

The counterintuitive role of sexual selection in species maintenance and speciation

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The pronounced and elaborate displays that often differ between closely related animal species have led to the common assumption that sexual selection is important in speciation, especially in geographically separated populations. We use population genetic models to examine the ability of Fisherian sexual selection to contribute to lasting species differentiation by isolating its effect after the onset of gene flow between allopatric populations. We show that when sexually selected traits are under ecologically divergent selection, the situation most favorable to speciation, mating preferences tend to introgress faster than trait alleles, causing sexual selection to counter the effects of local adaptation. As a consequence, the net amount of trait divergence often drops with stronger Fisherian sexual selection. Furthermore, alleles for progressively weaker preferences spread in this context until sexual selection is removed. The effects of pure Fisherian sexual selection on species maintenance are thus much more inhibitory than previously assumed.

secondary contact | mathematical model | premating isolation | mate choice | search costs

The importance of premating isolation as the first barrier to gene flow between species (1, 2), coupled with showy differences between closely related species in sexually selected characters, has led researchers to postulate a causal relationship between sexual selection and speciation (3). This hypothesized relationship seems particularly logical in the case of allopatric speciation; sexual selection may cause mating preferences (usually in females) and trait phenotypes (usually in males) to diverge quickly from one another in isolated populations (4, 5). If this divergence removes the potential of populations to interbreed, separate species would result under the biological species concept (6). In fact, a prominent review of the topic states that “the most obvious way in which sexual selection could accelerate speciation . . . is via increased coevolution of male traits and female preferences in allopatric populations or if traits involved in mate recognition were under direct environmental selection” (ref. 7, pp. 85–86). Under the latter suggestion, speciation would be particularly favored because divergent environmental selection on traits would maintain trait variation and could guide sexual selection in opposite directions in incipient species (8). In fact, trait alleles that are both under ecologically divergent selection and a component of premating isolation have been termed “magic traits” because of this dual function, which allows speciation to occur unusually easily (8–10).

Whereas it is well established that sexual selection alone is unlikely to drive sympatric speciation (e.g., refs. 10 and 11), the quotation above demonstrates that it is still considered a driving force in speciation that is largely allopatric. We ask the question of whether Fisherian sexual selection per se can really play the role ascribed to sexual selection above, of promoting speciation and species maintenance in allopatry, if species boundaries are tested by the onset of gene flow. Specifically, we consider secondary contact of allopatric populations that have already diverged in preferences and traits and concentrate on the most favorable case for divergence, when sexually selected traits are also locally adapted.

By “Fisherian sexual selection” we are referring to sexual selection in what can be considered its most basic form, in which a genetically encoded female preference imposes differential mating success with regard to a male trait. This nonrandom mating generates linkage disequilibrium, so that evolution by sexual selection on the male trait leads to concomitant evolution of the preference itself (ref. 12, pp. 136–137). To isolate the role of Fisherian sexual selection in species maintenance we primarily consider selectively neutral female preferences. Neutrality of preferences follows the classic scenario considered in early and influential sexual selection models (4, 12, 13) and is viewed as a null model for sexual selection in its simplest form (14). In particular, this is the form of sexual selection used in the model by Lande (4) that arguably first popularized the idea of sexual selection promoting speciation and is still widely cited for this today.

The goal of this study is thus to understand the role that this simplest form of sexual selection plays in speciation and species maintenance; this forms an essential basis upon which to understand deviations from the Fisherian scenario in the form of more complicated (and more realistic) sexual selection assumptions. We touch upon the effects of some of these deviations from the Fisherian model (e.g., search costs, expression of the trait in both sexes, and a best-of- n model) in the process of exploring the robustness of our basic result.

Using population genetic modeling techniques, we find that if allopatric populations come into contact via the onset of gene flow, sexual selection, in its purest form, takes on an inhibitory role, drastically reducing trait differentiation due to divergent local adaptation. This is due to the fact that under this Fisherian model, preferences, which are not under direct selection, equilibrate

Significance

Sexual selection is generally considered to be an important force in the maintenance of species differentiation. Using population genetic models, we show that when isolated in its purest form of Fisherian sexual selection, sexual selection inhibits rather than assists species maintenance and speciation when isolated populations begin to exchange migrants. The stronger this type of sexual selection becomes, the more it erases any effects of local adaptation that drive trait divergence. Furthermore, if the strength of Fisherian sexual selection itself is allowed to evolve, sexual selection is lost. These results emphasize that additional complications have to be added to sexual selection scenarios for sexual selection to contribute to divergence; Fisherian sexual selection alone has the opposite effect.

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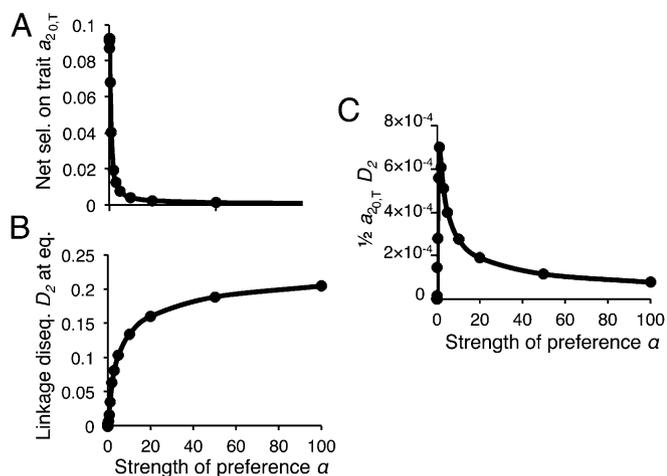


Fig. 3. Peaks in preference divergence between populations are due to the counteracting effects of the strength of female preference on selection in males and on linkage disequilibrium (Eq. 2). The points were calculated using the equilibrium values for the preference and trait allele frequencies and the linkage disequilibrium between them (note that Eq. 2 employs these values after migration rather than the equilibrium values, but these values are very similar because the migration rate is very small). (A) The net force of selection acting on the trait T_2 , $a_{2,0,T}$, for a set strength of preference α , using equilibrium values from numerical simulations of the exact recursion equations. (B) Equilibrium values for linkage disequilibrium between the preference and trait loci in population 2. (C) An approximation of the first term in Eq. 2, calculated as one-half of the product of the values plotted in A and B. For A–C the migration rate $m = 0.01$ and the selection coefficient for local adaptation $s = 0.1$.

selection (quasi-linkage equilibrium) and strong preference approximations (*SI Text*).

The explanations presented above for the patterns of trait and preference frequencies strongly suggest that although our models are haploid to facilitate analyses, our qualitative results are likely to be readily generalizable to diploids, although this remains to be confirmed. The presence of only low amounts of preference differentiation (and subsequently the loss of trait differentiation) between populations relies on the fact that selection on preferences is indirect. This is a characteristic of Fisherian systems that does not depend on ploidy. Additionally, linkage disequilibrium between preferences and traits, which determines the strength of indirect selection on preferences, has been shown to have the same magnitude in haploid and diploid models (21).

Although the goal of this paper is to explore the effect of Fisherian sexual selection per se, we also considered a variant of the model with selection on the preference in the form of search costs (*SI Text*). Concerns about the effects of costs in sexual selection models stem from early findings that the lines of equilibria present in classic Fisherian models become reduced to a point if costs to preferences are present, so that costly preferences cannot be maintained (24). We note that a line of equilibria is not present in our model; in fact, the equilibria are isolated and nondegenerate. Therefore, such a structural instability is not expected. Costs, however, provide a source of direct selection on preferences, which may overwhelm indirect selection as the primary determinant of preference evolution (25). We find that our results are robust to the addition of weak search costs; with such costs evolution arrives at approximately the same equilibria as shown in Fig. 1, constituting weaker differentiation with stronger preferences. Higher costs can, however, lead either to the loss of variation across both trait and preference loci (and hence no differentiation) or in some cases to stronger differentiation with stronger preferences (*SI Text* and Table S1). The ability of search

costs to promote species differentiation in some cases is consistent with the findings of previous models (26).

We additionally examined the results of a variant of our searching algorithm by exploring a best-of- n model (*SI Text*) (our original model is a “fixed relative preference” model in which all males are viewed, as assumed by refs. 4 and 13 and many subsequent papers). Best-of- n has been found in models of a single population to lead to very different results than does a fixed relative preference (27). We likewise find that best-of- n alters the results of our model (*SI Text* and Fig. S5), both when the sample of males n is small (in this case trait differentiation can either increase or decrease with stronger preferences, depending on the size of the sample and on preference strength) and when n is large (in this case preference variation or differentiation between populations is often lost, and when it is maintained trait differentiation decreases except at the very strongest preferences). We observed that with low n rare males have much lower mating success with rare females in the best-of- n model than with a fixed relative preference, which is consistent with the differences in the evolutionary effect of preference strength.

Our initial local adaptation model demonstrates that strong Fisherian sexual selection inhibits the maintenance of population differentiation between allopatric populations that come into contact, assuming preference strengths of a certain level. However, what if preference strength itself were to evolve? We addressed this possibility by adding a third locus that controls the value of the preference parameter α from the original model and allowed pairs of alleles at this locus to compete evolutionarily (*Methods*). Simulations of this model indicate that allelic variants for weaker and weaker preferences will successfully invade. Consistent with the results of the two-locus model above, these weaker preferences allow larger differences in the locally adapted traits to be maintained in each population. However, because preference strength evolves to zero, it is viability selection, not sexual selection that leads to these differences; traits no longer have a sexually selected function, only an ecological one.

Discussion

Speculation on the role of sexual selection in driving speciation and species maintenance traces back to the beginning of the explosion in sexual selection research seen in the past few decades (e.g., refs. 3, 4, 22, and 28). The more that this putative relationship is explored, however, the more tenuous it appears to be (e.g., refs. 10 and 11). Here we show that when sexual selection is isolated in a pure Fisherian form, it inhibits species maintenance in one of the situations in which its role seemed clearest, when the trait under sexual selection is also locally adapted. Furthermore, sexual selection is lost in this Fisherian system if preference strengths themselves are allowed to evolve.

What forces or scenarios may then explain the presence of sexually selected differences between species exchanging migrants? Our results suggest that researchers must look for more complicated scenarios than Fisherian sexual selection, even on a locally adapted trait, to explain an apparently divergent role of sexual selection between species with gene flow. Several candidates have been demonstrated or suggested to play such a role.

It has long been appreciated, for example, that preference differentiation, and consequently trait differentiation, may be maintained between populations when preferences themselves are under direct, divergent selection (9, 11, 29). This can occur when signal perception is affected by local environments that differ between sites (30). Search costs in the context of spatial structure may also cause direct selection on preferences that is divergent, as a result of positive frequency dependence (26); this effect can be seen in our model, in some cases, when costs are present and preferences are strong. We note, however, that the presence of search costs could exacerbate the loss of sexual selection through the evolution of weaker preference

strengths if preferences are more costly when they are stronger (19, 31, 32). We expect that deviations from polygyny may also result in direct selection on preferences; it is plausible that these may be frequency dependent and could lead to divergence.

More complicated sexual selection scenarios than the Fisherian models considered above may lead to divergence without direct selection on preferences being involved. Condition dependence in which trait expression is dependent upon local adaptation, for example, has been shown to allow sexually selected differences to evolve and be maintained (33). Preference and/or trait differentiation may also be driven by the process of reinforcement, due to selection against hybrids or hybridization (34–36). We note that avoidance of hybridization, direct selection on preferences, or another mechanism may be necessary for divergence in the case when unique sets of preference and trait loci lead to sexually selected differences between species (37) (e.g., large size is preferred in one population and red color is preferred in another); without these forces it seems that nothing would stop both sets of preferences and traits from sweeping through both populations. On the simpler side, as presented above, when preferences are already high, stronger preferences can increase trait differentiation when traits are expressed in females as well as males. Finally, as discussed below, the preference function may be of great importance in determining divergence (22). These factors, and doubtless others as yet to be recognized, should be sought and identified in empirical systems.

In the model most similar to the one considered here, Lande (22) showed using a quantitative genetic framework that some preference functions can increase divergence along a cline. Specifically, Lande found that when a female's preference for a male trait is an exponential function of the product of the preference and trait phenotypic values [a "psychophysical" mating preference (38)], differentiation of traits along a cline is exaggerated. Similar amplification along a cline can occur with a "relative" preference function, in which females prefer a male phenotype at a certain phenotypic distance from the mean phenotype in the population [as discussed above we also find increased divergence in some cases with a best-of- n model (27), in which the mating success of rare males with rare females is relatively low; see also ref. 23 for best-of-2 with density-dependent diffusion].

Although these results, in which sexual selection promotes diversification, form the primary message of his paper, Lande (22) also found that diversification is impeded when preferences are for specific male phenotypes ("absolute" mating preferences), provided that the covariance between preferences and traits is less than the genetic variance in the trait itself. Our model, which considers discrete instead of quantitative preferences and traits, matches the results of this final case, in which differentiation is inhibited. This suggests that discrete genetics of sexual selection best correspond to absolute preferences in a quantitative genetic model (and that, perhaps not surprisingly, covariances during Fisherian sexual selection are generally lower than trait variation). Lande (22) did not allow for the evolution of preference strength, so it is uncertain what effect this would have in the quantitative genetic framework.

Our models confirm (22, 23) that when local adaptation (viability selection) is absent, and Fisherian sexual selection alone drives divergence, population differentiation is lost after secondary contact regardless of the preference strength. This is entirely consistent with theory that finds that Fisherian sexual selection alone is also unable to drive de novo speciation with gene flow (10, 11); additional conditions are required (26, 33). Our result stresses that the rapid gain of premating isolation that may occur by pure Fisherian sexual selection alone in allopatry (4, 7) is very fragile indeed.

The finding of an inhibitory role for Fisherian sexual selection on species maintenance in our situation of geographically isolated populations exchanging migrants, although counterintuitive, falls

in line with a growing body of literature that casts doubt upon the common perception of a positive contribution of sexual selection to speciation. Recent theoretical studies have found that sexual selection often impedes sympatric speciation by eroding trait variation or generating stabilizing selection on traits (11, 16–19, 39, 40). Sexual selection has also been found to be ineffective at driving continued divergence after secondary contact when females prefer males that match their own phenotype, rather than when there are separate female preference and male trait loci (41). Likewise, comparative studies of sexual selection and speciation, which generally include fully allopatric taxa in which the inhibitory effects described above cannot act, have yielded mixed results (42).

By adding support to the idea that premating isolation may often be readily reversible (43), the results presented here inform a long-standing controversy in the speciation literature: whether premating or postzygotic isolation is more important in speciation (44). The finding that sexual selection in its purest form will tend to erase divergence by local adaptation contrasts with the permanence of intrinsic postzygotic isolation. Speciation researchers should look past the most basic forms of Fisherian sexual selection to gain a better understanding of specific circumstances that might lead sexual selection to establish more permanent isolation and thus play a more substantial role in species maintenance.

Methods

Preference and Trait Divergence. We model a deterministic system of two haploid populations exchanging migrants (a "two-island" model) with one locus for a preference, P , and one locus for a trait, T , each with two alleles. The frequencies of the four resulting genotypes P_1T_1 , P_1T_2 , P_2T_1 , and P_2T_2 are designated x_1 , x_2 , x_3 , and x_4 , respectively.

The life cycle begins with symmetric migration of individuals between the populations at rate m , which describes the proportion of each population that consists of migrants right after the migration event (slight departures from symmetry in migration rates between the populations were not found to have qualitatively different effects on the results of the model). Thus, the frequency of genotype i in population k is

$$x_{i,k}^* = (1 - m)x_{i,l} + mx_{i,l}, \quad [3]$$

where $l = 2$ when $k = 1$ and $l = 1$ when $k = 2$.

Migration is followed by local adaptation of the characteristic trait allele to the environment of each population. Thus, in males allele T_k is favored in population k with relative fitness $1 + s_k$. After this viability selection the genotypic frequencies in males (represented by subscript m) in population k are therefore

$$x_{i,k,m}^{**} = \frac{(1 + ds_k)x_{i,k}^*}{1 + s_k t_k^*}, \quad [4]$$

where $d = 1$ if genotype x_i has allele T_k and $d = 0$ otherwise (t_k^* represents the frequency of allele T_k after migration). The selection coefficients were generally set so that $s_1 = s_2$ (such symmetric viability selection is a best-case scenario for population differentiation; simulation results indicate that slight departures from symmetry in local adaptation do not qualitatively alter the results). As described above, the model was also analyzed assuming no local adaptation (sexual selection alone), by setting $s_1 = s_2 = 0$. Viability selection does not occur in females in the main model, so $x_{i,k,f}^{**} = x_{i,k}^*$ (but see *SI Text* for a version of the model in which the trait is expressed and selected upon in both sexes).

Fisherian sexual selection follows viability selection. Specifically, across both populations, allele P_i causes a female to be $1 + a_i$ times as likely to mate with a T_i male than with a male with the other trait allele if she encounters one of each. The preference alleles thus have the same effect regardless of the population in which they are found. This female choice results in a 4×4 matrix \mathbf{M} , the elements of which are the proportion of matings occurring between each pair of genotypes i in males and j in females, such that

$$M_{ij,k} = \frac{x_{i,k,m}^{**} x_{j,k,f}^{**} (1 + ba_1)(1 + ca_2)}{\sum_i x_{i,k,m}^{**} (1 + ba_1)(1 + ca_2)}, \quad [5]$$

where $b = 1$ if i is odd and $j = 1$ or 2 and $b = 0$ otherwise, and $c = 1$ if i is even and $j = 3$ or 4 and $c = 0$ otherwise. The normalization in the denominator

ensures that every female has equal mating success. For most of the analysis of the system $\alpha_1 = \alpha_2$. Spot checks of weakly asymmetric cases ($\alpha_1 \neq \alpha_2$) produce only weak deviations from the patterns with complete symmetry. Versions of this model that include costs to preferences incurred by lost mating opportunities (e.g., search costs) and that use a best-of- n searching algorithm are both described in *SI Text*.

Recombination and segregation follow mating, modeled using standard two-locus, two-allele equations for haploids, and leading to the production of zygotes in the next generation. Details of the numerical analysis of all model versions, which consisted of exact iterations of the recursion equations, are described in *SI Text*, as are details of approximations with weak and strong selection. All analyses were performed using *Mathematica* (45). Notebooks are archived in Dryad under 10.5061/dryad.mn643.

The Evolution of Preference Strength. Here we add an additional locus, A , which controls the strength of mating preferences in the system. Specifically, when allele A_1 at this locus is fixed in a population, the model behaves according to the equations in the two-locus model described above. P_1 and P_2 females that carry the A_2 allele instead have preference strengths of $1 + \alpha_3$ and $1 + \alpha_4$, respectively. There is no restriction on the relative strength of the four α parameters, although for most of the analyses $\alpha_3 = \alpha_4$ (simulations yield qualitatively identical results with slight departures from symmetry).

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In this three-locus system there are eight genotypes, ordered such that $A_1P_1T_1$, $A_1P_1T_2$, ... $A_2P_2T_2$ are represented by the frequencies x_1, x_2, \dots, x_8 , respectively. Eqs. 3 and 4 still hold. Mating now results in an 8×8 matrix \mathbf{M} , where the proportion of matings occurring between genotypes i in males and j in females is

$$M_{ij,k} = \frac{x_{i,k,m}^{**} x_{j,k,f}^{**} (1 + b\alpha_1)(1 + c\alpha_2)(1 + e\alpha_3)(1 + g\alpha_4)}{\sum_l x_{l,k,m}^{**} (1 + b\alpha_1)(1 + c\alpha_2)(1 + e\alpha_3)(1 + g\alpha_4)}, \quad [6]$$

where $b = 1$ if i is odd and $j = 1$ or 2 and $b = 0$ otherwise, $c = 1$ if i is even and $j = 3$ or 4 and $c = 0$ otherwise, $e = 1$ if i is odd and $j = 5$ or 6 and $e = 0$ otherwise, and $g = 1$ if i is even and $j = 7$ or 8 and $g = 0$ otherwise. Again the normalization in the denominator ensures strict polygyny. Recursion equations for the genotype frequencies are generated using the standard equations for free recombination and segregation, assuming three loci with two alleles each in haploids.

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Supporting Information

Servedio and Bürger 10.1073/pnas.1316484111

SI Text

The Effect of Sexual Selection on the Maintenance of Population Differentiation After Secondary Contact

Numerical Analysis, Basic Model. The models were primarily analyzed by numerical iterations of the exact recursion equations, run on *Mathematica* (1). We are particularly interested in the scenario of secondary contact in which alleles P_1 and T_1 are initially predominant in population 1 whereas alleles P_2 and T_2 are predominant in population 2. For a given set of parameter values, simulations were run with all pairwise starting combinations of allele frequencies of the T_2 and P_2 alleles in population 2 from the set $\{0.51, 0.6, 0.7, 0.8, 0.9, 0.99\}$ and linkage equilibrium. For all runs for a particular set of parameter values equilibrium values were found to match to within a difference in frequency of 0.001 regardless of these starting conditions. This indicates that the equilibria reached are robust to significant differences between the starting trait and preference frequencies (provided these are both noticeably above 0.5) and are very likely to be unique within these constraints. This has been further supported by multiple applications of the numerical equation-solving procedure FindRoot in *Mathematica*.

To ensure that the results did not depend on symmetry in the starting conditions between the populations, the starting frequency of the P_1 allele in population 1 was set as $p_{2,2}^0 + d$, where $p_{2,2}^0$ is the starting frequency of P_2 in population 2 and d is a deviation from symmetry (values of d between 0.001 and 0.02 were tested with no qualitative differences in the results, and d was then generally set at 0.001 to speed up computation time). Likewise the starting frequency of the T_1 allele in population 1 was set as $t_{2,2}^0 + 1.001d$, where $t_{2,2}^0$ is the starting frequency of T_2 in population 2. Runs were considered to have been completed when the difference between two subsequent generations in the frequency of the preference and trait alleles in either population had an absolute value of less than 10^{-9} .

Our aim is to examine whether stronger preferences decrease differentiation between populations. We thus focus, as reported in the main text, on situations at or close to symmetry in local adaptation (s_1, s_2) and preference (α_1, α_2) parameters because they present the best cases for preference and trait divergence. Indeed we find that simulations with large deviations from symmetry between the two adaptation parameters or between the two preference strength parameters lead to convergence in preferences and traits between the two populations [e.g., traits and preferences from populations 1 and 2 may both reach frequencies on the same side of 0.5; this was determined by spot checking deviations from symmetry in a small number of cases, ~ 35 parameter combinations, in addition to the ones described below for slight deviations from symmetry (see also the *Search Costs* section)]. Sexual selection thus also does not lead to divergence under very asymmetric conditions, although the patterns are different from those in the cases that are the focus of this study.

For example, we briefly investigated the role of unequal preferences, assuming strong preference strength. By fixing all parameters except α_2 , we found that increasing preference strength (α_2) leads to a decrease in the equilibrium frequencies of the corresponding preference and trait alleles (here, P_2 and T_2) in both populations. For instance, if $s = 0.2$, $m = 0.01$, $r = 0.5$, and $\alpha_1 = 50$, the frequencies of P_2 and T_2 in population 2 decrease from 0.888 and 0.900 respectively (for $\alpha_2 = 10$) to 0.324 and 0.326 respectively (for $\alpha_2 = 100$). The frequencies of both of these alleles are slightly smaller in the other population, where differentiation

is very weak. A lower migration rate ($m = 0.002$) has a very weak effect on the allele frequencies and increases differentiation only by a very small amount.

Altogether over 19,600 simulations were run and all results were consistent with those reported in the main text. The large majority of runs were performed in sets of 36 starting conditions per parameter set and were explorations of preference strength $\alpha_1 = \alpha_2$ for a given combination of migration and selection (see ranges below; many additional runs were done to narrow down the strength of preference that leads to peak preference divergence for Fig. S4). We also included ~ 500 runs (14 parameter sets with 36 sets of starting conditions each) with slight deviations from symmetry in the migration rates between the populations, $\sim 1,000$ runs with slight asymmetries in preference strengths, and ~ 500 runs with slight asymmetries in selection strengths, in addition to the spot checks with larger deviations described above. Parameter ranges investigated included migration rates m from the set $\{0.001, 0.01, 0.02, 0.05, 0.1, 0.2\}$, the selection coefficient for local adaptation s from the set $\{0.01, 0.05, 0.1, 0.2, 0.3, 0.5, 0.7, 0.9, 1.2, 1.5, 1.7, 2.0\}$, and preference strengths α between 0 and 200 (including in all cases all values of the set $\{0.001, 0.01, 0.1, 0.2, 0.5, 1, 2, 3, 5, 10, 20, 50, 100\}$).

The Net Selection Coefficient. Given the assumptions of the basic model, and using the notation of Barton and Turelli (2), the coefficient that describes net selection, from both natural and sexual selection, on the trait locus T is

$$a_{2,0T} = \frac{g(1 + bt_{2,2}^*) + cp_{2,2}^*}{(1 + \alpha_1 + gt_{2,2}^*)(1 + bt_{2,2}^*)}, \quad [S1]$$

where the coefficients $b = s + \alpha_2 + s\alpha_2$, $g = s - \alpha_1$, and $c = (1 + s)(\alpha_1 + \alpha_2 + \alpha_1\alpha_2)$. An asterisk indicates allele frequencies after migration. Thus, $t_{2,2}^* = mt_{2,1} + (1 - m)t_{2,2}$, $p_{2,2}^* = mp_{2,1} + (1 - m)p_{2,2}$, and $D_2^* = mD_1 + (1 - m)D_2 + m(1 - m)(p_{2,1} - p_{2,2})(t_{2,1} - t_{2,2})$ (equation 32 in ref. 3). The coefficients b and c are always positive, whereas g is negative if $\alpha_1 > s$. Because $1 + bt_{2,2}^* > 0$ and $1 + \alpha_1 + gt_{2,2}^* = 1 + \alpha_1(1 - t_{2,2}^*) + st_{2,2}^* > 0$, $a_{2,0T}$ is negative if and only if its numerator is negative. The latter is often the case if α_1 is much larger than s (Fig. S2), as would occur with strong sexual selection, because then g is highly negative.

Quasi-Linkage Equilibrium Analysis. In addition to numerical simulations, a weak selection analysis was performed to find an approximate equilibrium for the frequency of P_2 in population 2 and P_1 in population 1 when the selection coefficient for local adaptation s , the preference strengths $\alpha_1 = \alpha_2 = \alpha$, and the migration rate m are small. Using a perturbation analysis, the quasi-equilibrium value for the linkage disequilibrium in population i can be written as

$$D_{i,QLE} = \frac{m(1 - r)(p_{2,i} - p_{2,j})(t_{2,i} - t_{2,j}) + \alpha r p_{2,i}(1 - p_{2,i})t_{2,i}(1 - t_{2,i})}{r}, \quad [S2]$$

where the index j refers to the allele frequency in the other population and r is the recombination rate between the P and T loci. There is a curve of equilibria in each population to this order of approximation. If we apply the constraint that $p_{2,1} = 1 - p_{2,2}$ and $t_{2,1} = 1 - t_{2,2}$, the approximate equilibrium for the preference frequency in each population is $p_{1,i} = p_{2,i} = 1/2$. This

confirms that preference differentiation is expected to be very weak between the two populations when local adaptation is insignificant and is consistent with the results reported in the main text regarding the inability to maintain preference differentiation under the conditions of sexual selection alone. The trait frequency at QLE is

$$t_{2,2} = \frac{1}{2} - \frac{2m}{s} + \sqrt{\left(\frac{1}{2}\right)^2 + \left(\frac{2m}{s}\right)^2}, \quad [\text{S3}]$$

which is independent of the preference strength α . The value of linkage disequilibrium at QLE is thus

$$D_{2,\text{QLE}} = \frac{cm}{s} \left(\sqrt{\left(\frac{1}{2}\right)^2 + \left(\frac{2m}{s}\right)^2} - \frac{2m}{s} \right). \quad [\text{S4}]$$

Notably, the above equilibrium values are independent of the recombination rate r . It can be shown that this is true in general, although the recursion relations depend on r . The inherent model symmetry when the parameters are set symmetrically suggests that $p_{2,1} = 1 - p_{2,2}$, $t_{2,1} = 1 - t_{2,2}$, and $D_1 = D_2$ hold at polymorphic equilibria. Therefore, it is sufficient to solve the equations

$$\Delta p_{2,2} = 0, \quad \Delta t_{2,2} = 0, \quad \Delta D_2 = 0. \quad [\text{S5}]$$

It can be shown that

$$\Delta p_{2,2} = \Delta t_{2,2} \frac{D_2}{t_{2,2}(1 - t_{2,2})}$$

and

$$\Delta D_2 = \Delta p_{2,2} \left[1 - (2 + U)t_{2,2} + Ut_{2,2}^2 \right] + rV,$$

where $U = \Delta t_{2,2}/[t_{2,2}(1 - t_{2,2})]$, V is a complicated term, and $\Delta t_{2,2}$ is independent of r . It follows that if the allele frequencies are at equilibrium, the term in ΔD_2 that is independent of r vanishes, whence the equilibrium value of D_2 is obtained from the condition $V = 0$, which is independent of r . An analogous argument has been made by Kirkpatrick (4) in the absence of migration.

Approximation of Equilibrium Frequencies for Strong Preferences.

Here we assume that the preference α is much stronger than selection on the male trait (s) and the other evolutionary forces, i.e., recombination (r) and migration (m). Again, we assume that $p_{2,1} = 1 - p_{2,2}$, $t_{2,1} = 1 - t_{2,2}$, and $D_1 = D_2$ hold at equilibrium.

To implement the above assumption, we set $s = \varepsilon\sigma$, $m = \varepsilon\mu$, and $r = \varepsilon\rho$ in [S5] and develop the left-hand sides to Taylor series of first order in ε . Returning to the original parameters, we obtain the equilibrium equations governing the ‘‘strong-preference limit.’’ They are still very complicated, so we do not present them. However, a *Mathematica* notebook is available on Dryad.

Now we set $p_{2,2} = 1/2 + x/\alpha$ and $t_{2,2} = 1/2 + y/\alpha$, substitute into the equilibrium equations of the strong-preference limit, and solve for x , y , and D . The solution is $x = y = s/(4m)$ and $D = (\alpha - 2\sqrt{\alpha - 1})/[4(\alpha - 2)]$. Comparison with numerically determined solutions shows that x and y do not yet give satisfactory approximations, whereas the expression for D is quite accurate. To produce a better approximation, it turns out that we have to set $p_{2,2} = 1/2 + s/(4m\alpha) + x_1/\alpha^{3/2}$, $t_{2,2} = 1/2 + s/(4m\alpha) + y_1/\alpha^{3/2}$, and $D = (\alpha - 2\sqrt{\alpha - 1})/[4(\alpha - 2)] + z_1/\alpha^{3/2}$ and proceed as above.

The result is the following approximation for the equilibrium solution:

$$p_{2,2} \approx \frac{1}{2} + \frac{s}{4m\alpha} - \frac{s(\sqrt{\alpha}(1 + 2m) + 6m - 2)}{4m(2m\sqrt{\alpha} + 1 - 2m)} \frac{1}{\alpha^{3/2}}, \quad [\text{S6a}]$$

$$t_{2,2} \approx \frac{1}{2} + \frac{s}{4m\alpha} - \frac{s(1 - 2m)(\sqrt{\alpha}(1 + 2m) + 6m - 2)}{4m(1 + 2m)(2m\sqrt{\alpha} + 1 - 2m)} \frac{1}{\alpha^{3/2}}, \quad [\text{S6b}]$$

$$D_2 \approx \frac{1}{4} - \frac{1}{2\sqrt{\alpha}} + \frac{1}{2\alpha} - \frac{1}{4\alpha^{3/2}} + \frac{1}{\alpha^2}. \quad [\text{S6c}]$$

Notably, linkage disequilibrium depends only on the strength of the preference.

We assume that s is negligibly small, so that $p_{2,2} \approx 1 - p_{2,1} \approx 1/2$. Then the recursion relations yield the equilibrium value

$$D_1 = D_2 \approx \frac{2 + \alpha - 2\sqrt{\alpha + 1}}{4\alpha}. \quad [\text{S6d}]$$

This has the series expansion [S6c] but yields an approximation to the linkage disequilibria that is much more accurate than [S6c] if $\alpha \leq 20$. Because [S6a] and [S6b] are obtained by series expansion, they are independent of whether [S6c] or [S6d] is used.

The approximations [S6] are plotted against results of the numerical iterations of the exact recursion equations in Fig. S1. [S6] yields more accurate approximations for smaller values of α than in Fig. S1 if s/m is smaller.

We also note that the coefficient of $\alpha^{-3/2}$ of $p_{2,2}$ has a series expansion of the form $-s(1 + 2m)/(8m^2) + \tilde{x}/(2\sqrt{\alpha}) + O(1/\alpha)$. (and analogously for $t_{2,2}$). However, for small m it yields a much less accurate approximation than the more complicated expression in [S6a]. The reason is that in the limit $m \rightarrow 0$, the dynamical equations become degenerate because a curve of equilibria exists if $m = 0$.

Search Costs. The basic model presented above was modified to include costs to preferences in the form of search costs incurred from lost mating opportunities (using the form from ref. 5). However, we assumed symmetry, i.e., $\alpha_1 = \alpha_2 = \alpha$ and $s_1 = s_2 = s$. Search costs appear more reasonable to apply than absolute costs to preferences in this model, because both preference alleles P_1 and P_2 code for preferences of similar strengths (just for different types of males).

An initial matrix of mating coefficients was generated for genotypes i in males and j in females as

$$C_{ij} = \frac{1 + b\alpha}{1 + \alpha}, \quad [\text{S7}]$$

where $b = 1$ if (i) i is odd and $j = 1$ or 2 or (ii) i is even and $j = 3$ or 4 . Otherwise, $b = 0$. Incorporating costs, a matrix \mathbf{Q} is defined as $\mathbf{Q}_{ij,k} = \gamma_{j,k} \mathbf{C}_{ij}$, where relative costs γ are set as

$$\gamma_{j,k} = \frac{1 - \left(1 - \sum_i \mathbf{C}_{ij} x_{i,k,m}^{**}\right)^N}{\sum_i \mathbf{C}_{ij} x_{i,k,m}^{**}}; \quad [\text{S8}]$$

cf. equation 9 in ref. 6. Here N represents a fixed number of encounters that a female has before the end of the mating period. The resulting matrix of the proportion of matings occurring between each pair of genotypes i in males and j in females is $\mathbf{M}_{ij,k} = \mathbf{Q}_{ij,k} x_{i,k,m}^{**} x_{j,k,f}^{**}$; this replaces Eq. 5 in *Methods* in the main text.

Table S1 shows the effects of costs incurred by restricting mating opportunities, using a number of encounters N of 5, 10, 25, 50, or 100 males. We tested 10 different sets of starting conditions (Table S1). The results fall into three categories: (i) equilibria reached represent weak discrimination between populations (the equilibrium frequencies for traits and preferences in this case are very similar to those when $N = \infty$ as in Fig. 1; e.g., if $N = 100$ or 50 they are identical to those from $N = \infty$ to at least 6 digits, whereas if $N = 25$ the difference is at most 1%), (ii) the equilibria reached represent strong discrimination (P_k has a frequency of at least 70% in deme k , in most cases more than 95%), and (iii) one allele at the preference and at the trait locus is fixed across both populations (variation is lost). Which of the three types of equilibria is reached may depend on starting conditions. Higher asymmetry in the starting conditions favors convergence to a fixation equilibrium. High symmetry appears to slightly favor convergence to strong discrimination if weak and strong discrimination equilibria coexist.

It can be concluded that the results of the basic model are generally robust to weak costs (e.g., $N = 50, 100$), although when local adaptation is strong, they can tend to lead to a loss of variation. Strong differentiation is not an outcome when costs are low. When costs are moderate (e.g., $N = 25$), they can lead to either weak or strong differentiation or to fixation of one set of alleles if preferences are very strong. High costs can lead to strong differentiation if preference strengths are moderate or large.

Expression of the Trait in Both Sexes. A version of the basic model was developed in which the trait at the T locus was expressed in both sexes. In this version Eq. 4 in the main text was applied to the frequencies in both males and females. Parameter ranges investigated included migration rates m from the set {0.001, 0.01, 0.02, 0.05, 0.1, 0.2}, the selection coefficient for local adaptation s from the set {0.01, 0.1, 0.2, 0.5, 0.9}, and preference strengths α from the set {0.001, 0.01, 0.1, 0.2, 0.5, 1, 2, 3, 5, 10, 20, 50, 100, 200}. Starting conditions were the same as described above for the basic model.

When the trait is expressed in both sexes, stronger preferences again lower the frequency of the locally adapted trait, but this result is reversed when preferences are already high (e.g., $\alpha > \sim 10$, Fig. S3 A and C). Once preference strength is high, stronger sexual selection instead leads to a rise in the frequency of a locally adapted trait. As opposed to the case in which the trait is expressed in only one sex, the frequency of the “local” preference generally rises monotonically when preferences are stronger (Fig. S3 B and D). These results can be understood as follows. Females with the foreign trait allele are more likely to die due to local adaptation because the trait is expressed in females in this version of the model. Importantly, stronger preferences, which lead to stronger linkage disequilibrium, make it more likely that these females carry the foreign preference allele as well. Stronger preferences thus lead to a higher frequency of the local preference allele, and this frequency will now be particularly high right before mating occurs (after local adaptation). The higher frequency of the local preference at the time of mating in turn leads to stronger sexual selection tending to favor the locally adapted trait allele, as opposed to the foreign one, when preferences are already strong. In contrast, when preferences are weak, the frequency of the foreign preference is still relatively high in each population when mating occurs, leading to sexual selection tending to reduce the frequency of the locally adapted trait, as seen in the basic version of the model.

When local adaptation is very weak (e.g., $s = 0.01$), we observed that the frequency of the local preference allele can dip at moderate preference strengths before it rises again with stronger preferences (Fig. S3D, *Inset*). This again indicates that local adaptation has to be sufficiently strong to allow viability selection on females to drive the frequency of the local trait and preference

upward; in the absence of sufficiently strong viability selection the drop in the frequency of the locally adapted trait will lead to a drop in the frequency of the preference, as seen in the basic version of the model.

Best-of- n . The models considered so far assume that females choose a mate from among all males in the population. We also developed a “best-of- n ” model in which females choose from among a subsample of only n males in the population. Following Seger (7), we define $U_{xy,k}$ for all y as the proportion of P_x females that ultimately mate with T_y males, in population k . For a given n , we can set $U_{xx,k}$ as the sum of weighted binomial probabilities across samples where the n males consist of j preferred individuals of type T_x , as

$$U_{xx,k} = \sum_{j=1}^n \binom{n}{j} (t_{x,k,m}^{**})^j (t_{y,k,m}^{**})^{n-j} \frac{1}{n} \left(1 + \frac{c(n-j)}{j}\right) \tag{S9}$$

$$= t_{x,k,m}^{**} + c \left(t_{y,k,m}^{**} - (t_{y,k,m}^{**})^n \right),$$

where now $y \neq x$, and $t_{i,k,m}^{**}$ is the frequency of T_i males (males are denoted by the subscript m , following the main text) in population k , after viability selection (denoted by the superscript **, again following the main text). The parameter c represents the strength of preference; if $c = 0$, females mate randomly whereas if $c = 1$, they mate only with a preferred male if one is encountered. The proportion $U_{xy,k}$, where $y \neq x$ and thus females are mating with unpreferred males, is accordingly set as

$$U_{xy,k} = \sum_{j=1}^n \binom{n}{j} (t_{x,k,m}^{**})^j (t_{y,k,m}^{**})^{n-j} \frac{n-j}{n} (1-c) + (t_{y,k,m}^{**})^n \tag{S10}$$

$$= t_{y,k,m}^{**} - c \left(t_{y,k,m}^{**} - (t_{y,k,m}^{**})^n \right).$$

The last term on the first line, $(t_{y,k,m}^{**})^n$, accounts for the possibility that no preferred males are encountered, in which case a preference is not applied. Following Seger (7), we set $U'_{xy,k} = U_{xy,k}/t_{y,k,m}^{**}$ for all y and define the matrix of mated pairs \mathbf{M} as

$$\mathbf{M}_{ij,k} = x_{i,k,m}^{**} x_{j,k,f}^{**} U'_{xy,k}, \tag{S11}$$

where if $j = 1$ or 2, then the subscript $x = 1$, and otherwise the subscript $x = 2$, and if $i = 1$ or 3, then $y = 1$, and otherwise $y = 2$.

We investigated this model with parameter ranges including the selection coefficient for local adaptation s from the set {0.1, 0.2, 0.5, 0.9}, preference strengths c from the set {0.001, 0.01, 0.1, 0.2, 0.3, 0.5, 0.9, 1.0}, and the number of males in the sample observed by females n from the set {2, 3, 5, 7, 10, 50}. We used the migration rate $m = 0.01$ throughout these simulations. Starting conditions were the same as for the basic model.

Seger (7) demonstrated that best-of- n models can behave very differently from the fixed relative preference models developed by Kirkpatrick (4) and Lande (8), and we also find differences in the maintenance of species differences (see also ref. 9 for differences between best-of- n and sequential models in a sympatric speciation scenario). The expressions $U'_{xy,k}$ in the best-of- n model are strongly dependent on trait frequency. Numerical examination of the mating matrix \mathbf{M} gives the insight that, at least with relatively low n , rare males often have much lower mating success with rare females in the best-of- n model than in our fixed relative preference model. The presence of rare (foreign) females in each population therefore does not give as big a fitness advantage to rare (foreign) males, and divergence would not necessarily be expected to be reduced as much with stronger preferences with best-of- n as in our original model. We find that

with very low n ($n = 2$) in fact stronger preferences (higher c) lead to more trait differentiation (Fig. S5). As n increases we find that variation in preferences is often lost with low c . As c increases and preference variation appears, we see a drop in the magnitude of trait differentiation as preferences increase from a moderate c , but with very high c increased preference strength can still lead to an increase in trait differences between populations. This inflection point, when present, was not seen to vary with the strength of local adaptation, s (tested with $n = 2, 3$), although in general lower s leads to lower trait differentiation as in the main model. The frequency of the local preference generally increased in our simulations with higher preference strengths. When we increased n past 5 in our simulations, we tended to lose variation in preferences or lose preference and trait differentiation between populations.

The Evolution of Preference Strength

This version of the basic model was analyzed by numerical iterations of the exact recursion equations, using *Mathematica* (1). First, an initial equilibrium in the frequencies p_2 and t_2 was established with allele A_1 fixed in the population for a given set of parameters m , s , and $\alpha_1 = \alpha_2$, to set the stage for the introduction of allele A_2 . Simulations were started with A_2 introduced at a frequency of 0.01, and all disequilibria were initially set at 0. For simplicity the starting frequencies for these initial runs were generally set to be symmetric in the two populations ($p_{1,1}^0 = p_{2,2}^0$ and $t_{1,1}^0 = t_{2,2}^0$). These runs were considered to have reached the initial equilibrium point when the difference between any of the genotypes in either of the two populations between two subsequent generations was less than 10^{-11} .

The values of p_2 and t_2 in each population at the initial equilibrium were used as the starting conditions for the introduction of allele A_2 at a low frequency. The subsequent results were found to be robust to small deviations in symmetry between the frequencies in each population in spot checks (e.g., $p_{1,1}^0 = p_{2,2}^0 + d$ and $t_{1,1}^0 = t_{2,2}^0 + d$, where $d = 0.001$). After the introduction of A_2 , each simulation was run until the difference between any of the genotypes in either of the two populations between two subsequent generations was less than 10^{-11} . For these simulations the migration rate was $m = 0.01$, and s was equal to 0.1, 0.2, or 0.5. All nonidentical pairwise combinations of $\alpha_1 = \alpha_2$ (coded for in populations 1 and 2, respectively, by allele A_1) and $\alpha_3 = \alpha_4$ (coded for in populations 1 and 2, respectively, by allele A_2 ; runs with slight deviations from symmetry such that $\alpha_3 \neq \alpha_4$ did not change the results) were chosen from the set of possible preference strengths $\{0, 0.01, 0.1, 0.2, 0.5, 1.0, 2.0, 5.0, 10.0\}$. In each case the allele A_i that coded for the higher value of α dropped to a frequency of below 10^{-6} in both populations by the end of the simulation. The disequilibrium between the A locus and the T locus was noted in test cases to be positive in population 2 but negative in population 1 when allele A_2 leads to lower preference strength and negative in population 2 but positive in population 1 when A_2 leads to higher preference strength (see ref. 10). As the locally adapted T allele increases in each population, it thus drags along the allele at the A locus that codes for lower preference strength in each population, due to these genetic associations. Because the value 0 was included in the possible preference strengths, these simulations indicate that the populations will eventually evolve random mating.

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Table S1. Summary of data with costs

α	$M = \infty$			$M = 100$			$M = 50$			$M = 25$			$M = 10$			$M = 5$		
	wd	sd	fix	wd	sd	fix	wd	sd	fix	wd	sd	fix	wd	sd	fix	wd	sd	fix
$s = 0.9$																		
0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0
0.001	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0
0.01	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0
0.1	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0
0.2	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0
0.5	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0
1	10	0	0	9	0	1	10	0	0	10	0	0	10	0	0	0	10	0
2	10	0	0	8	0	2	10	0	0	10	0	0	0	10	0	0	10	0
3	10	0	0	8	0	2	10	0	0	10	0	0	0	10	0	0	10	0
5	10	0	0	8	0	2	10	0	0	0	0	10	0	9	1	0	10	0
10	10	0	0	9	0	1	10	0	0	0	0	10	0	9	1	0	10	0
20	10	0	0	8	0	2	10	0	0	0	8	2	0	9	1	0	10	0
50	10	0	0	7	0	3	8	0	2	0	8	2	0	9	1	0	10	0
100	10	0	0	7	0	3	5	3	2	0	8	2	0	9	1	0	10	0
$s = 0.2$																		
0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0
0.001	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0
0.01	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0
0.1	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0
0.2	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0
0.5	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	0	0	10
1	10	0	0	10	0	0	10	0	0	10	0	0	1	0	9	0	0	10
2	10	0	0	10	0	0	10	0	0	10	0	0	1	0	9	0	9	1
3	10	0	0	10	0	0	10	0	0	10	0	0	0	1	9	0	9	1
5	10	0	0	10	0	0	10	0	0	10	0	0	0	9	1	0	9	1
10	10	0	0	10	0	0	10	0	0	9	0	1	0	9	1	0	9	1
20	10	0	0	10	0	0	10	0	0	7	0	3	0	9	1	0	9	1
50	10	0	0	10	0	0	9	0	1	4	3	3	0	9	1	0	9	1
100	10	0	0	10	0	0	9	0	1	4	4	2	0	9	1	0	9	1

Each table entry shows the number of initial conditions of the following set of 10, which display different degrees of symmetry, for which the result in the column headings was attained (in each set the positions represent the following starting values $\{p_{2,1}^0, t_{2,1}^0, D_1^0, p_{2,2}^0, t_{2,2}^0, D_2^0\}$): $\{(0.2, 0.15, 0.05, 0.8, 0.9, 0.04), \{0.1, 0.05, 0.005, 0.95, 0.92, 0.002\}, \{0.55, 0.6, 0.1, 0.4, 0.45, 0.05\}, \{0.11, 0.1, 0.01, 0.9, 0.91, 0.005\}, \{0.02, 0.01, 0.01, 0.99, 0.98, 0.005\}, \{0.1, 0.01, 0.01, 0.99, 0.9, 0.005\}, \{0.999, 0.098999, 0.0, 0.9, 0.9, 0.0\}, \{0.999, 0.008999, 0.0, 0.9, 0.99, 0.0\}, \{0.009, 0.098999, 0.0, 0.99, 0.9, 0.0\}, \{0.009, 0.008999, 0.0, 0.99, 0.99, 0.0\}\}$. Column headings are as follows: wd, weak differentiation of preferences between demes (closer to 50:50 than 30:70); sd, strong differentiation of preferences between demes (more than 30:70); fix, fixation of one or the other allele in the total population (P_1 and T_1 or P_2 and T_2). The entries in italicized type are close to the boundary between sd and wd. If the result is wd or sd, then there is precisely one equilibrium solution of this type; i.e., all runs categorized as wd (or sd) converged to the same equilibrium. If the result is fix, there are two possibilities, either fixation of P_1 and T_1 or fixation of P_2 and T_2 (depending on initial conditions). Equilibria falling into the category sd have very low values of D , in sharp contrast to the high values for equilibria in category wd (Fig. S1C). However, this is deceptive because equilibria of type sd typically have very low allelic variation. If D is normalized by its maximum possible value given the allele frequencies, $D/\max[p(1-t), t(1-p)]$, then this normalized linkage disequilibrium reaches values of up to 0.7 in category sd, which is not much smaller than the maximum values of about 0.8 found in category wd.