 + r\hat{q}_{2L})\hat{q}_{1L}}{m_1m_2(\hat{q}_{1L} + \hat{q}_{2L}) + (m_1 + m_2)r\hat{q}_{1L}\hat{q}_{2L}} \right) \\ & + \left(\frac{\delta\alpha_{1H}}{(1 + \alpha_{1H})(2 + \alpha_{1H})} + \frac{\delta\alpha_{2H}}{(1 + \alpha_{2H})(2 + \alpha_{2H})} \right) \\ & \left\{ \frac{m_1m_2r\hat{q}_{1L}\hat{q}_{2L}}{m_1m_2(\hat{q}_{1L} + \hat{q}_{2L}) + (m_1 + m_2)r\hat{q}_{1L}\hat{q}_{2L}} \right\} + O(\epsilon^3) \end{aligned} \quad (A2)$$

The only costs that enter are those experienced by high-condition females, as they are most common. When these costs are the same in the two patches ($c_{11} = c_{22} = c_H$), the first line reduces to $1 - \frac{c_H}{2}$, otherwise the costs are a weighted average across the patches, with the weighting being higher for the patch receiving fewest migrants (parenthetical terms in the first two lines of A2). Indeed, if the wild-type population mates randomly and selection is equal in the two patches, (A2) simplifies to:

$$\begin{aligned} \lambda = & 1 - \frac{c_{11}}{2} \left(\frac{m_2}{m_1 + m_2} \right) - \frac{c_{22}}{2} \left(\frac{m_1}{m_1 + m_2} \right) \\ & + (\delta\alpha_{1H} + \delta\alpha_{2H}) \left\{ \frac{m_1m_2r(1 - s)}{2(m_1 + m_2)(r + s - rs)} \right\}, \end{aligned} \quad (A3)$$

where $\frac{m_2}{m_1 + m_2}$ and $\frac{m_1}{m_1 + m_2}$ represent the proportion of the population in the distant future that descends from individuals currently in patch 1 and 2, respectively, in a neutral model (Otto & Bourguet, 1999). Genetic associations that develop between the **P** and **E** loci [as described in the symmetric model by eqns (11b–11d)] are proportional to the migration rates and contribute only to the next order terms [$O(\epsilon^3)$] with weak migration.

Relative to the main results in the text (eqn (6)), when migration is rare, most females are locally adapted, and so eqn (A2) is dominated by their preferences ($\delta\alpha_{iH}$) and not by the preferences of locally maladapted females ($\delta\alpha_{iL}$). The term $\frac{\delta\alpha_{iH}}{(1 + \alpha_{iH})(2 + \alpha_{iH})}$ measures the proportional change in the amount of sexual selection against the locally maladapted allele at the **E** locus induced by the p_2 preference allele in patch i . The advantage of increasing the preference for locally adapted males depends on the term in braces, which rises with increases in either migration rate or recombination rate (see Supporting Information *Mathematica* package for proof).

Because we assume weak migration here, we only see the positive effects of increasing migration from low levels and not the negative effects that occur once migration becomes common, as observed in Fig. 1. Equation (A2) now allows us to see the effects of asymmetric migration. The advantage of preferring locally adapted males is generally weaker when migration is predominantly in one direction. Essentially, the patch

that receives fewer migrants serves as a genetic source population but exhibits less trait variation, reducing selection for females to prefer high-condition males. In the extreme, when migration is unidirectional, female preferences for the locally adapted allele are unable to spread (see Supporting Information *Mathematica* package), as found in the island-continent model of Servedio & Kirkpatrick (1997).

Finally, similarly to the symmetric model described in the main text, selection for condition-dependent preferences rises with the rate of recombination, because recombination again uncouples the new preference allele from the linked trait allele, which is especially

beneficial following migration when that trait allele tends to be poorly matched to the new environment.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Data S1. *Mathematica* 8.0 derivation of model, with additional figures and proofs.

Data deposited at Dryad: doi: 10.5061/dryad.2sj8r

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