

The effects of sexual selection on trait divergence in a peripheral population with gene flow

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The unique aspects of speciation and divergence in peripheral populations have long sparked much research. Unidirectional migration, received by some peripheral populations, can hinder the evolution of distinct differences from their founding populations. Here, we explore the effects that sexual selection, long hypothesized to drive the divergence of distinct traits used in mate choice, can play in the evolution of such traits in a partially isolated peripheral population. Using population genetic continent-island models, we show that with phenotype matching, sexual selection increases the frequency of an island-specific mating trait only when female preferences are of intermediate strength. We identify regions of preference strength for which sexual selection can instead cause an island-specific trait to be lost, even when it would have otherwise been maintained at migration-selection balance. When there are instead separate preference and trait loci, we find that sexual selection can lead to low trait frequencies or trait loss when female preferences are weak to intermediate, but that sexual selection can increase trait frequencies when preferences are strong. We also show that novel preference strengths almost universally cannot increase, under either mating mechanism, precluding the evolution of premating isolation in peripheral populations at the early stages of species divergence.

KEY WORDS: Assortative mating, continent-island model, mate choice, phenotype matching, preference, speciation.

Speciation has long been hypothesized to occur rather easily in peripherally isolated populations due to a number of factors, including founder effects and genetic revolutions (e.g., Mayr 1954, 1982; Carson 1975). In cases in which there is continued gene flow, however, the essentially unidirectional migration from founding populations into peripheral ones can make it difficult for such partially isolated populations to evolve or maintain differentiation. Even traits that are locally adapted in peripheral populations can retain substantial variation due to unidirectional migration (e.g., King and Lawson 1995). The evolution of premating isolation in a peripheral population faces similar difficulties. Premating isolation that results from selection can be thought of as a form of local adaptation, and it can likewise be swamped, at least to some degree, by migration from a larger population (Servedio and

Kirkpatrick 1997). The evolutionary divergence of traits and preferences involved in premating isolation during speciation with gene flow thus poses an interesting problem in the case of a peripheral population.

Theoretical studies of premating isolation have focused on several mechanisms, two of which can cause substantial sexual selection by mate choice. The first of these, phenotype matching, occurs when the choosing sex (hereafter assumed to be females) prefers a mate that matches some aspect of her own phenotype. This mechanism is commonly considered in mathematical models, especially in the case of sympatric speciation (e.g., Dieckmann and Doebeli 1999; Matessi et al. 2001; Kirkpatrick and Nuismer 2004; Bürger and Schneider 2006; Otto et al. 2008; Pennings et al. 2008; Kisdi and Priklopil 2011). The second, “preference/trait,” mechanism instead supposes that females have divergent preferences that are distinct from their own

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phenotypes (e.g., Lande 1981; Lande and Kirkpatrick 1988; Payne and Krakauer 1997; Kirkpatrick and Servedio 1999; van Doorn and Weissing 2001; van Doorn et al. 2004; Arnegard and Kondrashov 2004). Assortative mating results when females choose males with certain traits, as dictated by these preferences, and linkage disequilibrium builds between the trait and preference loci.

Theoretical work has shown that the sexual selection generated by these types of assortative mating can have unanticipated effects on speciation. Although sexual selection has often been hypothesized to be a driving force in speciation (e.g., Lande 1981; West-Eberhard 1983; Panhuis et al. 2001; Ritchie 2007; Safran et al. 2012; Seddon et al. 2013), recent models have shown that it may instead often inhibit divergence. During sympatric speciation with phenotype matching, sexual selection may eliminate trait variation (e.g., Kirkpatrick and Nuismer 2004; Schneider 2005; Bürger et al. 2006) or lead to stabilizing selection on trait phenotypes (e.g., Matessi et al. 2001; Otto et al. 2008; Pennings et al. 2008). During secondary contact, phenotype matching may instead be ineffective at driving divergence if preferences are very strong (Servedio 2011). With preference/trait mating, both sympatric speciation models (van Doorn and Weissing 2001; van Doorn et al. 2004) and secondary contact models (Servedio and Bürger 2014) have shown that it is very difficult to maintain preference variation. Preference homogenization can lead to stronger preferences eliminating more and more of the divergence caused by local adaptation of traits (Servedio and Bürger 2014), thus inhibiting population differentiation.

Because peripheral populations receiving ongoing gene flow can be described by a continent-island model, and population genetic dynamics can be quite different in single population (i.e., sympatric), two-island (i.e., vicariant), and continent-island models (e.g., Nagylaki 2009; Akerman and Bürger 2014, and references therein), it is unclear whether the effects of sexual selection on divergence in a peripheral population will be similar to those described above. Previous continent-island models of the evolution of premating isolation have concentrated primarily on the effects of selection against hybridization (e.g., reinforcement, Servedio and Kirkpatrick 1997; Kirkpatrick and Servedio 1999; Kirkpatrick 2000, 2001), and have not isolated the effects of sexual selection per se. There is thus an important gap in our understanding of this textbook case of speciation.

In this article, we examine the effects of the sexual selection generated by phenotype matching and preference/trait mechanisms of assortative mating on trait divergence between a peripheral and a founder population. We are particularly interested in whether sexual selection allows more or less trait divergence than would be expected under random mating, given local adaptation of the trait in the peripheral population. We also

examine the evolution of preference strength (choosiness) with both mating mechanisms. Our goal is to isolate the evolutionary effects of the sexual selection automatically generated by these two mechanisms of assortative mating, in models with discrete phenotypes. We thus examine these mechanisms in their most basic forms (i.e., basic phenotype matching and Fisherian sexual selection), and do not consider more elaborate cases of sexual selection such as condition dependence or costly preferences (but see Discussion). We also do not consider selection against hybrids, as we are interested in recently separated populations that have not yet developed postzygotic isolating barriers. We find that sexual selection has effects in the continent-island case that are undescribed in similar two-island models. With preference/trait mating, stronger sexual selection, under some conditions, can drive trait divergence when this was not possible in the two-island case. In contrast, with phenotype matching sexual selection can instead lead to unanticipated cases of trait loss.

Models

We first examine trait divergence by considering the simplest possible continent-island models of phenotype matching and preference/trait assortative mating in haploids (in a later section we extend these models to investigate the evolution of preference strength). The use of haploids eliminates intermediate phenotypes and hence selection against hybrids. Both models contain a locus *T* which controls a trait that serves as a marker of population identity during reproductive isolation. In the phenotype matching model, matching is based on the alleles in males and females at locus *T*, which is the only locus present. The preference/trait model contains a second locus, *P*, with alleles for female preferences for specific alleles at locus *T*. Because we later introduce a locus that codes for the *strength* of preferences, alleles at locus *P* can be best thought of as determining the *direction* of preference (see Edward 2015). Alleles *P*₂ and *T*₂ are generally characteristic of the island. We allow *P*₂ to be present on the continent with fixed frequency *p*_C in the preference/trait model, but consider the allele *T*₂ to be absent on the continent in both models. The frequencies of the genotypes on the island are denoted by *x*_{*i*}, where *i* represents a counter when the genotypes are ordered as *T*₁ and *T*₂ for the phenotype matching model and *P*₁*T*₁, *P*₁*T*₂, *P*₂*T*₁, and *P*₂*T*₂ for the preference/trait model. Genotype *i* has frequency *x*_{C,*i*} on the continent.

For both models, the life cycle consists of migration, viability selection, and mating, followed by recombination and zygote production. A fraction *m* of the island population each generation consists of newly arrived migrants from the continent, such that the frequency of genotype *i* on the island after migration is

$$x_i^{\text{mig}} = (1 - m)x_i + mx_{C,i}. \quad (1)$$

Viability selection subsequently acts in both models such that individuals expressing T_2 are locally adapted, and thus have an advantage s on the island (note that s can be negative, although we do not concentrate on this case). Locally adapted traits involved in premating isolation, called “magic traits” (Gavrilets 2004), are being found in an increasing number of study systems (Servedio et al. 2011). They present a best-case scenario for speciation by facilitating the evolution of assortative mating when divergent selection is present. In the phenotype matching model, both sexes express the trait, and the frequency of each genotype in both sexes after viability selection is

$$x_i^{vs} = \frac{(1 + d_i s)x_i^{\text{mig}}}{\sum_j (1 + d_j s)x_j^{\text{mig}}}, \quad (2)$$

where $d_i = 0$ if i is odd and $d_i = 1$ if i is even. In the preference/trait model, we concentrate on the case where only males express the trait and only females express the preference. Viability selection thus occurs only in males, following expression (2), whereas in females, $x_i^{f,vs} = x_i^{\text{mig}}$.

In the phenotype matching model, females prefer to mate with males that share their trait at locus T. A female is $1 + \alpha$ times as likely to mate with a male that she prefers, upon encounter with one of each male type. The frequency of mated pairs of females of genotype i and males of genotype j is thus

$$M_{ij} = \frac{(1 + d_{ij}\alpha)x_i^{vs}x_j^{vs}}{\sum_k (1 + d_{ik}\alpha)x_k^{vs}}, \quad (3)$$

where $d_{ij} = 1$ if $i = j$ and $d_{ij} = 0$ otherwise. The denominator of equation (3) ensures all females have equal mating success.

In the preference/trait model, assortative mating occurs because females that carry allele P_i prefer to mate with males with trait T_i . In the most general case, we allow the strength of preference to vary with the preference alleles, so that P_1 and P_2 females have preference strengths α_1 and α_2 , respectively. Specifically, females are $1 + \alpha_k$ times as likely to mate with a preferred versus an unpreferred male if they encounter one of each. Unless stated otherwise, however, we assume that the P allele of the female affects only the identity of the male preferred and not the preference strength, so that $\alpha_1 = \alpha_2 = \alpha$. The frequency of mated pairs of females of genotype i and males of genotype j is

$$M_{ij} = \frac{(1 + d_{ij}\alpha_1)(1 + g_{ij}\alpha_2)x_i^{f,vs}x_j^{vs}}{\sum_k (1 + d_{ik}\alpha_1)(1 + g_{ik}\alpha_2)x_k^{vs}}, \quad (4)$$

where $d_{ij} = 1$ if i is 1 or 2 and j is odd and $d_{ij} = 0$ otherwise, and $g_{ij} = 1$ if i is 3 or 4 and j is even and $g_{ij} = 0$ otherwise. As in equation (3), the denominator in equation (4) ensures strict polygyny.

Recombination and segregation follow assortative mating, using the standard equations for haploid genetics. The resulting recursions in terms of genotype frequencies are transformed into

recursions for the allele frequencies and the linkage disequilibrium D between loci P and T. These recursions are developed fully in Files S1 and S2.

Trait Divergence

By examining the trait divergence that can evolve between the continent and island populations with fixed (nonevolving) preference strengths, we can determine the extent to which the island can maintain a unique phenotypic identity under each assortative mating mechanism. Throughout our analyses, we consider evolution only on the island; continental genotype frequencies remain constant. All allele frequencies below thus refer to island frequencies unless specified otherwise. To measure trait divergence, we track the frequency t_2 of allele T_2 , which is not present on the continent. We find that phenotype matching and preference/trait mechanisms of assortative mating result in very different patterns of trait divergence with increasing preference strength.

PHENOTYPE MATCHING MODEL

A neutral trait

To fully understand the effects on trait divergence of sexual selection, per se, generated during phenotype matching, we first examine the case where the trait is selectively neutral ($s = 0$). In this case, the positive frequency-dependent sexual selection generated by phenotype matching is the only force present with the capability of allowing T_2 to be maintained on the island (there is no divergence with random mating). Depending on the preference strength α , we find one or three equilibria for t_2 (analyses presented in Appendix S1). The first equilibrium corresponds to loss of the allele T_2 ($\hat{t}_2 = 0$, where the caret indicates an equilibrium value). This equilibrium always exists, and, depending on α , may be locally or globally stable. If $\hat{t}_2 = 0$ is only locally stable, then there are two other equilibria. This may occur for an intermediate range of α that decreases as immigration from the continent (m) increases (Fig. 1). In this case, the equilibrium with the higher t_2 is locally stable, allowing differentiation between the island and continent (we call this the “differentiation equilibrium” below). Thus, T_2 can be maintained at high frequency on the island only at an intermediate range of preference strength α , and only if migration is weak; T_2 cannot be maintained if m increases above a critical value of $m_c \approx 0.0326$ (see eq. S3).

The frequency t_2 reaches a peak at an intermediate preference strength, α_{max} , which can be calculated from equation (S4) in Appendix S1. This maximum, which is usually very shallow (Fig. 1), decreases with increasing migration rate (Figs. 1, S1). Analysis of equation (S5) for relative fitness for this problem shows that α_{max} is the point at which frequency-dependent sexual selection favoring T_2 is maximized (Appendix S1).

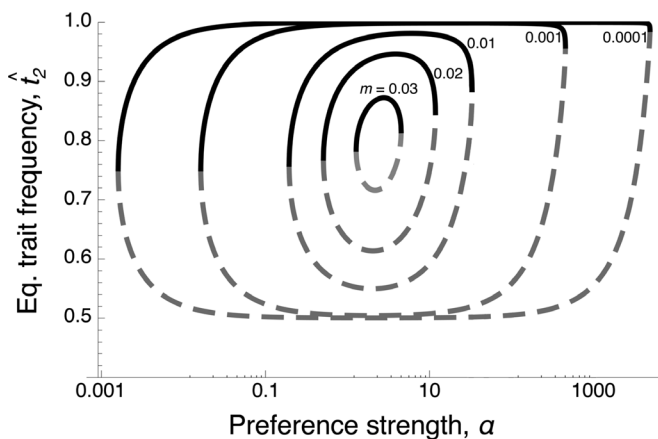


Figure 1. Equilibria in the continent-island phenotype matching model with no viability selection ($s = 0$). Black solid lines are stable equilibria and gray dashed lines are unstable equilibria, and each concentric curve represents the set of equilibria for a different migration rate, as labeled. There is always an equilibrium at $\hat{t}_2 = 0$, not shown in the figure. The nontrivial equilibria are calculated from equation (S2) in Appendix S1.

Trait divergence between the island and continent thus decreases when the preference strength deviates in either direction from the peak α_{\max} , and with low or high enough preferences, the only equilibrium in the system is when T_2 is lost. These results are qualitatively similar to those found in the two-island phenotype matching model of Servedio (2011), and can be explained as follows. With very weak preferences, positive frequency-dependent sexual selection (see eq. S6), the only force driving divergence when there is no local adaptation ($s = 0$), is not strong enough to maintain variation at the trait locus on the island. With moderately strong preferences, phenotype matching generates strong enough positive frequency-dependent sexual selection to allow divergence; common males are preferred by common females, and also have relatively high mating success with rare females because, although they are unpreferred, they are encountered often. As preferences increase even further, however, rare females will not mate until they can find a matching, rare male. The mating success of both male phenotypes thus starts to approach their respective frequencies in the population—positive frequency-dependent sexual selection declines (see Fig. S2). With strong enough preferences variation at locus T is lost (with infinitely strong preferences there would be no positive frequency-dependent sexual selection at all).

Note that even with intermediate preference strengths, and hence a stable differentiation equilibrium for T_2 , a sufficiently high initial t_2 is required for this equilibrium to be reached (Fig. 1). Divergence thus might be expected in the scenario of secondary contact, but we would not expect the de novo evolution of T_2 by mutation.

A locally adapted trait

When the trait has a selective advantage on the island ($s > 0$), the sexual selection generated during phenotype matching exhibits an even greater variety of effects. Interestingly, for some ranges of preference strength positive frequency-dependent sexual selection can lead to trait loss, even when the trait would have otherwise been maintained at migration-viability selection balance (henceforth called the "migration-selection" balance). Because it represents the amount of divergence under random mating ($\alpha = 0$), this balance is an important basis of comparison for the effects of sexual selection on divergence. It is denoted by

$$\hat{t}_{2,m/s}^{pm} = 1 - \frac{m}{s(1-m)} \tag{5}$$

(the superscript "pm" references the phenotype matching case), and is above 0 when migration is sufficiently weak relative to selection. First, we present a mathematical description of the equilibria when $s > 0$, and then discuss the biological interpretation of the resulting regimes.

When $s > 0$, the system again yields up to three equilibria (Appendix S2). One of these, at the loss of T_2 ($\hat{t}_2 = 0$), is stable only if the viability advantage s of T_2 is below a critical threshold (eq. S7 in Appendix S2), which increases with m and α (Fig. S3). When this is the only equilibrium, T_2 is lost independently of initial conditions. In contrast to the case where $s = 0$, there may be either one or two additional equilibria, depending on the migration rate and preference strength (Figs. 2, S4–S6). If there are two additional equilibria, the equilibrium with the higher t_2 is stable and maintains differentiation between the island and continent (similar to the case when $s = 0$). The frequency t_2 at this differentiation equilibrium is, as when $s = 0$, maximized at an intermediate value of preference strength, α_{\max} (Fig. S7), although this maximum is again generally very shallow. The other equilibrium (gray dashed lines in Figs. 2, S5) is unstable and separates the range of attraction of the differentiation equilibrium from that of $\hat{t}_2 = 0$. Thus, as in the case when $s = 0$, when there are three equilibria, a high enough initial frequency of T_2 is required to evolve differentiation. Finally, if there is a single equilibrium in addition to $\hat{t}_2 = 0$, it is globally stable and represents differentiation (Figs. 2, S5 when $\hat{t}_2 = 0$ is unstable). Only under these last conditions does differentiation of the trait on the island not require initial divergence in allopatry.

To understand the complicated patterns shown in Figure 2 biologically, it is important to remember two things. First, as in the case when $s = 0$, the positive frequency-dependent sexual selection generated by phenotype matching is maximized at intermediate preference strengths; it becomes weak and ineffective at leading to trait evolution if preferences are either too weak or too strong. Second, when positive frequency-dependent selection is strong enough to lead to substantial trait evolution, the *direction* of

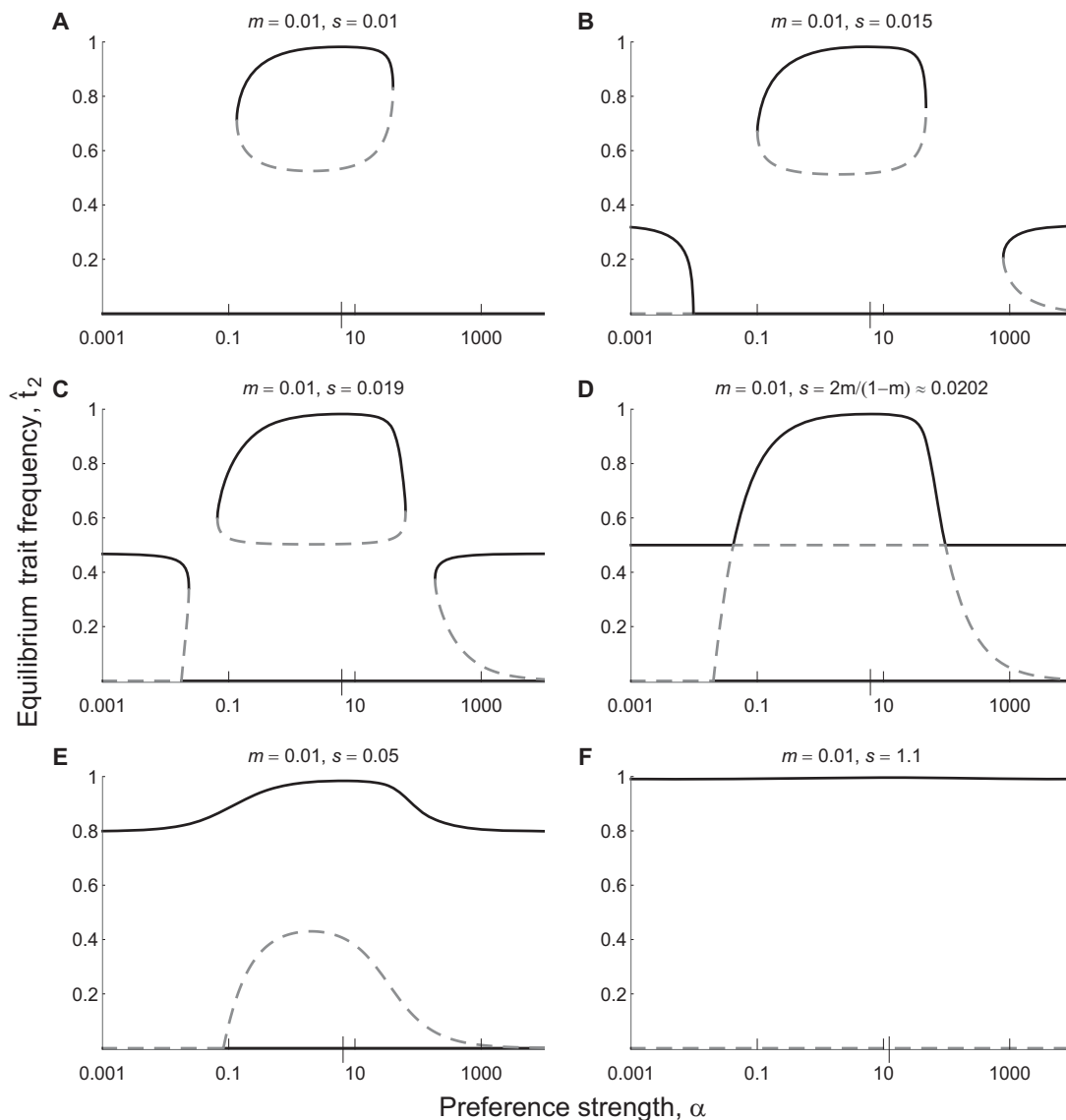


Figure 2. Equilibria in the phenotype matching model with local adaptation of the trait ($s > 0$). Black solid lines signify stable equilibria (loss of T_2 or differentiation), gray dashed lines signify unstable equilibria. If the loss of T_2 is unstable, differentiation is maintained independently of initial conditions. If all three equilibria exist, differentiation is maintained if and only if the initial frequency of T_2 is sufficiently high, that is, above the dashed line. The migration-selection balance $\hat{t}_{2,m/s}^{pm}$ (eq. 5) is essentially indistinguishable on these panels from the value at $\alpha = 0.001$ (in panel B it exceeds this value by 2.6%, and in other cases by less than 0.2%). The parameters m and s satisfy $s < m/(1 - m)$ in A, $m/(1 - m) < s < 2m/(1 - m)$ in B and C, $s = 2m/(1 - m)$ in D, $2m/(1 - m) < s < (1 + m)/(1 - m)$ in E, and $s > (1 + m)/(1 - m)$ in F; cf. Appendix S2. The long black tick marks indicate α_{max} . Their values increase from 6.10 in A to 12.33 in F. The corresponding maximum value of the stable polymorphic equilibrium for T_2 increases from 0.982 to 0.996. The nonzero equilibria are calculated from equation (S8) in Appendix S2. The analogous Figure S5 depicts the case of strong migration.

this evolution will depend upon the frequency t_2 because by definition common traits are favored by positive frequency dependence.

Keeping these facts in mind, we turn to the patterns in Figure 2. With very weak or very strong preferences, and hence very weak frequency-dependent sexual selection, we expect t_2 to be close to the migration-selection balance, $\hat{t}_{2,m/s}^{pm}$; this is what we see at the far left and far right of each panel in Figure 2 (in Fig. 2A, $\hat{t}_{2,m/s}^{pm} = 0$ because s is too small). Turning to the center

of each panel, with intermediate preference strengths near α_{max} , we see that a high equilibrium t_2 can be reached if the trait starts at a high frequency (as when $s = 0$). Here, positive frequency-dependent sexual selection is strong, and combines with viability selection to create a stable equilibrium where the balance between the net selection (viability and sexual) and migration is high. Interesting cases now arise on either side of the “bubble” present in Figure 2B, C. Here, the migration-selection balance is fairly low,

that is, $\hat{t}_{2,m/s}^{pm} < 1/2$ (note that in Fig. 2D, $\hat{t}_{2,m/s}^{pm} = 1/2$). When preference strengths are too far from α_{max} and thus are slightly off the bubble, positive frequency-dependent sexual selection is not strong enough to keep t_2 very high, so t_2 gets closer and closer to $\hat{t}_{2,m/s}^{pm}$. However, $\hat{t}_{2,m/s}^{pm} = 1/2$ is the critical threshold below which T_1 , and not T_2 , starts to be favored by positive frequency-dependent sexual selection. When t_2 approaches $\hat{t}_{2,m/s}^{pm} < 1/2$, positive frequency-dependent sexual selection thus contributes to the migration side of the migration-selection balance, not the viability selection side, and T_2 is lost. Because these cases require $\hat{t}_{2,m/s}^{pm} < 1/2$, they will occur only for a range of parameter values that is quite narrow with weak-migration rates (e.g., s between 0.0101 and 0.0202 with $m = 0.01$) but increases with higher migration rates (e.g., s between 0.25 and 0.5 with $m = 0.2$). When selection is relatively strong, the bubble can be completely absent, and the regime can shift to having a high equilibrium frequency t_2 uniformly present (see Fig. 2F). With high migration, the bubble is absent regardless of selection strength (Fig. S5).

In a continent-island scenario, we therefore expect the positive frequency-dependent sexual selection created by phenotype matching to be ineffective at changing trait frequencies when preferences are too weak or too strong, to contribute to divergence when it is maximized, but to actually lead to trait loss for certain ranges of preference strength when the migration-selection balance is low.

PREFERENCE/TRAIT MODEL

To assess the contribution of sexual selection from preference/trait mating to trait divergence on an island, we would again like to know when sexual selection will lead to more (or less) trait divergence than would be caused by local adaptation alone, given the migration of individuals with a maladapted trait. We thus again use the frequency of T_2 at migration-selection balance with random mating as a basis of comparison. For the preference/trait model (denoted by superscript "pt"),

$$\hat{t}_{2,m/s}^{pt} = \frac{s(1-m) - 2m}{s(1-m^2)} \approx 1 - \frac{(2+s)m}{s}, \tag{6}$$

which requires $m < s/(2+s)$. Note that $\hat{t}_{2,m/s}^{pt}$ differs from $\hat{t}_{2,m/s}^{pm}$ because in the latter case viability selection occurs in both sexes.

General conditions for sexual selection to increase versus decrease trait divergence

First, we explore conditions for the equilibrium trait frequency \hat{t}_2 to be greater than $\hat{t}_{2,m/s}^{pt}$. Rearrangement of the recursion equation for $\Delta\hat{t}_2$ shows that in any given generation, T_2 will increase in frequency due to sexual selection when the frequency of the

preference, p_2 , in females after viability selection, and thus at the time of sexual selection, is greater than

$$p_2^{ss*} = \frac{1 + t_2^{vs}\alpha}{2 + \alpha} \tag{7}$$

(see Appendix S3). Here, t_2^{vs} is the frequency t_2 in males after viability selection and the preference strengths are assumed to be symmetrical ($\alpha_1 = \alpha_2 = \alpha$). The value of p_2^{ss*} is often rather high (Fig. S8), especially when local adaptation is strong (leading to a high t_2^{vs}), so p_2 must be high if sexual selection is to contribute to trait divergence.

By the arguments and substitutions presented in Appendix S3, it follows from equation (7) that sexual selection will cause the equilibrium trait frequency to be above $\hat{t}_{2,m/s}^{pt}$ when

$$\hat{p}_2 > \frac{h(1 - m p_C(2 + \alpha)) + \alpha(1 + s)(1 - m)\hat{t}_2}{h(1 - m)(2 + \alpha)}, \tag{8}$$

where

$$h = 1 + (1 - m)s\hat{t}_2.$$

Although general expressions for the preference and trait frequencies at equilibrium cannot be obtained, weak-migration analyses, analyses with strong preferences, and numerical analyses can give insight into when condition (8) is met (see Appendix S4 and below) and sexual selection contributes to, versus detracts from, trait divergence.

We see from such analyses there is a large range of preference strengths α for which sexual selection depresses the trait frequency below $\hat{t}_{2,m/s}^{pt}$ (Figs. 3, S9, Appendix S4, File S2). In fact, a weak-migration approximation shows that the equilibrium frequency \hat{t}_2 always decreases as α increases when α is small (Appendix S4, Fig. S10). In general, this decrease may be small or moderate (if p_C is sufficiently large) or may lead to loss of T_2 for an intermediate range of values α when p_C is low enough (see eq. S21 in Appendix S4, Figs. 3, 4). There are also, however, cases with strong preferences where conditions (7) and (8) are met, and sexual selection causes an increase in trait frequency above migration-selection balance. This occurs for relatively weaker preferences when migration is higher (Fig. 5A). In all cases, the trait and preference frequencies are heavily influenced by the frequency of the preference on the continent, p_C (Fig. 4, 5B).

The equilibria shown in Figures 3, 4, S9, and S10 are globally stable. However, they represent differentiation only if $\hat{t}_2 > 0$. If $\hat{t}_2 = 0$ (hence, $\hat{p}_2 = p_C$), T_2 is lost from any initial condition. This occurs when p_C is below a critical threshold,

$$p_C < p_{C,crit} = \frac{\alpha - s + m(2 + s + \alpha)}{\alpha(2 + \alpha)(1 - m)(1 + s)}, \tag{9}$$

where $p_{C,crit}$ is given in more general form by equation (S19) in Appendix S4. We note that $p_{C,crit}$ is maximized at intermediate or low values of α . Therefore, $p_C < p_{C,crit}$ often holds for a range

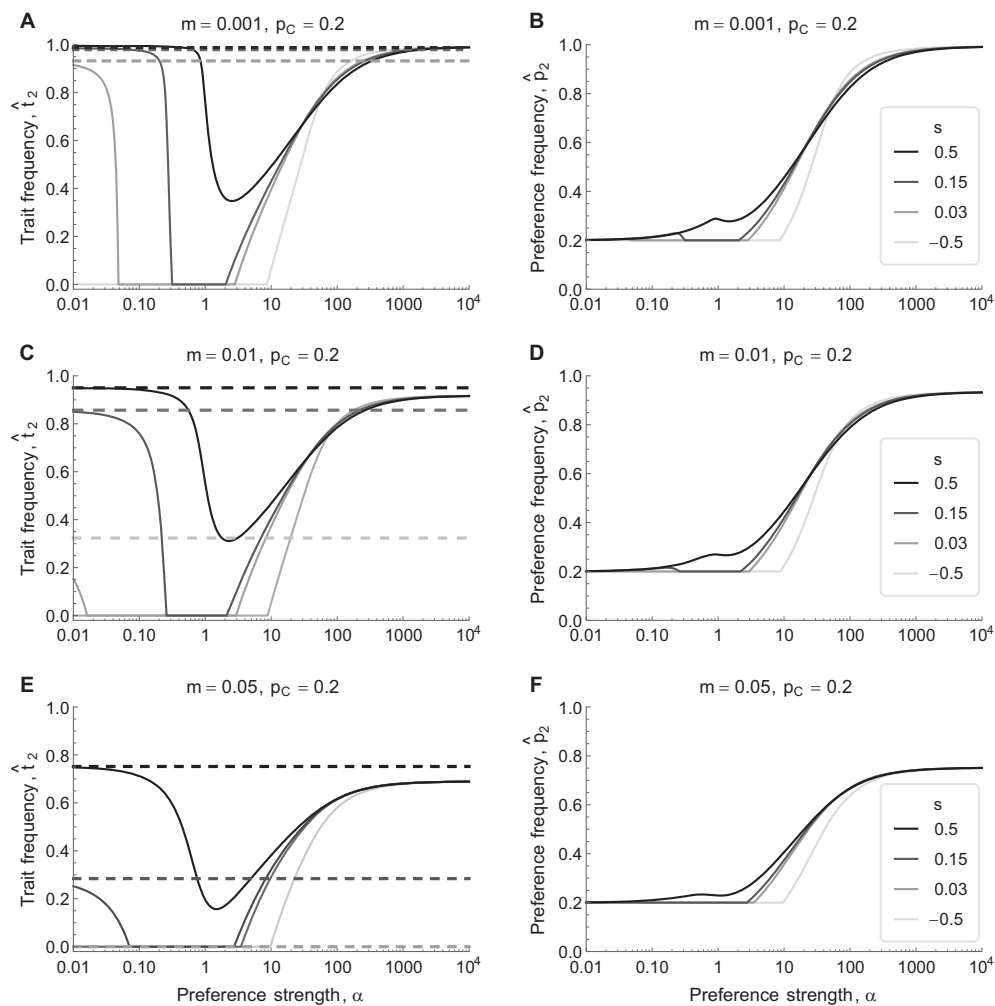


Figure 3. Stable equilibria in the preference/trait model with viability selection. Solid lines signify equilibrium trait frequencies \hat{t}_2 (left column) and equilibrium preference frequencies \hat{p}_2 (right column) as functions of the preference strength α . Dashed lines show migration-selection balance of the trait under random mating, $\hat{t}_{2,m/s}^{pt}$; equation (6). Shades of gray indicate the strengths of selection (see legend). The stable equilibrium is calculated by solving a very complicated cubic equation, as described in Section 3 in File S2. Numerics suggest that it is globally asymptotically stable if it exists ($\hat{t}_2 > 0$). The small peaks in \hat{p}_2 at low-to-moderate α can be explained by the fact that in this region the net selection on T_2 goes from high to low while the linkage disequilibrium that transmits these selective forces to P_2 already starts to increase (cf. Figs. S9 and 3 in Servedio and Bürger 2014).

of intermediate values α (Figs. 3, 4, S9, Appendix S4). At these values, differentiation is completely erased. More insights both into the effects of p_C on the equilibrium values of the trait and preferences, and into the fall and rise in the trait frequency with increasing preferences, can be gained by considering the cases with low and high p_C separately.

The effects of preference frequencies on trait divergence

First, we consider the case where p_C is relatively low; this case is of particular interest as the preference for the locally adapted island trait may be expected to be rare in the mainland population. With very weak preferences (very low α), the preference frequency at

equilibrium is very close to p_C , whereas the equilibrium frequency \hat{t}_2 is very close to the migration-selection balance $\hat{t}_{2,m/s}^{pt}$, which can be high (Figs. 3 and 4). As the preference strength α starts to increase, \hat{t}_2 drops due to the fact that with low p_C the frequency of p_2 in females at the time of sexual selection is much lower than p_2^{SS*} (eq. (7) and Fig. S8). In short, under these conditions, the low frequency of the island preference P_2 , and consequently high frequency of the continental preference P_1 , leads to high mating success of the continental type T_1 on the island. The trait divergence caused by local adaptation on the island is thus depressed or erased by sexual selection at these weak to moderate preference strengths. This same effect was seen in the two-island preference/trait model of Servedio and Bürger (2014), in which

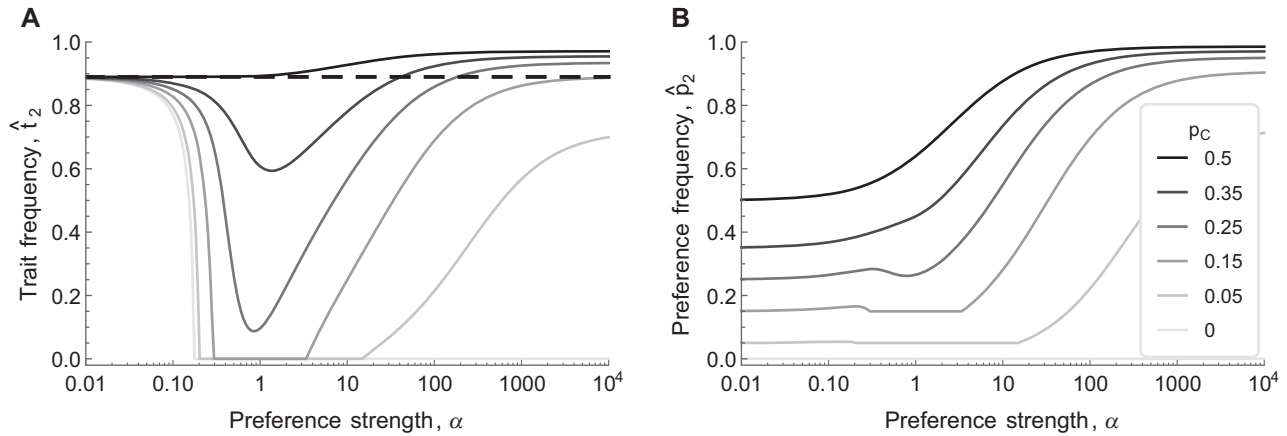


Figure 4. Stable equilibria in the preference/trait model with viability selection. Solid lines signify equilibrium trait frequencies \hat{t}_2 (A) and equilibrium preference frequencies \hat{p}_2 (B) as functions of the preference strength α . The black dashed line shows migration-selection balance of the trait under random mating, $\hat{t}_{2,m/s}^{pt}$; equation (6). Shades of grey indicate the frequency p_C of the preference allele P_2 on the continent. In both (A) and (B), $m = 0.01$ and $s = 0.2$.

trait homogenization increased with stronger preferences, due to the fact that under Fisherian sexual selection preferences become more homogenized than traits.

Even with weak to moderate preferences, the frequency of P_2 is noticeably affected by evolution at locus T. The nonrandom mating generated by female preference leads to positive linkage disequilibrium between loci P and T (Fig. S9). When viability selection is strong relative to migration, the increase in T_2 due to local adaptation can lead to an increase in the frequency of P_2 as well, even in ranges of α for which sexual selection subsequently lowers T_2 (Figs. 3, 4).

When preferences are strong (high α), the equilibrium preference frequency \hat{p}_2 can be far above its frequency on the continent, p_C (Figs. 3, 4). Strong preferences generate high levels of linkage disequilibrium, so local adaptation increasing the frequency of T_2 boosts the level of P_2 greatly as well. If p_2 in females at the time of sexual selection becomes greater than p_2^{ss*} , sexual selection will have a positive, rather than negative, effect on t_2 . In this case, both viability selection and sexual selection lead to an increase in t_2 , and hence p_2 via linkage disequilibrium (Figs. 3, S9). We note that in a version of the model in which we also allowed viability selection on the trait in females (so that $x_i^{f,vs} = x_i^{vs}$), we find the same pattern as in Figure 3, but \hat{t}_2 and \hat{p}_2 are higher and rise slightly faster (see Fig. S11).

Interestingly, when preference strengths are very high, the frequency of P_2 at equilibrium can increase even above that of T_2 . This can occur at lower values of α than are necessary for \hat{t}_2 to increase above $\hat{t}_{2,m/s}^{pt}$. The approximate preference strength at which this occurs, when migration m is weak, is

$$\alpha \approx \frac{(1 - p_C)(1 + s)}{(2 - p_C)m} \tag{10}$$

(see Section 4.4.1 in File S2). The cause of this effect is as follows. First, migration lowers the trait frequency t_2 more than it does the preference frequency p_2 because P_2 , but not T_2 , is polymorphic on the continent. Because linkage disequilibrium between P and T is very high with strong preferences, p_2 increases at a similar magnitude as does t_2 from the joint effects of viability and sexual selection. The frequency p_2 can thus, from these combined effects, remain above t_2 at equilibrium.

Second, we consider the case where the preference P_2 is common on the continent (p_C is high, which is likely to be of less interest in the context of speciation in nature). In this case, we see that \hat{t}_2 can increase above its value at migration-selection balance, $\hat{t}_{2,m/s}^{pt}$, at much lower levels of preference strength α than are required with a low p_C (Figs. 4, 5B). When p_C is high, migration depresses p_2 much less than when p_C is low, and it becomes easier for conditions (7) and (8) to be met. For infinitely high α , we can show that $\hat{t}_2 > \hat{t}_{2,m/s}^{pt}$ when

$$p_C > \frac{s - m(2 + s)}{(1 - m)(1 + s)} \tag{11}$$

(Appendix S4). In these cases, \hat{t}_2 converges to the value given in equation (S22) in Appendix S4 (Fig. S12). For small m , condition (11), shown in Figure S13, becomes approximately $p_C > (s - 2m)/(1 + s)$, which requires large p_C if selection is strong.

If viability selection is sufficiently weak relative to migration, such that migration-selection balance does not allow T_2 to persist in the island population, strong sexual selection still induces trait divergence on the island (Figs. 3C, E, 5, S12C–F). Sexual selection is thus particularly important in these cases, in which it is a uniformly positive force for divergence. Interestingly, strong sexual selection can additionally allow the trait to reach a high frequency on the island when it is selectively neutral, or even

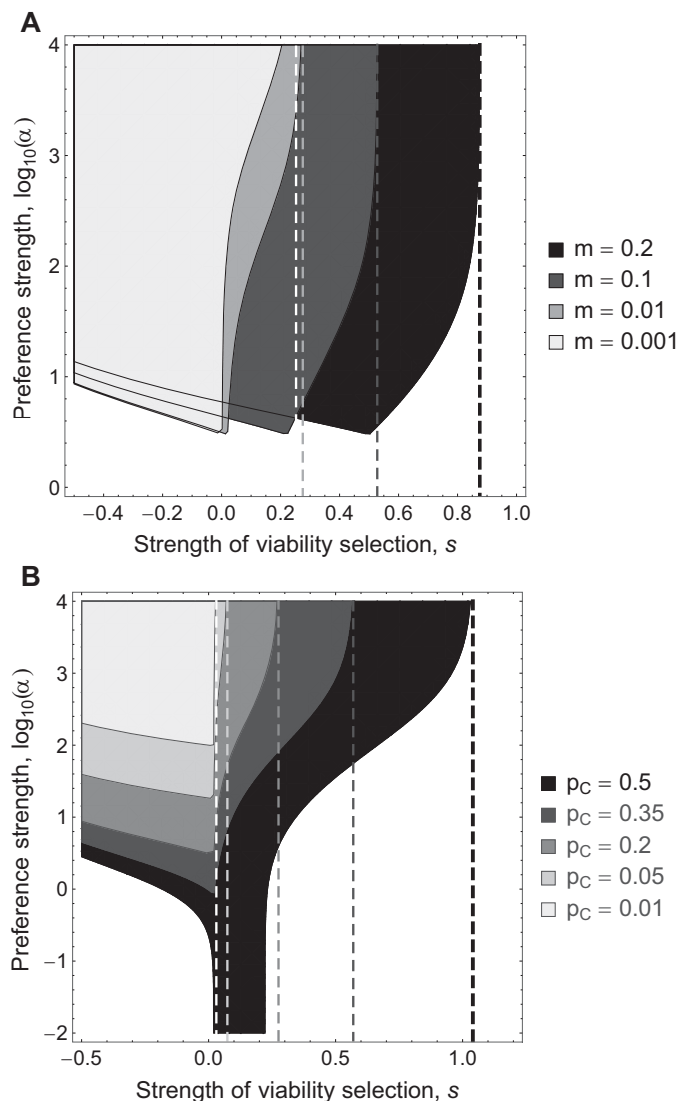


Figure 5. Regions in which the equilibrium trait frequency \hat{z}_2 exceeds its value $z_{2,m/s}^{pt}$ at migration-selection balance. In A, p_C is fixed at 0.2; in B, m is fixed at 0.01. In the shaded regions, $\hat{z}_2 > z_{2,m/s}^{pt}$ holds. To the left of the minimum of each region in A and B, $z_{2,m/s}^{pt} = 0$, where the minimum is attained $s = 2m/(1 - m)$. The straight line that is the lower boundary of this region is obtained by solving $p_C = p_{C,crit}$ for α ; see equation (9). To the right of these minima, $z_{2,m/s}^{pt} > 0$ is increasing, causing $\hat{z}_2 > z_{2,m/s}^{pt}$ only at higher preference strengths. The dashed lines indicate the critical value s , below which $\hat{z}_2 > z_{2,m/s}^{pt}$ holds for infinitely large preference strength α . It is obtained by solving equation (11) for s . Panel B indicates that for negative s , $\hat{z}_2 > z_{2,m/s}^{pt} = 0$ holds for sufficiently large α even if p_C is arbitrarily close to 0. This is indeed the case and follows from equation (S22) in Appendix S4.

selected against (Fig. 3). This contrasts with the two-island case (Servedio and Bürger 2014) and with the case of Fisherian sexual selection along a cline (Lande 1982; Payne and Krakauer 1997), in which trait differentiation cannot be maintained with selectively neutral traits. Trait divergence in the continent-island model is possible because the reservoir of P_2 on the continent, if it exists ($p_C > 0$), prevents the complete loss of P_2 on the island. This allows T_2 to be maintained on the island regardless of whether it is present on the continent, while the lack of back migration prevents trait homogenization.

Increased preference strength only for the island trait

Above, we assumed $\alpha_1 = \alpha_2 = \alpha$ and varied the parameter α . This can be interpreted as variation in the degree of choosiness. However, α_1 and α_2 may also be specific preference strengths for particular traits that vary independently. In fact, much of the mathematical theory has been developed for general values of α_1 and α_2 (File S2 and Appendix S4). If α_1 , the strength of the preference for the continental trait T_1 , is fixed at some (low) value and $p_C > 0$, then an increasingly stronger preference α_2 for the island trait T_2 leads to increased differentiation in trait and

preference frequencies, once α_2 is high enough to allow divergence (Fig. S14). This scenario constitutes another instance in which stronger sexual selection always increases divergence. The simple explanation is that if only α_2 , and not α_1 , increases, the rare and maladapted males with T_1 lose their disproportionately high mating opportunities.

Evolution of Preference Strength

In the presentation above, we evaluate the extent of trait divergence between a continent and island when the strength of preference is fixed. It is also, however, important to assess whether preference strength can evolve, to obtain a better understanding of the level of trait divergence that will ultimately result. To evaluate the evolution of preference strength, we added an additional choosiness locus, *A*, to both mating models. The alleles at this locus, which we assume are selectively neutral, determine different values of α . Full equations for these versions of the models are presented in Appendix S5, and files containing the simulation code are available on Dryad.

In brief, in almost no case, with either mating model, was an allele for a novel preference strength able to evolve to a nontrivial frequency on the island; ancestral continental preference strengths could not be displaced in the island populations. As detailed in Appendices S6 and S7, large ranges of resident values of α were tested numerically and by simulation against invasion by many other α values in both models.

In the phenotype matching model, the resident and invasive values of α examined included α_{\max} , which had been found to be the preference strength ultimately reached by evolution in a two-island phenotype matching model (Servedio 2011). Although it does not have this property in the continent-island model, it did have some effect of note when we allowed the continental population to be polymorphic at locus *A*. In this case, an allele at locus *A* that is closer to α_{\max} will reach a higher frequency on the island, although frequency differences obtained by such an allele between the island and continent are always very modest (see Appendix S6). The only case found in the phenotype matching model in which the evolution of a novel, high α was possible was when the allele determining it was introduced in complete linkage disequilibrium with allele T_2 and the recombination rate between loci *T* and *A* was very low (e.g., $r < 0.0001$).

In the preference/trait model, we also examined the case in which the continental allele was polymorphic at locus *A*, to assess whether there would be a departure from continental allele frequencies on the island. We found that as in the phenotype matching model, the forces of indirect selection on the island only allowed departures from the continental frequencies by a small absolute amount (in this case of less than 0.1) with the

parameters tested (see Appendix S7). It is difficult, however, to see clear patterns regarding when alleles for stronger preferences increase versus decrease in frequency on the island (even by these slight amounts), although the behavior of the model is somewhat elucidated by re-writing the recursion equations using the multi-locus notation of Barton and Turelli (1991); for more detail see Appendix S7.

The failure of evolution of a novel preference strength on the island in these models can be attributed to the fact that such alleles are only favored by indirect selection; this indirect selection is mediated by the strength of linkage disequilibrium between the choosiness locus *A* and other loci in the system, and is consequently weak. The direct force of migration of alleles for the preference strength characteristic of the continent will generally overwhelm any indirect selection that favors an allele for novel preference strength on the island. This result obviously hinges on the assumption that there is no direct selection favoring a novel preference strength. For the primary case of interest, the evolution of stronger preferences, and hence potentially stronger assortative mating, it is indeed not likely that stronger preferences would confer a direct viability, fecundity, or mating advantage in nature; if anything, the opposite might be expected to be true, as individuals with stronger preferences might pay higher costs in searching for mates. The fact that we did not include search costs in the model thus only makes the conclusion that stronger assortative mating is not likely to evolve conservative.

Discussion

Peripheral isolation has remained a situation of interest in empirical speciation research (e.g., Hodge et al. 2012; Bowen et al. 2013; Farrington et al. 2014; Tyers et al. 2014), and several theoretical studies have noted that strongly asymmetric migration patterns can have important consequences for the speciation process (e.g., Servedio and Kirkpatrick 1997; Kirkpatrick 2000; Bank et al. 2012; Guerrero and Kirkpatrick 2014). We examine the effect of sexual selection on the amount of trait divergence between a partially isolated population and a founding population, using a continent-island model, under two commonly considered forms of assortative mating. We find that the positive frequency-dependent sexual selection generated by phenotype matching can increase the frequency of a locally adapted trait on the island, but generally only under an intermediate range of preference strengths. Similarly, when there are separate preference and trait loci only a limited range of preference strengths, in this case strong preferences, can allow sexual selection to increase island trait frequencies above migration-selection balance, and this furthermore requires that the preference be polymorphic on the continent ($p_C > 0$). Under other conditions, the sexual selection generated by both of these forms of assortative mating can instead reduce

trait divergence between an island and continent, especially in the case of separate preferences and traits. These results broaden our understanding of the conditions under which partially isolated populations can evolve unique traits involved in mate choice.

When assortative mating occurs by phenotype matching, as is commonly assumed in many theoretical models (e.g., see Introduction, also Servedio 2000, 2004; Bolnick 2004; Goumbiere 2004; Rettelbach et al. 2013, and “similarity based” models in Gavrillets 2004), trait divergence is close to migration-selection balance with both very weak and very strong preferences, and has a peak at intermediate preference strengths. These results are very similar to those that occur under phenotype matching with a two-island migration pattern (Servedio 2011). Additionally, in both cases initial trait differentiation, as might occur under secondary contact, is required for trait divergence. Unlike in the two-island case, however, we find a range of preference strengths at some distance from either side of the peak for which sexual selection drives trait loss, even when the trait would otherwise be maintained at migration-selection balance under random mating. The width of these ranges of trait loss, when present, increase with increasing migration rate. As detailed above, all of these results can be explained by the fact that phenotype matching generates positive frequency-dependent sexual selection, which is maximized at intermediate preference strengths. Critically, when preferences are too strong, positive frequency-dependent selection begins to weaken, due to the fact that the mating success of rare males begins to match the frequency of the rare females that prefer them. In the range of preference strengths that leads to trait loss there is still enough sexual selection to significantly affect trait frequencies. However, because trait frequencies are otherwise low in this range due to unidirectional migration (not present in the two-island model), this positive frequency-dependent sexual selection further lowers the frequency of the trait instead of increasing it. We thus arrive at two counterintuitive conclusions: (1) very strong preferences can lead to less trait divergence than intermediate ones (as in the two-island case), and (2) in the range of trait loss, sexual selection can directly counter local adaptation and lead to the elimination of the island-specific trait.

With preference/trait mating, the results of the continent-island model also bear some similarity to the case when two populations are exchanging roughly equal proportions of migrants, but again demonstrate important differences. In the two-island case, increasingly strong preferences lead to a decrease in trait divergence under Fisherian sexual selection (Servedio and Bürger 2014). Trait loss occurs because preferences, which are only under indirect selection that is naturally fairly weak, maintain little divergence across populations. Stronger preferences thus serve to increase the power of these homogenized preference frequencies to in turn homogenize trait frequencies, countering local

adaptation of the trait. We find that a similar effect occurs with low-to-moderate preference strengths under unidirectional migration; high frequencies of the foreign preference tend to result in trait frequencies dropping below the migration-selection equilibrium that they would have reached under random mating. Trait differentiation can be lost entirely, especially with higher migration or weaker viability selection. Strong preferences can, though, allow the trait to reach frequencies above migration-selection balance, especially when preferences are polymorphic at higher frequencies on the continent. Unlike in the phenotype matching case, where differentiation requires secondary contact, the polymorphic trait equilibrium on the island can be reached even from a low initial frequency, and thus could originate by mutation. Moreover, strong sexual selection can allow the trait to be maintained on the island even when it would be lost under random mating. Under these conditions, which occur when there is weak local adaptation of the trait relative to migration, or even if the trait is costly and selected against on the island, sexual selection can be considered to play a uniformly positive role in allowing trait differentiation between the island and the continent.

Our primary findings for both models center on the effects of fixed preference strengths. The relevance of these analyses is confirmed by our finding that it is very difficult for preference strength on an island to evolve away from the value present on the continent. We allow preference strength to evolve at a separate locus, which can be thought of as controlling “choosiness,” especially in the case of symmetric strengths across preference alleles. Because we do not assume that alleles for preference strength are under direct selection, they evolve only through linkage disequilibrium between this choosiness locus and the other loci in the system; the effective strength of selection on them is thus weak, and easily overcome by migration. Note that in natural systems, the most likely selection to be present on choosiness alleles would be selection against greater choosiness or stronger preferences due to search costs; by not assuming search costs in our models we are therefore being conservative with regard to the likelihood of evolving stronger preferences (e.g., Kopp and Hermisson 2008; Otto et al. 2008). Also note that because we have unidirectional migration, we do not have a line of preference and trait equilibria in our model (as in Lande 1981; Kirkpatrick 1982), and thus small costs of preferences in the preference/trait model are not likely to substantially alter the dynamics we see here.

The preference strengths present on a continent are therefore very likely to determine at least the upper bound of preference strength that can evolve on an island, at least in the early stages of the speciation process. We assume in our models that the preference strength present on the continent is under the control of forces not considered in the system. We note that when trait variation is absent, as we assume on the continent, preference

alleles in the preference/trait model would be neutral and could thus remain polymorphic at equilibrium, as assumed when we set $p_C > 0$ (a low p_C will be more feasible than a high p_C under trait absence, Kirkpatrick 1982). It is still possible that choosiness on the continent may, however, be under selection due to search costs in both the phenotype matching and preference/trait models, if the biology of females is such that they will delay mating if the preferred male is not present; in this case, we would expect the continent to evolve to $p_C = 0$.

In later stages of the speciation process, there may be strong evolutionary pressure to avoid hybridization because the buildup of postzygotic isolation renders hybrids less fit (Dobzhansky 1940). This process of reinforcement has been shown to lead to stronger choosiness in continent-island models of phenotype matching (e.g., Kirkpatrick 2000; Servedio 2000). In preference/trait models, island-specific preference alleles can also increase in frequency by reinforcement (Servedio and Kirkpatrick 1997; Kirkpatrick and Servedio 1999, for extrinsic postzygotic isolation, see Kirkpatrick 2001). Higher preference frequencies on the island would subsequently tend to increase the frequency of island-specific traits. Kirkpatrick and Servedio (1999) showed that even when selection against hybrids is absent, preferences on the island can maintain a higher frequency than those on the continent if a set amount of trait divergence is present. Our results support this finding, while elaborating on the degree of trait divergence that it is possible to maintain.

Although our interest is in the effects of sexual selection given the migration pattern typical of a continent-island scenario, we do not consider other factors that have been hypothesized to be important in speciation in peripheral isolates. Several authors have focused, for example, on the importance of genetic drift due to bottlenecks occurring during the colonization of a new area (e.g., Mayr 1954, 1963; Kaneshiro 1976, 1980; Templeton 1980), and on the relaxed selection that may accompany subsequent population expansion (Carson 1982; see Barton and Charlesworth 1984; we hold population size constant). The equilibria that allow divergence in our models can always be reached from the assumptions of secondary contact, and so are consistent with factors such as the ones above playing a role in an initial allopatric phase of divergence.

The relevance of the models considered in this study depends on how often the basic scenarios assumed occur in nature. Although not thought to be very common, support for peripheral isolate speciation, which may have the unidirectional pattern of gene flow assumed in these models, is found across diverse groups of taxa (e.g., birds: Chesser and Zink 1994, felids: Mattern and McLennan 2000, *Rana*: Austin et al. 2003, marine species: Bowen et al. 2013). Formal estimates of the prevalence of the phenotype matching and preference/trait mechanisms in nature have not yet been made, although the importance of mate choice

as a component of premating reproductive isolation (e.g., Coyne and Orr 2004) indicates that one or the other is likely often at play.

The very simple models of assortative mating considered in this article are not meant to match specific cases in nature, but instead to isolate the effects on trait divergence of the sexual selection generated by phenotype matching and preference/trait mechanisms. It thus becomes possible to better understand the causes of the underlying dynamics of more realistic, and hence more complicated, biological scenarios. In the phenotype matching model, we expect that biological phenomena that alter trait frequencies between males and females, such as sex-specific selection or migration, may alter the equilibrium trait conditions, although analysis of the two-island case shows that trait divergence still peaks at an intermediate preference strength with moderately different migration rates between the sexes (Yeh and Servedio, 2015). There are many different sexual selection scenarios that build upon the Fisherian preference/trait model that we use here, which has indeed been considered a “null model” for sexual selection (Prum 2010). Servedio and Bürger (2014) found that several departures from the classic Fisherian sexual selection assumptions of the discrete model of Kirkpatrick (1982) led to stronger sexual selection increasing trait divergence in certain areas of the parameter ranges, but not others (e.g., with traits expressed in females, with search costs, with a best-of- n mating rule). Alternative or more complicated sexual selection scenarios, including different preference functions with continuous traits (e.g., Lande 1982), condition dependence without preference variation (e.g., van Doorn et al. 2009) or deviations from polygyny may also produce departures from the current findings (or may not), and would be worth exploring in future analyses.

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DATA ARCHIVING

The data are archived on Dryad: doi:10.5061/dryad.4km38.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Appendix S1. Trait divergence during phenotype matching in the absence of selection—equilibria and stability.

Appendix S2. Trait divergence during phenotype matching with selection—equilibria and stability.

Appendix S3. Trait divergence in the preference/trait model.

Appendix S4. The preference/trait model: important properties and approximations.

Appendix S5. The evolution of assortative mating—models.

Appendix S6. The evolution of assortative mating—phenotype matching.

Appendix S7. The evolution of assortative mating—preference/trait model.

File S1. The phenotype matching model.

File S2. The preference/trait model.

Figure S1. Preference strength, α_{\max} , that leads to the maximum level of trait divergence between the continent and island in the phenotype matching model with no viability selection ($s = 0$).

Figure S2. Sexual selection coefficient, $a_{\phi,T}$ (eq. S6), in males in the phenotype matching model without viability selection ($s = 0$) as a function of the trait frequency \hat{t}_2^{mig} after migration.

Figure S3. Threshold level of selection comprising local adaptation of T2, s_{crit} (eq. S7).

Figure S4. Regions of the three different equilibrium configurations in the phenotype matching model with viability selection.

Figure S5. Equilibria in the phenotype matching model with viability selection and strong migration.

Figure S6. Equilibria in the phenotype matching model with viability selection.

Figure S7. Preference strength, α_{\max} , that leads to the maximum level of trait divergence between the continent and the island in the phenotype matching model with viability selection.

Figure S8. Threshold preference in females at the time of sexual selection, p_2^{ss*} (eq. 7) in the preference/trait model.

Figure S9. Stable equilibria in the preference/trait model with viability selection. Solid lines signify equilibrium trait frequencies \hat{t}_2 (left column), equilibrium preference frequencies \hat{p}_2 (middle column), and equilibrium values of linkage disequilibrium \hat{D} (right column) as functions of the preference strength α . Dashed lines show migration-selection balance of the trait under random mating, $\hat{t}_{2,m/s}^{\text{pt}}$ (eq. 6). Colors indicate the strength of selection (see legends in the middle column).

Figure S10. Stable equilibria in the preference/trait model with viability selection. Solid lines signify the equilibrium trait frequency, \hat{t}_2 , as a function of the preference strength α . Dashed lines show the weak-migration approximation $\hat{t}_{2,\text{weakmig}}$ (first expression in eq. S20 in Appendix S4). Colors indicate the frequency p_C of the preference allele P₂ on the continent. The values $m = 0.01$ and $s = 0.5$ are fixed.

Figure S11. Stable equilibria in the preference/trait model with viability selection on both sexes.

Figure S12. Stable equilibria in the preference/trait model with viability selection. Solid lines signify equilibrium trait frequencies \hat{t}_2 (left column) and equilibrium preference frequencies \hat{p}_2 (right column) as functions of the preference strength α . Dotted lines show the strong-preference limits $\hat{t}_{2,\alpha \rightarrow \infty}$ and $\hat{p}_{2,\alpha \rightarrow \infty}$ (eqs. S22 and S23 in Appendix S4). Notably, these depend only on m and p_C , but not on s . Different colors indicate different values of p_C .

Figure S13. Preference frequency on the continent, p_C , above which $\hat{t}_{2,\alpha \rightarrow \infty} > \hat{t}_{2,m/s}^{\text{pt}}$ holds, that is, more differentiation can be maintained for sufficiently strong preferences than for random mating (see eq. 11).

Figure S14. Stable equilibria in the preference/trait model with viability selection.

Figure S15. Three-dimensional representation of the stable equilibria in the preference/trait model with viability selection.

Table S1. Phenotype matching invasion analyses with $s = 0$.

Table S2. Phenotype matching invasion analyses with $s > 0$.

Table S3. Phenotype matching invasion analyses with $s > 0$ and the A locus polymorphic.

Table S4. Preference/trait invasion analyses.