

## REINFORCEMENT AND SEX LINKAGE

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**Abstract.**—We present a general model for the effect of sex linkage on the evolution of reinforcement of mating preferences on an island. We find that the level of reinforcement can vary up to 80% depending on the mode of inheritance of the female preference and male trait. When reinforcement is driven mainly by selection in the male trait and intrinsic hybrid incompatibilities are weak, sex-linked preferences and autosomal male traits are the most conducive to reinforcement, whereas autosomal preferences and X-linked traits are the least. Surprisingly, the effect of mode of inheritance on reinforcement is poorly predicted by its effect on the genetic correlation between the male trait and female preference. Sex-linkage of genetic incompatibility loci increases reinforcement, though this is not due solely to the occurrence of Haldane's rule. We find that reinforcement can lead to complete reproductive isolation in some cases but not others and that the mode of inheritance can determine which outcome occurs.

**Key words.**—Good genes, hybrid incompatibility, mating preferences, quasi-linkage equilibrium, sexual selection.

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There is currently a renaissance of interest in the role that reinforcement plays in speciation (Kirkpatrick and Ravigne 2002; Servedio and Noor 2003; Coyne and Orr 2004). The interest was sparked largely by Coyne and Orr's (1989, 1997) reviews of mating behavior in sympatric and allopatric species pairs of *Drosophila* that found compelling evidence for reinforcement. Numerous other studies have subsequently found similar patterns in other groups, suggesting that reinforcement is common (reviewed in Coyne and Orr 2004).

A striking empirical observation is that the genes affecting female preferences and male display traits are often sex linked (Grula and Taylor 1980; Heisler 1984; Reinhold 1998; Iyengar et al. 2002; Lindholm and Breden 2002; but see Fitzpatrick 2004). It is plausible that sex linkage could have substantial effects on reinforcement. Theory has already established that sex linkage substantially alters the genetic correlation that arises between mating preferences and display traits (Kirkpatrick and Hall 2004), and it seems likely that it may influence other factors known to affect reinforcement.

Motivated by these considerations, this paper studies how reinforcement is impacted by the sex linkage of preference and display genes. Building on the island-continent model of reinforcement of Kirkpatrick and Servedio (1999), we develop a model that is quite general with regard to assumptions about genetics and behavior, though we do assume that selection is weak at individual loci and that the migration (or hybridization) rate is small. Although sex linkage causes the genetic correlation between mating preferences and display traits to vary over a five-fold range, we find that its overall impact on the level of reinforcement is moderate, up to 80%. A complementary study of the effects of sex linkage of hybrid incompatibility loci is presented elsewhere (Lemmon and Kirkpatrick 2006).

### THE MODEL

There are three sets of loci in our model: those affecting female preference, those affecting male display traits, and those affecting hybrid incompatibility. These sets are assumed to be disjoint, that is, there is no pleiotropy. There

can be any number of loci within each set. Each locus segregates two alleles, which we denote 0 and 1. Loci can be autosomal or sex linked. To simplify the comparison of different kinds of sex linkage, we assume all loci affecting the preference have the same mode of inheritance, and likewise for the display trait. We do not make this assumption for the set of incompatibility loci because many instances of hybrid incompatibility are known to involve both autosomal and sex-linked loci (reviewed in Coyne and Orr 2004).

We assume additive effects at each of the display trait and preference loci, but make no assumptions about the distribution of the effects of each locus. The display trait is expressed only in males. The incompatibility loci can have any form of gene action, including arbitrary patterns of dominance and epistasis. Selection coefficients (denoted by  $a$ ) are assumed to be much smaller than one. We make no assumptions about the rates of recombination among loci, except that linkage is not too tight relative to the selection coefficients.

The model allows for any type of mating system in which females determine what male they mate with. Our definition for the female mating preference is general: it can be any phenotypic aspect of the female that affects the type of male she is likely to mate. We will see that for our model a key quantity determined by the preference is  $\rho$ , the phenotypic correlation between the preference in females and the display trait in males in mated pairs. We assume the preference genes are free of direct selection. That is, a female's preference genotype does not alter her probability of survival or the number of eggs she lays. We make this assumption to isolate the effects of reinforcement in the absence of other evolutionary forces acting on the preference genes.

Our model follows the evolution of a population on an island that receives migrants from an unchanging continental population. Each generation, a fraction  $m$  of the individuals on the island arrive as migrants from the continent. We can also interpret  $m$  as a hybridization rate if we define it to be the frequency of matings between the focal species and pure individuals of the other species. This rate is assumed to be sufficiently small that swamping of alleles favored by selec-

tion on the island does not occur. That is,  $m$  is much smaller than the strength of selection acting at each locus on the island ( $m \ll a$ ).

The life cycle is migration, followed by natural selection, mating pair formation (sexual selection), and finally the production of offspring to begin the next generation. The population is censused at the zygote stage. Genetic drift and mutation are assumed to be weak enough that they can be neglected.

Hybridization with continental immigrants causes the preferences on the island to evolve toward those on the continent. Reinforcement, in contrast, favors the evolution of preferences that discriminate against mating with immigrants. We therefore seek to determine the difference between the mean preference on island, denoted  $\bar{P}$ , and the mean preference on the continent, denoted  $P^C$ , at equilibrium. This is our measure for the strength of reinforcement. Later in the paper we will relate this difference to the hybridization rate.

A detailed derivation of the model is given in Appendix 1. It is based on the quasi-linkage equilibrium (QLE) approximation of Barton and Turelli (1991) and Kirkpatrick et al. (2002), which can be consulted for the full details about the notation and approach. Briefly, we say that the genes at a given locus occupy different positions, depending on how they were inherited. At an X-linked locus  $i$ , for example, a female has two positions, one for the gene inherited from her mother, denoted  $i_{ff}$ , and one for that inherited from her father,  $i_{fm}$ . For the same X-linked locus, a male has only a single position, which carries the gene he inherited from his mother,  $i_{mf}$ . We use  $n_i$  to denote the number of positions at locus  $i$  (e.g.,  $n_i = 3$  for an X-linked locus in a diploid dioecious population).  $\mathbb{P}_f$  denotes the set of all positions carried by females that affect the preference (e.g., with  $n$  Z-linked loci, there are  $n$  positions in  $\mathbb{P}_f$ , while with  $n$  X-linked loci, there are  $2n$  positions).  $\mathbb{W}$  is the set of all positions under direct selection: those for the male trait and all others that affect hybrid fitness.

A key advantage of our approach is that it can accommodate all forms of selection and nonrandom mating. We use  $a_{\mathbb{A}}$  to denote the selection coefficients (both natural and sexual) acting on the positions in set  $\mathbb{A}$ . Given any particular assumptions about selection and mating, these selection coefficients can be calculated using the methods described by Kirkpatrick et al. (2002).

Finally, we use  $D'_{\mathbb{A}, \mathbf{j}}$  to denote the genetic association (linkage disequilibrium) after migration between positions in the set that includes  $\mathbb{A}$  and  $\mathbf{j}$ . Due to typeface limitations, single positions are indicated by bold characters rather than the double-struck characters used in Kirkpatrick et al. (2002).

### Reinforcement at Equilibrium

To find the equilibrium, we begin with an equation describing the per-generation change in the mean preference on the island. Appendix 1 shows that this change is

$$\Delta \bar{P} = m(P^C - \bar{P}) + \sum_{\mathbf{i} \in \mathbb{P}_f} b_{\mathbf{i}} \frac{1}{n_{\mathbf{i}}} \sum_{\mathbf{j}: \mathbf{j}=\mathbf{i}} \sum_{\mathbb{A} \subseteq \mathbb{W}} a_{\mathbb{A}} D'_{\mathbb{A}, \mathbf{j}}, \quad (1)$$

where  $\bar{P}$  is the average preference in females on the island and  $P^C$  is the average on the continent and  $b_{\mathbf{i}}$  is the difference

in the preference of carrying allele 1 rather than allele 0 at position  $\mathbf{i}$ . On the right, the terms involved in the summation are written in the notation of Kirkpatrick et al. (2002), which can be consulted for more detail. The outer summation includes one term for each of the positions  $\mathbf{i}$  in females affecting the preference. With  $n$  X-linked loci,  $\mathbf{i} \in \mathbb{P}_f$  is comprised of positions  $i_{ff}$  and  $i_{fm}$  at each of the  $n$  loci and thus contains  $2n$  elements. The second summation is over all positions  $\mathbf{j}$  that share the same locus as position  $\mathbf{i}$ , and the inner summation is over all sets and subsets of positions that experience direct selection in either sex.

Equation (1) shows that the preference evolves under the sway of two forces. One is introgression, represented by the first term on the right. This force draws the preference toward the value of the continental population. In our model, introgression is caused by the migration of continental individuals onto the island, but the exact same force acts on a population that is hybridizing with another species with which it co-occurs. The second term on the right represents the impact on the preference of all forms of selection acting on the genome. Although the preference genes are selectively neutral (by assumption), indirect selection acts on them via their statistical associations (the  $D$  values) with other genes under direct selection. These other genes include the display trait and all hybrid incompatibility genes. The associations are created by introgression (or migration) and, in the case of the associations with display trait genes, by sexual selection. Although the preference is only expressed in females, it experiences indirect selection in both sexes.

To measure reinforcement, we set equation (1) to zero to solve for the difference in the mean preference of the island and mainland at equilibrium. It is convenient to standardize this difference by the phenotypic standard deviation of the preference,  $\sigma_P$ , which expresses the result as a dimensionless quantity that allows comparisons across different taxa and different types of preferences (Kirkpatrick and Servedio 1999). At equilibrium, this measure is either zero, in which case there is no reinforcement, or positive, indicating reinforcement has evolved. An equilibrium value of 0.2, for example, would indicate that the preference on the island is 0.2 standard deviations greater than the preference on the continent. Using this measure of reinforcement, we obtain

$$\frac{(\hat{P} - P^C)}{\sigma_P} = \frac{\sqrt{F_P(1 - F_P)} \beta_T \hat{r}_{PT}^{m'} \sqrt{\hat{G}_T} h_P}{[1 - F_P I_f - (1 - F_P) I_m] m} + O(a^2), \quad (2)$$

where  $\hat{P}$  is the mean preference on the island at equilibrium and  $O(a^2)$  denotes terms that are of the order of  $a^2$ . In the numerator on the right,  $F_P$  is the proportion of preference genes carried in females (e.g.,  $2/3$  for X-linkage),  $\beta_T$  is the lifetime directional selection gradient acting on the male display trait,  $\hat{r}_{PT}^{m'}$  is the QLE value of the genetic correlation in males between the preference and trait after migration,  $\hat{G}_T$  is the equilibrium additive genetic variance for the display trait in males, and  $h_P$  is the square root of the heritability of the female preference. In the denominator,  $F_P I_f$  and  $(1 - F_P) I_m$  are, respectively, the effect of incompatibility on reinforcement through females and males (see Appendix 1). These terms are either zero or positive, implying that genetic incompatibility acts to increase the level of reinforcement at

equilibrium. The values of  $I_f$  and  $I_m$  depend on the strength of selection at the incompatibility loci, the mode of inheritance of both the preference and incompatibility loci, and the level of recombination between them. Methods for calculating their values are given in Lemmon and Kirkpatrick (2006). Several of these quantities are dynamic (e.g.,  $\beta_T$  and  $\hat{r}_{PT}^m$ ). Equation (2) implicitly assumes their equilibrium values, and we give explicit expressions for them below.

This result shows immediately that the amount of reinforcement is changed by sex linkage of the preference.  $F_p$ , which is the fraction of preference genes carried by females, is 1/2 when preferences are autosomal. For every other mode of inheritance, however,  $F_p$  has a value other than 1/2, and so the amount of reinforcement will be different. We will see shortly that other terms in equation (2) are also affected by sex linkage of the preference and trait.

One important result is immediately obvious from equation (2). Reinforcement can evolve even in the absence of genetic hybrid incompatibility, that is, when the term  $F_p I_f + (1 - F_p) I_m$  is zero, because hybrids have suboptimal values of the male display trait. Even in the absence of those incompatibilities, island females that avoid mating with migrants produce sons with higher fitness than females that mate with migrants. Reinforcement in this case evolves in response to these extrinsic incompatibilities.

We can make further progress by calculating explicit expressions for the selection gradient,  $\beta_T$ , and the genetic correlation between the male trait and female preference,  $\hat{r}_{PT}^m$ . Appendix 3 shows that at equilibrium the selection gradient is

$$\beta_T \approx \frac{m(\hat{T} - T^C)}{(1 - F_T)\hat{G}_T}, \quad (3)$$

where  $\hat{T}$  and  $T^C$  are, respectively, the mean of the display trait in males on the island and continent at equilibrium, and  $F_T$  is the proportion of display trait genes carried in females (e.g., 1/2 for autosomal and 2/3 for X-linked traits). Under our weak migration assumption, the average phenotypic value of the male display on the island at equilibrium is close to its optimal value on the island, and thus  $(\hat{T} - T^C)$  will not differ significantly under different modes of inheritance of the male display trait.

The genetic correlations under different modes of inheritance are calculated in Appendix 2 and given in Table A1 of the Appendix. The expressions for the correlations contain two terms. One is identical to that found by Kirkpatrick and Hall (2004, table 1) and represents the contribution of sexual selection to the genetic correlation. The other term captures the contribution to the genetic correlation that is due to migration. With our assumption that the migration rate is much smaller than the strength of selection ( $m \ll a$ ), the effect of migration on the genetic correlation is small, and we thus use the values for the genetic correlation calculated in Kirkpatrick and Hall (2004) to simplify the remainder of the analysis:

$$\hat{r}_{PT}^m \approx \frac{k}{2} h_p h_T \rho, \quad (4)$$

where  $h_p$  and  $h_T$  are the square roots of the heritability for the preference and trait, respectively, and  $\rho$  is the phenotypic

correlation between the preference in females and display trait in males among mated pairs;  $k$  is a constant factor that varies with the mode of inheritance for the preference and display trait genes, and it is given in column 3 of Table 1.

Substituting those results into equation (2), we find that the amount of reinforcement at equilibrium is

$$\frac{(\hat{p} - p^C)}{\sigma_p} = \frac{\sqrt{F_p(1 - F_p)} h_p^2 \rho k (\hat{T} - T^C)}{2[1 - F_p I_f - (1 - F_p) I_m](1 - F_T) \sigma_T} + O(a^2). \quad (5)$$

A comparison of the level of reinforcement for different modes of inheritance obtained from equation (5) is shown in Table 1 (column 6).

This result is quite general: it allows for any number of loci, any form of female choice, and any form of selection against hybrids. Given values for the parameters that appear on the right of equation (5), we can predict how many phenotypic standard deviations the preference will evolve in response to reinforcement.

The predicted level of reinforcement depends upon a number of terms, each of which appears in equation (5) in an intuitive manner. In the numerator, the fraction of preference genes carried in females,  $F_p$ , enters the equation such that there is no reinforcement when  $F_p$  is zero or one. When  $F_p = 0$ , the preference cannot evolve because females carry no genes for it. When  $F_p = 1$ , the only correlation causing the evolution of female preference is between the preference and hybrid incompatibility in females. This correlation is proportional to the difference in the preference on the island and continent, which is reduced each generation by migration and thus precludes reinforcement at equilibrium. The heritability of the female preference also appears in the numerator because the higher its value, the more that the preference can respond to selection and thus the higher the level of reinforcement.

The other terms in the numerator of equation (5) are the phenotypic correlation between the preference and display among mated pairs ( $\rho$ ), the constant that reflects the mode of inheritance ( $k$ ), and the mean trait difference between the island and continent ( $\hat{T} - T^C$ ). The larger the phenotypic correlation between the male display trait and female preference in mated pairs, the stronger the sexual selection. The  $k$  factor relates the strength of sexual selection to the size of the genetic correlation between the female preference and male display in males given the modes of inheritance of the preference and display (eq. 4). The larger the value of  $k$ , the larger the genetic correlation and the more the female preference will evolve in response to selection acting on the male display. The trait difference between the island and continent allows females to distinguish migrant and resident males. As the difference in the mean trait increases, island females can better distinguish (and avoid) migrant males, particularly if the mean trait difference is large relative to the phenotypic standard deviation in the display, increasing the fitness of their offspring and resulting in higher levels of reinforcement.

In the denominator of equation (5) are two terms, one involving intrinsic incompatibilities and the other involving the proportion of trait loci found in males ( $1 - F_T$ ). As expected, intrinsic incompatibilities act to enhance the level

TABLE 1. The level of reinforcement on the island under different modes of inheritance. Columns 1 and 2 show the mode of inheritance of the preference and male display trait respectively. Column 3 gives the value of the constant  $k$  that varies with the mode of inheritance for the preference and display trait genes. The relative size of the genetic correlation between the male display trait and female preference is found by multiplying  $k$  by  $\frac{1}{2}h_p h_T \rho$  (Appendix 2; Kirkpatrick and Hall 2004). Columns 4 and 5 give the proportion of preference positions found in females or trait positions in males respectively. Column 6 shows the level of reinforcement expected under the different modes of inheritance. Note that  $I = F_p I_f + (1 - F_p) I_m$ . Column 7 is the amount of reinforcement expected under different modes of inheritance, relative to the case where both the preference and trait loci are autosomal, assuming that the heritabilities of the preference and trait and  $(\hat{T} - T^C)$  do not vary with mode of inheritance and that  $I_f$  and  $I_m$  are sufficiently small that they can be ignored. A, loci are autosomal; X, loci are on the X chromosome, the (usually large) sex chromosome present found in both sexes in species with heterogametic males (such as mammals and flies); Y, loci are on the Y chromosome, which is present only in males in species with heterogametic males; Z, loci are on the Z chromosome, the (usually larger) sex chromosome present in both sexes in species with heterogametic females (such as birds and butterflies); W, loci are on the W chromosome, which is present only in females in species with heterogametic females.

Preference	Trait	$k$	$\sqrt{F_p(1 - F_p)}$	$(1 - F_T)$	Reinforcement	Relative reinforcement
A	A	1	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{h_p^2 \rho (\hat{T} - T^C)}{2(1 - I)\sigma_T}$	1
	X	$\frac{2}{5} = 0.4$	$\frac{1}{2}$	$\frac{1}{3}$	$\frac{3h_p^2 \rho (\hat{T} - T^C)}{10(1 - I)\sigma_T}$	$\frac{3}{5} = 0.6$
	Z	$\frac{6}{5} = 1.2$	$\frac{1}{2}$	$\frac{2}{3}$	$\frac{9h_p^2 \rho (\hat{T} - T^C)}{20(1 - I)\sigma_T}$	$\frac{9}{10} = 0.9$
	Y	2	$\frac{1}{2}$	1	$\frac{h_p^2 \rho (\hat{T} - T^C)}{2(1 - I)\sigma_T}$	1
X	A	$\frac{\sqrt{32}}{5} = 1.13$	$\frac{\sqrt{2}}{3}$	$\frac{1}{2}$	$\frac{8h_p^2 \rho (\hat{T} - T^C)}{15(1 - I)\sigma_T}$	$\frac{16}{15} = 1.07$
	X	$\frac{1}{\sqrt{2}} = 0.707$	$\frac{\sqrt{2}}{3}$	$\frac{1}{3}$	$\frac{h_p^2 \rho (\hat{T} - T^C)}{2(1 - I)\sigma_T}$	1
	Y	$\sqrt{2} = 1.41$	$\frac{\sqrt{2}}{3}$	1	$\frac{h_p^2 \rho (\hat{T} - T^C)}{3(1 - I)\sigma_T}$	$\frac{2}{3} = 0.67$
Z	A	$\frac{\sqrt{32}}{5} = 1.13$	$\frac{\sqrt{2}}{3}$	$\frac{1}{2}$	$\frac{8h_p^2 \rho (\hat{T} - T^C)}{15(1 - I)\sigma_T}$	$\frac{16}{15} = 1.07$
	Z	$\sqrt{2} = 1.41$	$\frac{\sqrt{2}}{3}$	$\frac{2}{3}$	$\frac{h_p^2 \rho (\hat{T} - T^C)}{2(1 - I)\sigma_T}$	1
W	A	—	0	$\frac{1}{2}$	0	0
	Z	—	0	$\frac{2}{3}$	0	0

of reinforcement, because there is a greater advantage to avoiding hybridization if there are intrinsic as well as extrinsic incompatibilities. As the proportion of trait loci found in males increases, the display trait loci spend more time under selection and the mean male trait will be closer to its optimum. The closer the male trait is to its optimum, the smaller the selection gradient and the less it responds to selection. If the male trait responds less, the correlated response of the female preference will also be less, leading to less reinforcement.

*Reinforcement under Different Modes of Inheritance*

In principle, we can use these results to determine how reinforcement changes depending on how the preference and trait are inherited. To do that, we would evaluate equation (5) using values for the parameters appropriate to the different cases. We do not yet have data, however, for several of the parameters from any population. Until those data become available, we can make further progress by making the sim-

plifying assumption that the only factors that are systematically affected by sex linkage are  $F_p$  (the fraction of preference alleles carried by females),  $F_T$  (the fraction of display trait alleles carried by females), and  $k$  (the constant factor that depends on the mode of inheritance). We will assume that the other parameters, such as the heritability of the preference, do not change systematically with sex linkage. If data or theory become available that allow us to predict how those parameters change with sex linkage, those results can be used with equation (5) in place of this simplifying assumption.

A second simplification we will make at this point is to assume that hybrid incompatibility is very weak ( $I_m, I_f \ll 1$ ), so that reinforcement is driven only by selection on the male trait. This allows us to avoid having to specify how the hybrid incompatibilities are inherited, which is a factor that interacts with the sex linkage of the trait and preference. We relax this assumption in the next section to study several specific kinds of hybrid incompatibilities, and further results can be found in Lemmon and Kirkpatrick (2006).



TABLE 2. The fitness of the various genotypes with two hybrid incompatibility loci. For simplicity, we assume selection coefficients in males and females are the same, and that loci have equal effects. We assume complete dosage compensation such that hemizygosity and homozygosity are equivalent phenotypically. With one locus sex-linked, the homogametic sex exhibits the same fitnesses as with two autosomal loci. The continental alleles,  $A_0$  and  $B_0$ , are assumed to be fixed on the continent and the island alleles,  $A_1$  and  $B_1$ , are assumed to be at high frequency on the island.

Both loci autosomal				One locus sex-linked (heterogametic sex)		
Locus 1 genotype	Locus 2 genotype			Locus 1 genotype	Locus 2 genotype	
	$B_0B_0$	$B_0B_1$	$B_1B_1$		$B_0$	$B_1$
$A_0A_0$	1	$1 - s_{01}$	$1 - s_{02}$	$A_0A_0$	1	$1 - s_{02}$
$A_0A_1$	$1 - s_{01}$	$1 - s_{11}$	$1 - s_{12}$	$A_0A_1$	$1 - s_{01}$	$1 - s_{12}$
$A_1A_1$	$1 - s_{02}$	$1 - s_{12}$	1	$A_1A_1$	$1 - s_{02}$	1

To compare the outcome under different forms of inheritance, it is convenient to standardize the results by the case in which both preference and display trait genes are autosomal. This gives a relative measure of how much different forms of sex linkage affect reinforcement. The results are shown in the last column of Table 1. Sex linkage causes the amount of reinforcement to vary by up to 80% (Table 1, last column). All else equal, the highest levels of reinforcement occur when the preference is X or Z linked and the display is autosomal, though these levels are not much higher than seen under several other modes of inheritance. Reinforcement is particularly ineffective in two situations: when the preference is autosomal and the male display is X linked and when the preference is X linked and the trait Y linked.

*Effects of Hybrid Incompatibilities*

Intrinsic hybrid incompatibility is thought to play a critical role in the evolution of reinforcement. A general discussion of the role of intrinsic incompatibility on reinforcement is beyond the scope of this paper, and it is considered elsewhere (Lemmon and Kirkpatrick 2006). However, to give some insight into the effects of these incompatibilities, we present results for a very simple scenario: two hybrid incompatibility loci in which one locus is autosomal and the other is either autosomal or sex linked. This situation includes the Dobzhansky-Muller incompatibilities, in which epistatic interactions among loci reduce fitness, that have been found in many hybrid crosses (Bateson 1909; Orr 1996; Coyne and Orr 2004).

We assume that these two loci have equal effects, identical dominance relationships, and identical effects on fitness in males and females and exhibit complete dosage compensation. Further, we assume that the continent is fixed for the 0 allele at both loci, and the 1 allele is at high frequency on the island. Intrinsic incompatibilities will only be exhibited when an individual carries a mixture of 0 and 1 alleles at different loci. With these assumptions, the nine possible fitnesses in each sex reduce to only four. The notation for these fitnesses is shown in Table 2.

To further simplify, we consider three dominance scenarios: additivity ( $s_{01} = s_{12} = s_{11} = s_{02}/2$ ), continental alleles dominant ( $s_{01} = s_{11} = 0$  and  $s_{02} = s_{12}$ ), and island alleles

dominant ( $s_{11} = s_{12} = 0$  and  $s_{02} = s_{01}$ ). In the additive case, every mismatched pair of alleles contributes the same amount to incompatibility. Thus, genotypes that are heterozygous at one or both loci, in which there are two pairs of incompatibilities between the loci, are assumed to have equal fitness. Genotypes that are homozygous 00 at one locus and homozygous 11 at the other, in which there are four pairs of interlocus incompatibilities, will have twice the loss of fitness. With continental alleles dominant, heterozygous loci behave as if they were homozygous for the continental allele. In this scenario, continental alleles should be most visible to selection. With island alleles dominant, heterozygous loci behave as if they were homozygous for the island allele. In this scenario, continental alleles should be least visible to selection. We note that with nonadditivity and one incompatibility locus sex-linked, the  $F_1$  individuals exhibit Haldane’s rule (Haldane 1922), in which the average fitness of the homogametic sex is greater than the average fitness of the heterogametic sex ( $2s_{11} < s_{01} + s_{12}$ ). With these simplifications, we can use the results from Lemmon and Kirkpatrick (2006) to calculate  $I_f$  and  $I_m$  and the effect of incompatibility on reinforcement ( $F_p I_f + [1 - F_p] I_m$ ). The results of these calculations are shown in Appendix 4.

To explore how much the level of reinforcement can increase with genetic incompatibility, we calculated the level of reinforcement assuming the strength of selection on the incompatibility loci is quite strong ( $s_{02} = 0.1$ ), but still weak enough that our approximations should hold. The results are shown in Table 3, where each entry is the level of reinforcement standardized to the autosomal preference, autosomal trait case with no incompatibility. The level of reinforcement in the absence of incompatibility is shown in the last column. To determine the effect of extrinsic incompatibility on reinforcement, compare any entry in Table 3 with the entry in the last column of the same row. To compare how different modes of inheritance of the incompatibility affect reinforcement, compare entries in the same row. To compare how the mode of inheritance of the preference and trait affect reinforcement, compare entries in the same column. Under some scenarios, postzygotic incompatibility results in increases in reinforcement of almost 50% relative to the case with no incompatibility (Table 3).

One general pattern that emerges from Table 3 is that sex linkage of one of the incompatibility loci results in higher levels of reinforcement, though the effect is small, not more than 13%. One might be tempted to attribute this to Haldane’s rule, in which the heterogametic sex is doing poorly, causing incompatibility through that sex to have a greater impact on reinforcement. With sex-linked preferences, however, the contribution to reinforcement through the heterogametic sex is actually less than through the homogametic sex (Appendix 4). Further, with additivity (where Haldane’s rule does not occur), reinforcement is still higher with a sex-linked incompatibility locus when the preference is sex linked. The reason is that the incompatibility terms involve both selection coefficients and associations between incompatibility and preference loci. These associations are affected by the mode of inheritance of both the preference and incompatibility loci, making the results more difficult to predict. Further discus-

TABLE 3. The amount of reinforcement expected under different modes of inheritance and under three different forms of hybrid incompatibility, relative to the case where both the preference and trait loci are autosomal and there is no postzygotic incompatibility (such that  $I_f$  and  $I_m = 0$ ). The heritabilities of the preference and trait and  $(\hat{T} - T^C)$  are assumed to not vary with mode of inheritance. The three scenarios correspond to those outlined in Appendix 4, assuming  $s_{02} = 0.1$ . The (A, A) columns consider two autosomal incompatibility loci and the (A, X) columns consider one autosomal and one sex-linked incompatibility locus. The last column gives the expected levels of reinforcement when there is no hybrid incompatibility (that is  $s_{02} = 0$ ); these values are the same as in the last column of Table 1.

Preference	Trait	Genetics of incompatibility						No incompatibility ( $I_m = I_f = 0$ )
		Additive		Continental alleles dominant		Island alleles dominant		
		A, A	A, X	A, A	A, X	A, A	A, X	
A	A	1.36	1.36	1.36	1.43	1.00	1.11	1.00
A	X	0.82	0.82	0.82	0.86	0.60	0.67	0.60
A	Z	1.22	1.22	1.22	1.29	0.90	1.00	0.90
X	A	1.38	1.56	1.38	1.56	1.07	1.17	1.07
X	X	1.29	1.46	1.29	1.46	1.00	1.11	1.00
Z	A	1.38	1.56	1.38	1.56	1.07	1.17	1.07
Z	Z	1.29	1.46	1.29	1.46	1.00	1.11	1.00

sion of these patterns can be found in Lemmon and Kirkpatrick (2006).

Another pattern to emerge is that nonadditivity at the incompatibility loci rarely increases the level of reinforcement. Only when the preference is autosomal, one of the incompatibility loci is sex linked, and the island incompatibility alleles is recessive is reinforcement larger in the nonadditive than in the additive case. Even in this situation, the effect is not great, on the order of 5%. The reason is that continental alleles are not visible to selection in the homogametic sex in the  $F_1$  because the double heterozygous  $F_1$  behaves as if homozygous 00 at both incompatibility loci ( $s_{01} = 0$ ). With recessive continental incompatibility alleles, the expected level of reinforcement is actually substantially lower than in the additive case. This is because there is no incompatibility through the homogametic sex and only a small amount through the heterogametic sex (Appendix 4). Thus, even though nonadditivity causes Haldane’s rule to be observed

because of the unmasking of Dobzhansky-Muller incompatibilities in the heterogametic  $F_1$  (see Coyne and Orr 2004), there is at most only minor enhancement of reinforcement.

*Reinforcement and the evolution of prezygotic isolation*

Our model measures reinforcement in terms of the changes in the mean female preference. How do those changes translate into reproductive isolation? Because our model is very general about how females choose mates, additional assumptions would be required to answer that question quantitatively.

We can, however, use a qualitative argument to draw three general conclusions. The first is that the reinforcement of the preference predicted by our model can lead to complete reproductive isolation. In this case, the mode of inheritance can have a large qualitative impact on speciation. Second, there are cases in which total isolation cannot evolve. Then reinforcement will have a quantitative effect on the amount of introgression but might not qualitatively change the outcome of speciation. The third conclusion is that when complete isolation can be achieved, different modes of inheritance can lead to the same evolutionary outcome despite the differences seen in Table 1.

We begin this qualitative analysis with the reasonable assumption that the hybridization rate (measured by  $m$ ) is a monotonic function of the mean preference. Figure 1 shows two cases that can result. In case 1, the hybridization rate goes to zero if the amount of reinforcement (measured by  $[\hat{P} - P^C]/\sigma_P$ ) exceeds a certain value, which we denote  $R^*$ . Analysis of equations (1–4) shows that if the amount of reinforcement predicted by equation (5) is greater than  $R^*$ , then the amount of reinforcement will evolve to  $R^*$  and  $m$  will evolve to zero.

In this case, the mode of inheritance could have a major qualitative effect on speciation. Depending on how the preference and trait are inherited, the equilibrium for the preference might lie above or below  $R^*$ . All else equal, those combinations that show greater reinforcement in Table 1 will be more likely to achieve complete isolation.

Our second qualitative conclusion is that there are situations in which complete isolation can never evolve by re-

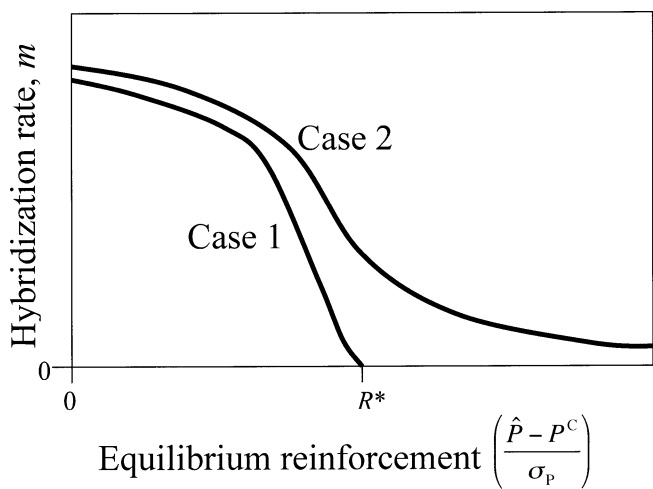


FIG. 1. Hypothetical relationship between the hybridization rate ( $m$ ) and the level of reinforcement. In case 1, island females will completely avoid mating with continental males if the amount of reinforcement is sufficiently large ( $\geq R^*$ ), implying hybridization will be zero. In case 2, regardless of the amount of reinforcement, there is always some chance that females will mate with continental males, implying that the hybridization rate will never reach zero.

inforcement. To see this, consider case 2 of Figure 1. Here the hybridization rate declines with greater reinforcement, but it never completely vanishes. (This case applies to the preference functions introduced by Lande [1981], for example, in which there is always some probability that a female will mate with a given male.) Then reinforcement will decrease the amount of introgression quantitatively, but might not have a qualitative impact on speciation. Whether a situation like case 1 or case 2 prevails depends on details such as the female's sensory system and the phenotypic distribution of the male trait.

Our third conclusion is that there are situations in which the evolutionary outcome will be the same despite the differences predicted by Table 1. Return to case 1 and consider the outcome for two modes of inheritance that Table 1 predicts will cause different amounts of reinforcement. If both equilibria are greater than  $R^*$ , then both modes of inheritance will cause the preference to evolve to  $R^*$ .

#### DISCUSSION

Our analysis shows that sex linkage can affect the level of reinforcement by up to 80% (Table 1). When reinforcement is driven mainly by selection in the male trait and intrinsic hybrid incompatibilities are weak ( $I_m, I_f \ll 1$ ), sex-linked preferences and autosomal male traits are the most conducive to reinforcement, while autosomal preferences and X-linked traits are the least. (Those statements neglect the case of W-linked preferences, which prevents reinforcement entirely.)

Reinforcement evolves because females increase their fitness by avoiding the production of hybrid offspring. Hybrid offspring have reduced fitness due to (intrinsic) hybrid incompatibilities and due to male trait values that are further from the optimum than island males. Offspring of females with strong preferences for island males will carry alleles for higher fitness at both the trait and incompatibility loci, and alleles for stronger preferences. Thus, stronger preferences will evolve as a correlated response to selection acting through the male trait and the incompatibility loci.

Equation (5) shows that the amount of reinforcement depends on three general factors: the ability of females to distinguish island and continental males, the strength of selection acting directly on the male trait and hybrid incompatibility, and the genetic correlations between the those traits and the female preference. The first factor is captured by the difference in the mean display trait between the island and continent,  $(\hat{T} - T^C)/\sigma_T$ , and the phenotypic correlation between the male trait and female preference in mated pairs,  $\rho$ . If island and continental males do not differ too much, or if mating preferences are not accurate, then females will not be able to distinguish between island and continental males. They will be less able to avoid producing low fitness offspring, and the amount of reinforcement will be less.

The second factor is the strength of direct selection on the male trait and hybrid incompatibility. The contribution from the male trait is captured in equation (5) by the term  $(1 - F_T)$ , which is the proportion of trait loci found in males. As it increases, the display trait loci spend more time under selection, and the mean male trait on the island will be closer to its optimum. This results in a smaller selection gradient

on the male trait, leading to a smaller correlated response of the female preference and so less reinforcement. The contribution to reinforcement from hybrid incompatibility genes (i.e., all fitness-affecting loci other than the male trait) appears in equation (5) as  $[F_P I_f + (1 - F_P) I_m]$ . As we expect intuitively, greater hybrid incompatibility produces more reinforcement.

The third general factor affecting reinforcement is the efficiency with which selection on the male trait and incompatibility genes is transmitted to the preference. This depends on the genetic correlations with the preference. The correlation between the male trait and preference loci is affected by how they are inherited (i.e., sex linkage), and that effect appears in the factor  $k$  (defined in Table 1). Genetic correlations with the preference are prevented entirely if there is no genetic variance for the preference ( $h_p^2 = 0$ ), or if preference genes spend either none or all of their time in females ( $F_P = 0$  or 1). The term  $\sqrt{F_P(1 - F_P)}$  has nearly the same value with autosomal inheritance ( $=1/2$ ) as with X and Z linkage of the preference ( $=\sqrt{2}/3 \approx 0.48$ ), and so it changes little across different modes of inheritance. The conclusions drawn from Table 1 assume weak intrinsic incompatibility ( $I_m, I_f \ll 1$ ). Similar qualitative conclusions also hold when intrinsic incompatibility is moderately strong (Table 3).

We can extract several conclusions from equation (5) and Table 1. With autosomal displays, sex linkage of the preference facilitates the evolution of reinforcement. This result suggests we might expect the sex chromosome to play a larger role in reinforcement than expected based on its size. The logic here is that loci that alter female preferences are more likely to contribute to reinforcement if they are sex linked than otherwise. Likewise, with X- or Z-linked displays, we expect that the sex chromosome will play a higher role in reinforcement. In contrast, with Y-linked displays, X linkage of the preference reduces the amount of reinforcement, implying that the X chromosome will play a much lesser role in reinforcement. In situations in which the display and preference have the same mode of inheritance (e.g., both Z linked), we expect no difference in the amount of reinforcement that will evolve. With W linkage of the female preference, reinforcement cannot evolve, implying that we should never see W-linked preferences playing a role in reinforcement.

We emphasize that these predictions come with an important caveat. To simplify comparisons between modes of inheritance, we have assumed that several factors (e.g., heritability of the preference) do not change in a systematic way with mode of inheritance. If later theoretical or empirical progress challenges this assumption, such that the last column of Table 1 is no longer an appropriate comparison, the general result of equation (5) will still stand.

While the 80% difference between the smallest and highest levels of reinforcement predicted under different forms of sex linkage is substantial, there are many cases in which the effect of sex linkage is small. For example, with an autosomal trait, there is no difference in the level of reinforcement between X- and Z-linked preferences and only a 7% difference compared to autosomal preferences (Table 1). These results are perhaps surprising given that the mode of inheritance causes up to five-fold differences in the genetic correlation

between the preference and display in males and three-fold differences in the selection gradient on the male trait. Why is the overall strength of reinforcement affected so little by the mode of inheritance of the preference and display trait? The basic reason is that sex linkage has two main effects on reinforcement, and they tend to cancel each other. The first of these enters through the genetic correlation between the preference and trait, whereas the second enters through the selection gradient on the male trait.

To see these effects, consider Z-linked preferences and Z-linked traits. The first effect of sex linkage is on the genetic correlation between the preference and trait. In this case, this correlation is 41% larger than with both sets of loci autosomal (Table 1). An intuitive explanation for this effect is given in Kirkpatrick and Hall (2004). In part, Z linkage of the preference results in females passing all of their preference alleles to their sons. Because the preference alleles were expressed in females and the phenotypic correlation between mated pairs causes the genetic correlation, this increases the correlation between the preference and the trait in sons.

The second effect of sex linkage is on the directional selection gradient on the male trait. There is persistent directional selection on the trait at equilibrium because it is pulled from its selection optimum by migration (or hybridization), and this contributes to reinforcement of the preference. When the trait is Z linked, its mean will be closer to the optimum because the genes are more often in the sex where they are expressed and subject to selection. This generates a selection gradient that is 25% smaller than for autosomal displays. Thus, even though the genetic correlation is larger with Z linkage of preferences and displays, the selection gradient is smaller and these two offset one another, resulting in levels of reinforcement that are the same as with autosomal preferences and displays. Similar patterns are seen with other modes of inheritance: high genetic correlations tend to be associated with small selection gradients. An important conclusion is that knowing the genetic correlation alone, either by empirical measurement or theoretical calculation, is not sufficient to gauge how efficient reinforcement might be.

Hybrid incompatibility acts to enhance reinforcement, but in a nonintuitive manner. Simply knowing that male  $F_1$  hybrids are less fit than females does not allow one to predict whether incompatibilities acting through males will contribute more to reinforcement than those acting through females. There are other factors that must be considered, such as which genotypes are formed in the  $F_2$  and the magnitudes of the associations between the incompatibility loci and the preference alleles. In addition, the effect of dominance at incompatibility loci on reinforcement is complex. While departure from additivity cause Haldane's rule to be observed, it is not able to enhance reinforcement that much, as compared to the additive case (Table 3). In fact, with recessive continental alleles, there is a significant reduction in the amount of reinforcement due to incompatibilities as compared to the additive case (Table 3).

Much of the interest in reinforcement lies in the question of whether it leads to the complete closure of genetic introgression between two populations. Dobzhansky (1940) argued that it does and indeed saw reinforcement as a key step in most speciation events. The genetic model developed here

focuses on the evolution of mating preferences, rather than on the hybridization rate. Our qualitative analysis, however, shows how evolution of the preference can cause complete prezygotic isolation in some cases but not others. The outcome depends in part on behavioral details of how female choose their mates. There are cases in which sex linkage of the preference and male trait can play a decisive role in determining whether reinforcement will achieve complete isolation.

To isolate the effects of reinforcement from other evolutionary forces, our model assumes that the preference genes are free of direct selection. There are many ways that natural selection on preference genes can arise, however, including search costs and pleiotropy (e.g., Kirkpatrick 1987; Kirkpatrick and Ryan 1991; Hall et al. 2000; Gavrillets 2004, ch. 10; Kirkpatrick and Nuismer 2004). When direct selection happens at the same time as reinforcement, we expect intuitively that the equilibrium for the preference will be a compromise between the two. Direct selection may often predominate when genetic variance in fitness is generated by the evolutionary forces that are typical in many populations (Kirkpatrick and Barton 1997). But hybridization might generate much higher levels of genetic variance in fitness, making reinforcement a potentially powerful form of indirect selection on preferences. The many empirical cases of reinforcement that have been documented (Coyne and Orr 2004) show that it is strong enough to have substantial evolutionary effects, despite any direct selection that may operate.

It is helpful to compare our results with those of a good-genes model of sexual selection analyzed in an earlier study (Kirkpatrick and Hall 2004). In that model, we examined the rate at which the female preference evolves because of genetic correlations that exist between the male trait and fitness. We might expect those results to be similar to the ones presented here because the preference on the island is evolving to avoid hybridization with continental males who carry low-quality genes. Avoidance of bad genes is essentially a good genes mechanism of sexual selection. Despite the appeal of that intuition, our results here show that there are critical differences between the reinforcement and good-genes mechanisms. The models differ in two respects. First, our earlier model is dynamic, examining a rate of change rather than an equilibrium level of preference. Second, our earlier model assumes a fixed value for the mean male trait, and that the genetic correlations between the male trait and fitness are constant. In the present model, we allow for the evolution of the male trait in response to selection and migration.

There are two reasons for the difference with our present results. First, the selection gradient on the male trait varies with mode of inheritance in our present model, whereas it was assumed (implicitly) to be constant in the previous model. Thus, the mode of inheritance of the male trait cannot act through this factor in that model. Second, in our previous model, the genetic correlation between the preference and display trait in females plays an important role. With a genetic correlation between the preference and trait in females, extreme mating preferences can still evolve even in the absence of a preference-trait correlation in males because of the correlation between the trait and good genes in females (Kirk-



patrick and Hall 2004; eq. 2). The genetic correlation in females, which is substantially changed by the mode of inheritance, does not enter when reinforcement is driven only by selection on the male trait, because the male trait is not subject to selection in females. When genetic incompatibilities are present, the genetic correlation in females enters in the  $F_p I_f$  term, but is unable to cause reinforcement in the absence of a genetic correlation in males (eq. 5). We thus found that the good-genes mechanism is facilitated by W-linked preferences in the dynamic model (Kirkpatrick and Hall 2004, table 1), whereas in the equilibrium model presented here, we find that W-linkage precludes reinforcement.

Servedio and Saetre (2003) studied the effects of sex linkage on reinforcement using simulations of a four-locus model. They find that Z linkage of the preference, trait, and incompatibilities causes greater reinforcement compared to the case where all genes are autosomal. We do not see that difference when intrinsic incompatibility is very weak ( $I_m, I_f \ll 1$ ). The analytic results of Lemmon and Kirkpatrick (2006), however, confirm that adding Z-linked incompatibility (with Z-linked preferences and displays) does lead to more reinforcement.

Our analytic approach is based on the QLE approximation, which assumes weak selection. Servedio (2004) criticized the weak selection approach as a method to study reinforcement. She found (as we do) that the relative contributions of the male trait and hybrid incompatibility to reinforcement are sensitive to the values of the parameters used. She concluded from that observation that weak selection approximations do not give robust predictions and do not "allow generalization to large parameter values."

Servedio's (2004) criticism is unjustified on two grounds. First, she does not directly compare the predictions of a weak selection analysis with numerical results for cases involving moderate to strong selection. In fact, the QLE approach seems to do quite well. Servedio's own simulations show that the QLE approximation is very accurate when selection coefficients are on the order of 1–2%, and other work shows the results are quite good even with selection coefficients of  $s = 0.1$  or larger (Kirkpatrick and Servedio 1999; Nuismer and Otto 2004; Lemmon and Kirkpatrick 2006). Second, even in cases where the QLE approximation does not give good quantitative results, it may still provide a good qualitative guide. For example, our conclusion that X-linked preferences are especially conducive to reinforcement may be robust far outside the range of parameters where the model makes quantitatively satisfying predictions. If so, then the weak selection approximation is accurate in terms of our biological understanding of the processes involved. Simulations by Lemmon and Kirkpatrick (2006) indicate that these qualitative predictions do hold for selection coefficients that are substantially larger than 0.1.

The genetic correlation between the male display and female preference is often considered to be a crucial parameter in models of indirect sexual selection (Andersson 1994). However, our analysis indicates that even though the mode of inheritance has a substantial impact on the correlation, it has only a moderate impact on the predicted level of reinforcement. Explanations of other evolutionary phenomena that invoke mode of inheritance as an important factor should

be considered with caution unless a full theoretical analysis has been presented.

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#### APPENDIX 1

This appendix outlines the derivation of equations (1) and (2). The notation follows Kirkpatrick et al. (2002), which can be consulted for further details.

We assume two alleles segregate at each preference locus, denoted alleles 0 and 1, that have additive but possibly unequal effects. We say that genes carried by an individual occupy positions. An individual carries one or two positions at each locus, depending on the mode of inheritance. At an X-linked locus  $i$ , for example, a female has two positions, one inherited from her mother, denoted  $i_{ff}$ , and one inherited from her father, denoted  $i_{fm}$ . For the same X-linked locus, a male has only a single position, which he inherited from his mother, and is denoted  $i_{mf}$ . The set of all positions that affect the female preference is written  $\mathbb{P}$ , while the set of preference positions carried by females is written  $\mathbb{P}_f$ . With  $n$  X-linked loci, there are  $3n$  positions in set  $\mathbb{P}$  and  $2n$  in set  $\mathbb{P}_f$ . On the island, the frequency of allele 1 at position  $\mathbf{i}$  (where  $\mathbf{i}$  could represent  $i_{ff}$ ,  $i_{fm}$ , or  $i_{mf}$ ) is denoted  $p_i$  with  $q_i = 1 - p_i$ . The corresponding frequencies in the continental population are denoted with a C superscript.

The preference phenotype of a particular female can be written

$$P = \bar{P} + \sum_{i \in \mathbb{P}_f} b_i \zeta_i, \quad (\text{A1})$$

where  $\bar{P}$  is the mean preference at birth among females in the current generation,  $b_i$  is the difference in the preference of carrying allele 1 rather than allele 0 at position  $\mathbf{i}$ , and  $\zeta_i = q_i$  if the individual carries allele 1 at position  $\mathbf{i}$  and  $-p_i$  otherwise. The summation includes one term for each of the positions affecting the preference in females.

The change in the mean preference in females from the start of one generation to the next is

$$\Delta \bar{P} = \sum_{i \in \mathbb{P}_f} b_i \Delta p_i, \quad (\text{A2})$$

where  $\Delta p_i$  is the change in allele frequency at position  $\mathbf{i}$  from the start of one generation to the start of the next. This change is caused by forces acting within a generation (migration and selection) and by transmission between generations. To make progress, we will use the quasi-linkage equilibrium (QLE) approximation (Barton and Turelli 1991; Kirkpatrick et al. 2002). The QLE approximation assumes that selection and migration are weak and recombination rates are not too small (so that genetic disequilibria evolve rapidly compared to allele frequency changes). When transmission is conservative (i.e., all positions contribute equally to the next generation), then one can show that at QLE the change in allele frequency across a generation at any position at a locus is equal to the average change across all positions within a generation:

$$\Delta p_i = \frac{1}{n_i} \sum_{j: j=i} (p_j'' - p_j), \quad (\text{A3})$$

where  $n_i$  is the number of positions at locus  $i$  (e.g.,  $n_i = 3$  for an X-linked locus in a diploid dioecious population) and  $p_j''$  is the

frequency of allele 1 at position  $\mathbf{j}$  in mated pairs. The summation is over all positions  $\mathbf{j}$  that are at the same locus as position  $\mathbf{i}$ . For proof of (A3), consult the online materials of Lemmon and Kirkpatrick (2006).

The term within the parentheses of equation (A3) represents the within-generation change in allele frequency at position  $\mathbf{j}$ , which is

$$(p_j'' - p_j) = m(p_j^C - p_j) + \sum_{\mathbb{A} \subseteq \mathbb{W}} a_{\mathbb{A}} D'_{\mathbb{A}, j}, \quad (\text{A4})$$

where  $m$  is the migration rate from the continent,  $p_j^C$  is the frequency of allele 1 at position  $\mathbf{j}$  on the continent,  $\mathbb{W}$  is the set of all positions under selection, and the  $D'_{\mathbb{A}, j}$  are the genetic associations after migration but before selection among positions in the set that includes  $\mathbf{j}$  and  $\mathbb{A}$ . The  $a_{\mathbb{A}}$  values are selection coefficients defined by equation (7) of Kirkpatrick et al. (2002). A key point is that they can describe any form of selection and nonrandom mating. That is, given any set of specific assumptions about natural and sexual selection, these selection coefficients can be calculated by the methods described in Kirkpatrick et al. (2002).

Substituting (A4) into (A2) and using (A3) gives:

$$\Delta \bar{P} = m(P^C - \bar{P}) + \sum_{i \in \mathbb{P}_f} b_i \frac{1}{n_i} \sum_{j: j=i} \sum_{\mathbb{A} \subseteq \mathbb{W}} a_{\mathbb{A}} D'_{\mathbb{A}, j}, \quad (\text{A5})$$

where  $\bar{P}$  is the average preference of females on the island and  $P^C$  is the average on the continent. Equation (A5) is equation (1) of the text.

To arrive at equation (2), first split the selection term (the second term on the right side of eq. A3) into selection on the display trait loci and incompatibility loci in males and females:

$$\Delta \bar{P} = m(P^C - \bar{P}) + \sum_{i \in \mathbb{P}_f} \frac{b_i}{n_i} \sum_{j: j=i} \left( \sum_{\mathbb{A} \subseteq \mathbb{H}_f} a_{\mathbb{A}} D'_{\mathbb{A}, j} + \sum_{\mathbb{A} \subseteq \mathbb{H}_m} a_{\mathbb{A}} D'_{\mathbb{A}, j} + \sum_{\mathbb{A} \subseteq \mathbb{T}_f} a_{\mathbb{A}} D'_{\mathbb{A}, j} + \sum_{\mathbb{A} \subseteq \mathbb{T}_m} a_{\mathbb{A}} D'_{\mathbb{A}, j} \right), \quad (\text{A6})$$

where  $\mathbb{H}_f$  and  $\mathbb{H}_m$  are, respectively, the sets of all hybrid incompatibility positions carried by females and males, and  $\mathbb{T}_f$  and  $\mathbb{T}_m$  are the sets of all male display trait positions carried by females and males. Because there is no direct selection on the display trait in females,  $a_{\mathbb{A}} = 0$  for  $\mathbb{A} \subseteq \mathbb{T}_f$  and we obtain

$$\Delta \bar{P} = m(P^C - \bar{P}) + \sum_{i \in \mathbb{P}_f} \frac{b_i}{n_i} \sum_{j: j=i} \left( \sum_{\mathbb{A} \subseteq \mathbb{H}_f} a_{\mathbb{A}} D'_{\mathbb{A}, j} + \sum_{\mathbb{A} \subseteq \mathbb{H}_m} a_{\mathbb{A}} D'_{\mathbb{A}, j} + \sum_{\mathbb{A} \subseteq \mathbb{T}_m} a_{\mathbb{A}} D'_{\mathbb{A}, j} \right). \quad (\text{A7})$$

At equilibrium,  $\Delta \bar{P} = 0$ . Setting the left side of (A7) equal to zero and rearranging gives our measure for the amount of reinforcement at equilibrium, the difference in the mean level of preference between the island and the continent, measured in units of the standard deviation of the preference:

$$\frac{(\hat{P} - P^C)}{\sigma_P} = \frac{1}{m \sigma_P} \sum_{i \in \mathbb{P}_f} \frac{b_i}{n_i} \left[ \left( \sum_{\mathbb{A} \subseteq \mathbb{T}_m} \sum_{j: j=i} a_{\mathbb{A}} \hat{D}'_{\mathbb{A}, j} \right) + \left( \sum_{\mathbb{A} \subseteq \mathbb{H}_f} \sum_{j: j=i} a_{\mathbb{A}} \hat{D}'_{\mathbb{A}, j} \right) + \left( \sum_{\mathbb{A} \subseteq \mathbb{H}_m} \sum_{j: j=i} a_{\mathbb{A}} \hat{D}'_{\mathbb{A}, j} \right) \right], \quad (\text{A8})$$

where  $\sigma_P$  is the phenotypic standard deviation of the preference in females,  $\hat{P}$  is the average preference in females at equilibrium, and the  $\hat{D}$  values are the disequilibria values at equilibrium.

Inside the square brackets of (A8) are three terms. The first represents the impact on the preference of natural and sexual selection acting on the male display trait. The second and third represent the effects of selection on hybrid incompatibility genes in females and males, respectively. These latter two quantities are calculated in Lemmon and Kirkpatrick (2006). They show:

$$\sum_{i \in \mathbb{P}_f} \frac{b_i}{n_i} \left[ \left( \sum_{\mathbb{A} \subseteq \mathbb{H}_f} \sum_{j: j=i} a_{\mathbb{A}} \hat{D}'_{\mathbb{A}, j} \right) + \left( \sum_{\mathbb{A} \subseteq \mathbb{H}_m} \sum_{j: j=i} a_{\mathbb{A}} \hat{D}'_{\mathbb{A}, j} \right) \right] = [F_P I_f + (1 - F_P) I_m] m (\hat{P} - P^C), \quad (\text{A9})$$

where  $F_p$  is the proportion of preference alleles carried in females (2/3 for X-linkage for example).  $I_f$  and  $I_m$  are measures of the effect of incompatibility on reinforcement acting through females and males, respectively. Their values are

$$I_f = - \sum_{A \in \mathbb{H}_f} a_A d_A \phi_A^f \quad \text{and} \quad I_m = - \sum_{A \in \mathbb{H}_m} a_A d_A \phi_A^m,$$

where

$$d_U = \prod_{i \in U} (p_i^C - p_i).$$

The constants  $\phi_A^f$  and  $\phi_A^m$  depend on the mode of inheritance of the female preference and incompatibility loci and level of recombination among them. Their values and the resulting values of  $I_f$  and  $I_m$  can be found in the online materials and in tables 1 and 2 of Lemmon and Kirkpatrick (2006), and that paper should be consulted for details.

Substituting (A9) into equation (A8) and rearranging gives

$$\frac{(\hat{P} - P^C)}{\sigma_P} = \frac{1}{[1 - F_p I_f - (1 - F_p) I_m] m \sigma_P} \times \sum_{i \in \mathbb{P}_f} \frac{b_i}{n_i} \left( \sum_{j: j'=i} \sum_{A \in \mathbb{T}_m} a_A \hat{D}'_{Aj} \right) + O(a^2). \quad (\text{A10})$$

We can rewrite equation (A10) as

$$\frac{(\hat{P} - P^C)}{\sigma_P} = \frac{F_p}{[1 - F_p I_f - (1 - F_p) I_m] m \sigma_P} \times \sum_{i \in \mathbb{P}_m} b_i \sum_{A \in \mathbb{T}_m} a_A \hat{D}'_{Ai} + O(a^2). \quad (\text{A11})$$

The selection coefficients for single preference positions are  $a_j = b_j \beta_T$ , where  $\beta_T$  is the selection gradient (including both natural and sexual selection) for the male display trait. If we assume that the fitness function is approximately linear over the display trait's range of phenotypic variation, then selection coefficients involving more than one position are zero, and

$$\sum_{i \in \mathbb{P}_m} b_i \sum_{j \in \mathbb{T}_m} a_j \hat{D}'_{ij} = \beta_T \sum_{i \in \mathbb{P}_m} \sum_{j \in \mathbb{T}_m} b_i b_j \hat{D}'_{ij} + O(a^2). \quad (\text{A12})$$

The double summation term on the right side of (A12) is equal to the genetic covariance between the preference and trait in males after migration,  $\hat{G}_{PT}^m$ , and thus (A11) becomes

$$\begin{aligned} \frac{(\hat{P} - P^C)}{\sigma_P} &= \frac{F_p \beta_T \hat{G}_{PT}^m}{[1 - F_p I_f - (1 - F_p) I_m] m \sigma_P} + O(a^2) \\ &= \frac{F_p \beta_T \hat{r}_{PT}^m \sqrt{\hat{G}_T} \sqrt{\hat{G}_P^m}}{[1 - F_p I_f - (1 - F_p) I_m] m \sigma_P} + O(a^2) \\ &= \frac{\sqrt{F_p(1 - F_p)} \beta_T \hat{r}_{PT}^m \sqrt{\hat{G}_T} h_P}{[1 - F_p I_f - (1 - F_p) I_m] m} + O(a^2), \quad (\text{A13}) \end{aligned}$$

where  $\hat{r}_{PT}^m$  is the equilibrium value of the genetic correlation between the preference and trait in males after migration and  $h_P$  is the heritability of the female preference ( $h_P = \sqrt{G_P}/\sigma_P$ ).  $\hat{G}_P^m$  and  $\hat{G}_T$  are the additive genetic variances for the female preference and male trait in males at equilibrium. The last simplification to obtain (A13) assumes that linkage disequilibrium is small, in which case the genetic variance for the female preference in females,  $G_P = [F_p/(1 - F_p)] G_P^m$ . Equation (A13) is equation (2) of the text.

## APPENDIX 2

In this appendix, we calculate the genetic correlation between the preference and display in males following migration and show that it can be approximated by the value calculated in Kirkpatrick and Hall (2004). This result is used to arrive at equation (5) of the text. The notation and several results we use come from Kirkpatrick et al. (2002) and Kirkpatrick and Hall (2004), which give further details.

We begin with the genetic covariance between the male trait and female preference in males following migration:

$$G_{PT}^m = \sum_{i \in \mathbb{P}_m} \sum_{j \in \mathbb{T}_m} b_i b_j D'_{ij}, \quad (\text{A14})$$

where  $D'_{ij}$  is the value of the association between preference position  $i$  and trait position  $j$  after migration, and  $b_i$  and  $b_j$  are, respectively, the additive effect of position  $i$  on the preference and of position  $j$  on the display. The two summations are over preference positions and display trait positions carried by males. Because the preference is not expressed in males, the values for the  $b_i$  are arbitrary. It will be convenient later if we define them as equal to the corresponding positions in females, for example,  $b_{int} = b_{if}$ .

To determine the values of the associations  $D'_{ij}$  at QLE, we derive a recursion for them over a complete generation. We start with the association in zygotes in the next generation, denoted  $D''_{ij}$ , and work backward to express that value in terms of associations among mated pairs (i.e., after natural and sexual selection) in the current generation, denoted  $D'''_{ij}$ :

$$D''_{ij} = \sum_{U: U=i, j} t_{U \leftarrow \mathbb{T}} D'''_{U}, \quad (\text{A15})$$

where the transmission coefficient  $t_{S \leftarrow \mathbb{T}}$  is the probability that positions in set  $S$  were inherited from those in set  $\mathbb{T}$ , and the summation is over all sets  $U$  that consist of one position at locus  $i$  and one at locus  $j$ . Next we need to write the association after sexual and natural selection,  $D''_{ij}$ , in terms of its value before selection but after migration,  $D'_{ij}$ . Recalling that  $i$  is a preference position and  $j$  is a display trait position, if  $i$  is in a female and  $j$  is in a male we have

$$D''_{ij} = D'_{ij} + a_{ij} p q_{ij} + O(a^2), \quad (\text{A16a})$$

and if not

$$D''_{ij} = D'_{ij} + O(a^2), \quad (\text{A16b})$$

where  $p q_{ij} = p_i(1 - p_i)p_j(1 - p_j)$  (Kirkpatrick et al. 2002, eq. 11). Because  $i$  is a preference position and  $j$  is a display trait position, the only selection coefficients that are nonzero are those in which  $i$  is carried by a female and  $j$  is carried by a male. We assume that the sex-of-origin does not affect the expression of the preference or display. Thus, we write the nonzero selection coefficients as  $a_{ifj_m}$ . These selection coefficients represent the force of sexual selection that brings together a preference gene in a female with a trait gene in the male she has chosen to mate, and are given by

$$a_{ifj_m} = \rho \frac{b_{if} b_{j_m}}{\sigma_P \sigma_T}, \quad (\text{A17})$$

where  $b_{if}$  and  $b_{j_m}$  are, respectively, the effects of locus  $i$  on the preference in females and of locus  $j$  on the display trait in males,  $\sigma_P$  is the phenotypic standard deviation of the preference in females, and  $\sigma_T$  is the phenotypic standard deviation of the display trait in males (Kirkpatrick et al. 2002, eq. 48).

The last step of the recursion is to write  $D'_{ij}$  in terms of associations in zygotes of the current generation,  $D_{ij}$ . Migration generates associations between positions within individuals. Thus,

$$D_{ij} = D_{ij} + m d_{ij} + O(a^2), \quad (\text{A18a})$$

if  $i$  and  $j$  are in the same sex of carrier, and

$$D'_{ij} = D_{ij} + O(a^2), \quad (\text{A18b})$$

if not, where  $d_{ij} = (p_i^C - p_i)(p_j^C - p_j)$  (Kirkpatrick et al. 2002, eq. 31).

At QLE, the differences in allele frequencies between positions at the same locus are  $O(a)$ , so we can write  $d_{ij} = (p_i^C - p_i)(p_j^C - p_j) + O(a)$  where  $p_i$  is the average allele frequency among positions at locus  $i$ .

We can now solve for the QLE values of the associations. The number of values depends on the mode of inheritance for the preference and display trait. To illustrate the method, in the remainder of this appendix we will assume both the female preference and male display are autosomal. Other cases are solved using the same method.

We begin by neglecting terms  $O(a^2)$  and setting the value of the

associations among zygotes in the next generation equal to their corresponding values in the current one  $D_{ij}''' = D_{ij} = \hat{D}_{ij}$ . (The number of resulting equations depends on the mode of inheritance for the preference and display trait.) In the case where both the female preference and male display are autosomal, we obtain

$$\begin{aligned} \hat{D}_{i_{ff}j_{ff}} &= t_{i_{ff}j_{ff} \leftarrow i_{ff}j_{ff}} \hat{D}_{i_{ff}j_{ff}} + t_{i_{ff}j_{ff} \leftarrow i_{ff}j_{fm}} \hat{D}_{i_{ff}j_{fm}} + t_{i_{ff}j_{ff} \leftarrow i_{ff}j_{ff}} \hat{D}_{i_{ff}j_{ff}} \\ &\quad + t_{i_{ff}j_{ff} \leftarrow i_{ff}j_{fm}} \hat{D}_{i_{ff}j_{fm}} \\ &\quad + md_{ij}(t_{i_{ff}j_{ff} \leftarrow i_{ff}j_{ff}} + t_{i_{ff}j_{ff} \leftarrow i_{ff}j_{fm}} + t_{i_{ff}j_{ff} \leftarrow i_{ff}j_{ff}} + t_{i_{ff}j_{ff} \leftarrow i_{ff}j_{ff}}), \end{aligned} \quad (A19a)$$

$$\begin{aligned} \hat{D}_{i_{fm}j_{fm}} &= t_{i_{fm}j_{fm} \leftarrow i_{fm}j_{fm}} \hat{D}_{i_{fm}j_{fm}} + t_{i_{fm}j_{fm} \leftarrow i_{fm}j_{mm}} \hat{D}_{i_{fm}j_{mm}} \\ &\quad + t_{i_{fm}j_{fm} \leftarrow i_{fm}j_{mf}} \hat{D}_{i_{fm}j_{mf}} + t_{i_{fm}j_{fm} \leftarrow i_{fm}j_{mm}} \hat{D}_{i_{fm}j_{mm}} \\ &\quad + md_{ij}(t_{i_{fm}j_{fm} \leftarrow i_{fm}j_{mf}} + t_{i_{fm}j_{fm} \leftarrow i_{fm}j_{mm}} + t_{i_{fm}j_{fm} \leftarrow i_{fm}j_{mf}} \\ &\quad + t_{i_{fm}j_{fm} \leftarrow i_{fm}j_{mm}}), \end{aligned} \quad (A19b)$$

$$\begin{aligned} \hat{D}_{i_{mf}j_{mf}} &= t_{i_{mf}j_{mf} \leftarrow i_{mf}j_{mf}} \hat{D}_{i_{mf}j_{mf}} + t_{i_{mf}j_{mf} \leftarrow i_{mf}j_{fm}} \hat{D}_{i_{mf}j_{fm}} \\ &\quad + t_{i_{mf}j_{mf} \leftarrow i_{mf}j_{ff}} \hat{D}_{i_{mf}j_{ff}} + t_{i_{mf}j_{mf} \leftarrow i_{mf}j_{fm}} \hat{D}_{i_{mf}j_{fm}} \\ &\quad + md_{ij}(t_{i_{mf}j_{mf} \leftarrow i_{mf}j_{ff}} + t_{i_{mf}j_{mf} \leftarrow i_{mf}j_{fm}} + t_{i_{mf}j_{mf} \leftarrow i_{mf}j_{ff}} \\ &\quad + t_{i_{mf}j_{mf} \leftarrow i_{mf}j_{fm}}), \end{aligned} \quad (A19c)$$

$$\begin{aligned} \hat{D}_{i_{mm}j_{mm}} &= t_{i_{mm}j_{mm} \leftarrow i_{mm}j_{mm}} \hat{D}_{i_{mm}j_{mm}} + t_{i_{mm}j_{mm} \leftarrow i_{mm}j_{mf}} \hat{D}_{i_{mm}j_{mf}} \\ &\quad + t_{i_{mm}j_{mm} \leftarrow i_{mm}j_{mf}} \hat{D}_{i_{mm}j_{mf}} + t_{i_{mm}j_{mm} \leftarrow i_{mm}j_{mm}} \hat{D}_{i_{mm}j_{mm}} \\ &\quad + md_{ij}(t_{i_{mm}j_{mm} \leftarrow i_{mm}j_{mf}} + t_{i_{mm}j_{mm} \leftarrow i_{mm}j_{mf}} + t_{i_{mm}j_{mm} \leftarrow i_{mm}j_{mf}} \\ &\quad + t_{i_{mm}j_{mm} \leftarrow i_{mm}j_{mm}}), \end{aligned} \quad (A19d)$$

$$\begin{aligned} \hat{D}_{i_{ff}j_{fm}} &= t_{i_{ff}j_{fm} \leftarrow i_{ff}j_{mf}} a_{i_{ff}j_{mf}} pq_{ij} + t_{i_{ff}j_{fm} \leftarrow i_{ff}j_{mm}} a_{i_{ff}j_{mm}} pq_i pq_j \\ &\quad + t_{i_{ff}j_{fm} \leftarrow i_{ff}j_{mf}} a_{i_{ff}j_{mf}} pq_{ij} + t_{i_{ff}j_{fm} \leftarrow i_{ff}j_{mm}} a_{i_{ff}j_{mm}} pq_{ij}, \end{aligned} \quad (A19e)$$

$$\hat{D}_{i_{fm}j_{ff}} = 0, \quad (A19f)$$

$$\begin{aligned} \hat{D}_{i_{mf}j_{mm}} &= t_{i_{mf}j_{mm} \leftarrow i_{mf}j_{mf}} a_{i_{mf}j_{mf}} pq_{ij} + t_{i_{mf}j_{mm} \leftarrow i_{mf}j_{mm}} a_{i_{mf}j_{mm}} pq_{ij} \\ &\quad + t_{i_{mf}j_{mm} \leftarrow i_{mf}j_{mf}} a_{i_{mf}j_{mf}} pq_{ij} + t_{i_{mf}j_{mm} \leftarrow i_{mf}j_{mm}} a_{i_{mf}j_{mm}} pq_{ij}, \end{aligned} \quad (A19g)$$

and

$$\hat{D}_{i_{mm}j_{mf}} = 0. \quad (A19h)$$

With autosomal inheritance, the transmission coefficients that involve the inheritance of both genes from the same parent are

$$\begin{aligned} t_{i_{ff}j_{ff} \leftarrow i_{ff}j_{ff}} &= t_{i_{ff}j_{ff} \leftarrow i_{ff}j_{fm}} = t_{i_{mf}j_{mf} \leftarrow i_{mf}j_{ff}} = t_{i_{mf}j_{mf} \leftarrow i_{mf}j_{fm}} \\ &= (1 - r_{ij}^f)/2, \end{aligned} \quad (A20a)$$

$$\begin{aligned} t_{i_{ff}j_{ff} \leftarrow i_{ff}j_{fm}} &= t_{i_{ff}j_{ff} \leftarrow i_{ff}j_{ff}} = t_{i_{mf}j_{mf} \leftarrow i_{mf}j_{ff}} = t_{i_{mf}j_{mf} \leftarrow i_{mf}j_{ff}} \\ &= r_{ij}^f/2, \end{aligned} \quad (A20b)$$

$$\begin{aligned} t_{i_{fm}j_{fm} \leftarrow i_{fm}j_{mf}} &= t_{i_{fm}j_{fm} \leftarrow i_{fm}j_{mm}} = t_{i_{mm}j_{mm} \leftarrow i_{mm}j_{mf}} \\ &= t_{i_{mm}j_{mm} \leftarrow i_{mm}j_{mm}} = (1 - r_{ij}^m)/2, \quad \text{and} \end{aligned} \quad (A20c)$$

$$\begin{aligned} t_{i_{fm}j_{fm} \leftarrow i_{fm}j_{mm}} &= t_{i_{fm}j_{fm} \leftarrow i_{fm}j_{mf}} = t_{i_{mm}j_{mm} \leftarrow i_{mm}j_{mf}} \\ &= t_{i_{mm}j_{mm} \leftarrow i_{mm}j_{mf}} = r_{ij}^m/2, \end{aligned} \quad (A20d)$$

where  $r_{ij}^m$  and  $r_{ij}^f$  are the recombination rates between loci  $i$  and  $j$  in males and females, respectively. The sixteen other transmission coefficients that appear in equations (A19) involve inheritance of the two genes from different parents (e.g.,  $t_{i_{ff}j_{fm} \leftarrow i_{ff}j_{mf}}$ ), and they are all equal to 1/4. With other modes of inheritance, there will be less than eight associations to determine. For example, with autosomal preference and X-linked display, there are four associations in females and only two in males, giving six associations in total.

Equations (A19) represent a linear system in eight variables, which are the associations in zygotes at QLE. The system can be solved, for example using Mathematica (Wolfram Research 2003), to give

$$\hat{D}_{i_{ff}j_{fm}} = \hat{D}_{i_{mf}j_{mm}} = \rho \frac{b_{i_{ff}} b_{j_{mm}}}{\sigma_P \sigma_T} pq_{ij}, \quad (A21a)$$

$$\begin{aligned} \hat{D}_{i_{ff}j_{ff}} &= \hat{D}_{i_{fm}j_{fm}} = \hat{D}_{i_{mm}j_{mm}} = \hat{D}_{i_{mf}j_{mf}} \\ &= \frac{1}{2} \rho \frac{b_{i_{ff}} b_{j_{mm}}}{\sigma_P \sigma_T} pq_{ij} + \frac{md_{ij}}{\bar{r}_{ij}}, \quad \text{and} \end{aligned} \quad (A21b)$$

$$\hat{D}_{i_{fm}j_{ff}} = \hat{D}_{i_{mm}j_{mf}} = 0, \quad (A21c)$$

where  $\bar{r}_{ij}$  is the recombination rate averaged across males and females. Equations (A21) are consistent with our previous results (Kirkpatrick and Hall 2004) for a model without migration.

Our ultimate goal is to find the genetic covariance between the preference and display in males after migration but before selection. Continuing with the example of an autosomal preference and display, equations (A14) and (A18) give

$$\begin{aligned} \hat{G}_{PT}^{m'} &= \sum_{i \in P_m} \sum_{j \in T_m} b_{i_m} b_{j_m} (\hat{D}_{i_{mm}j_{mf}} + \hat{D}_{i_{mm}j_{mm}} + \hat{D}_{i_{mf}j_{mf}} \\ &\quad + \hat{D}_{i_{mf}j_{mm}} + 4md_{ij}). \end{aligned} \quad (A22)$$

Here we have written the summations over the sets  $P_m$  and  $T_m$ , which are, respectively, the preference loci and display loci carried by males. Then substituting the QLE values for the  $\hat{D}$  from equations (A21) gives:

$$\begin{aligned} \hat{G}_{PT}^{m'} &= 2 \sum_{i \in P_m} \sum_{j \in T_m} b_{i_m} b_{j_m} \left[ \rho \frac{b_{i_{ff}} b_{j_{mm}}}{\sigma_P \sigma_T} pq_{ij} + md_{ij} \left( 2 + \frac{1}{\bar{r}_{ij}} \right) \right] \\ &= \frac{\rho}{2\sigma_P \sigma_T} \left[ 2 \sum_{i \in P_m} (b_{i_m} \sqrt{pq_i}) (b_{i_{ff}} \sqrt{pq_i}) \right] \left( 2 \sum_{j \in T_m} b_{j_m}^2 pq_j \right) \\ &\quad + m \left( 2 \sum_{i \in P_m} b_{i_m} d_i \right) \left( 2 \sum_{j \in T_m} b_{j_m} d_j \right) + 2m \sum_{i \in P_m} \sum_{j \in T_m} b_{i_m} b_{j_m} \frac{d_{ij}}{\bar{r}_{ij}}. \end{aligned} \quad (A23)$$

The last term shows that the genetic covariance increases with tighter linkage between the preference and trait loci. For simplicity, we assume free recombination,  $\bar{r}_{ij} = 1/2$ , which gives:

$$\begin{aligned} \hat{G}_{PT}^{m'} &= \frac{\rho}{2\sigma_P \sigma_T} \left[ 2 \sum_{i \in P_m} (b_{i_m} \sqrt{pq_i}) (b_{i_{ff}} \sqrt{pq_i}) \right] \left( 2 \sum_{j \in T_m} b_{j_m}^2 pq_j \right) \\ &\quad + 2m \left( 2 \sum_{i \in P_m} b_{i_m} d_i \right) \left( 2 \sum_{j \in T_m} b_{j_m} d_j \right). \end{aligned} \quad (A24)$$

In the autosomal preference case, the genetic variance for the preference in males is  $G_P^m = 2 \sum_{i \in P_m} b_{i_m}^2 pq_i$  and in females is  $G_P = 2 \sum_{i \in P_m} b_{i_{ff}}^2 pq_i$ . With an autosomal trait, the genetic variance for the trait in males is  $G_T = 2 \sum_{j \in T_m} b_{j_m}^2 pq_j$ . For any mode of inheritance in which preference positions are found in both males and females,

$$\sum_{i \in P_m} b_{i_m} d_i = \left( \frac{1 - F_P}{F_P} \right) \sum_{i \in P_f} b_{i_{ff}} d_i.$$

Substituting into (A24) gives

$$\begin{aligned} \hat{G}_{PT}^{m'} &\approx \frac{\rho}{2\sigma_P \sigma_T} \sqrt{\hat{G}_P} \sqrt{\hat{G}_P^m} G_T \\ &\quad + 2m \left( \frac{1 - F_P}{F_P} \right) (\hat{P} - P^C) (\hat{T} - T^C), \end{aligned} \quad (A25)$$

where  $\hat{T}$  is the mean male trait value at equilibrium on the island and  $T^C$  is the mean trait value on the continent. The last step is an approximation that assumes the associations are small so that the genetic variances are close to the values they would have at equilibrium under random mating and with no migration. With autosomal preference,  $F_P = 1/2$  and  $[(1 - F_P)/F_P] = 1$ . Nevertheless, we leave the term in the equation to show how the calculation works with other modes of inheritance.

Because  $h_T^2 = G_T/\sigma_T^2$  and  $h_P^2 = G_P/\sigma_P^2$ , then



$$\hat{G}_{PT}^{m'} = \frac{1}{2}\hat{h}_p\hat{h}_T\sqrt{\hat{G}_P^m}\sqrt{\hat{G}_T^m}\rho + 2m\left(\frac{1-F_P}{F_P}\right)(\hat{P}-P^C)(\hat{T}-T^C) \quad \text{and} \quad (\text{A26})$$

$$\hat{r}_{PT}^{m'} = \frac{1}{2}\hat{h}_p\hat{h}_T\rho + \frac{2m\sqrt{(1-F_P)}(\hat{P}-P^C)(\hat{T}-T^C)}{\sqrt{F_P}\sqrt{\hat{G}_P^m}\sqrt{\hat{G}_T^m}}. \quad (\text{A27})$$

To obtain the second term of (A27), note that  $\hat{G}_P^m = [(1-F_P)/F_P]\hat{G}_P$ . Values for the genetic correlation under other modes of inheritance are derived analogously. With our assumption that  $m \ll a$ , the second term will be much smaller than the first and will be

TABLE A1. The genetic correlation under different modes of inheritance. Columns 1 and 2 show the mode of inheritance of the preference and male display trait respectively. Column 3 gives the equilibrium value of the genetic correlation,  $\hat{r}_{PT}^{m'}$ , between the male display trait and female preference after migration. Note that with W-linked preferences, there is no genetic correlation between the male trait and female preference in males, because there are no female preference alleles in males.

Preference	Trait	$\hat{r}_{PT}^{m'}$
A	A	$\frac{2m(\hat{P}-P^C)(\hat{T}-\bar{T}^C)}{\sqrt{G_P}\sqrt{G_T}} + \frac{h_ph_T\rho_{PT}}{2}$
	X	$\frac{2m(\hat{P}-P^C)(\hat{T}-\bar{T}^C)}{\sqrt{G_P}\sqrt{G_T}} + \frac{h_ph_T\rho_{PT}}{5}$
	Z	$\frac{2m(\hat{P}-P^C)(\hat{T}-\bar{T}^C)}{\sqrt{G_P}\sqrt{G_T}} + \frac{3h_ph_T\rho_{PT}}{5}$
X	Y	$\frac{2m(\hat{P}-P^C)(\hat{T}-\bar{T}^C)}{\sqrt{G_P}\sqrt{G_T}} + h_ph_T\rho_{PT}$
	A	$\frac{2m(\hat{P}-P^C)(\hat{T}-\bar{T}^C)}{\sqrt{2}\sqrt{G_P}\sqrt{G_T}} + \frac{4h_ph_T\rho_{PT}}{5\sqrt{2}}$
	X	$\frac{7m(\hat{P}-P^C)(\hat{T}-\bar{T}^C)}{2\sqrt{2}\sqrt{G_P}\sqrt{G_T}} + \frac{h_ph_T\rho_{PT}}{2\sqrt{2}}$
Z	Y	$\frac{m(\hat{P}-P^C)(\hat{T}-\bar{T}^C)}{\sqrt{2}\sqrt{G_P}\sqrt{G_T}} + \frac{h_ph_T\rho_{PT}}{\sqrt{2}}$
	A	$\frac{4\sqrt{2}m(\hat{P}-P^C)(\hat{T}-\bar{T}^C)}{\sqrt{G_P}\sqrt{G_T}} + \frac{4h_ph_T\rho_{PT}}{5\sqrt{2}}$
	Z	$\frac{5\sqrt{2}m(\hat{P}-P^C)(\hat{T}-\bar{T}^C)}{\sqrt{G_P}\sqrt{G_T}} + \frac{h_ph_T\rho_{PT}}{\sqrt{2}}$
W	A	—
	Z	—

ignored. The Supplemental materials of Kirkpatrick and Hall (2004) give the calculations for all modes of inheritance in a model that has no migration but that is otherwise identical; it can be consulted for further details.

The values for  $\hat{r}_{PT}^{m'}$  obtained from the other analyses are shown in Table A1, with the appropriate value of  $F_P$  substituted.

### APPENDIX 3

This appendix derives an expression for  $\beta_T$ , the selection gradient on the male trait, at a migration-selection equilibrium. The result appears as equation (3) in the text. Denote the average trait value in the island population at birth equal to  $\bar{T}_m$  and  $\bar{T}_f$ , and at birth in the next generation equal to  $\bar{T}_m''$  and  $\bar{T}_f''$  in males and females respectively. The following equations describe the relationship between the trait values at the start of one generation and the start of the next

$$\bar{T}_m'' = t_{m \leftarrow m}[\bar{T}_m + m(T_m^C - \bar{T}_m) + G_T^m\beta_T] + t_{m \leftarrow f}[\bar{T}_f + m(T_f^C - \bar{T}_f)] \quad \text{and} \quad (\text{A28a})$$

$$\bar{T}_f'' = t_{f \leftarrow m}[\bar{T}_m + m(T_m^C - \bar{T}_m) + G_T^m\beta_T] + t_{f \leftarrow f}[\bar{T}_f + m(T_f^C - \bar{T}_f)], \quad (\text{A28b})$$

where  $t_{x \leftarrow y}$  is the proportion of alleles in sex  $x$  obtained from sex  $y$ . Thus, with an X-linked trait,  $t_{m \leftarrow m} = 0$ ,  $t_{m \leftarrow f} = 1$ ,  $t_{f \leftarrow m} = 1/2$ , and  $t_{f \leftarrow f} = 1/2$ .

We can solve equations (A28) to obtain an expression for  $\beta_T$  at equilibrium, assuming that the trait value in males is the same as in females on the continent and using the fact that  $t_{m \leftarrow m} + t_{m \leftarrow f} = 1$  and  $t_{f \leftarrow m} + t_{f \leftarrow f} = 1$ . Setting  $\bar{T}_m'' = \bar{T}_m = \hat{T}_m$  and  $\bar{T}_f'' = \bar{T}_f = \hat{T}_f$  and ignoring terms of order  $m^2$ ,

$$\beta_T \approx \frac{m(t_{f \leftarrow m} + t_{m \leftarrow f})(\hat{T}_m - T_m^C)}{t_{f \leftarrow m}\hat{G}_T^m}. \quad (\text{A29})$$

Now,  $t_{f \leftarrow m}/(t_{f \leftarrow m} + t_{m \leftarrow f}) = (1 - F_T)$  (the derivation of this result is given in the supplemental materials for Kirkpatrick and Hall 2004). (This relationship among the transmission coefficients does not hold for Y and W linkage, though the same result [A30] is obtained.) Thus,

$$\beta_T \approx \frac{m(\hat{T}_m - T_m^C)}{(1 - F_T)\hat{G}_T^m}, \quad (\text{A30})$$

where  $\hat{T}_m$  is the value of the mean male trait on the island at equilibrium.

Since  $\hat{T}_m$  will vary depending on the mode of inheritance of the display trait, we can calculate an expression for  $(\hat{T}_m - T_m^C)$  in terms of  $(T_{\text{opt}} - T_m^C)$ , where  $T_{\text{opt}}$  is the value of the male trait favored on the island by natural and sexual selection. It is straightforward to show that with low levels of migration ( $m \ll a$ ), the difference between  $(\hat{T}_m - T_m^C)$  and  $(T_{\text{opt}} - T_m^C)$  is negligible and can be ignored. The reason is that migration is the only force acting to move the mean male display trait away from the optimum, and thus the difference between the mean display trait and optimal trait value will be order  $m$ .

## APPENDIX 4

The effect of incompatibility on reinforcement through females and males, and their sum as it appears in equation (5) under different modes of inheritance of the female preference (column 1) and incompatibility loci (column 2), assuming additivity, dominance of the continental alleles, and dominance of the island alleles. The  $F_p I_f$  and  $(1 - F_p) I_m$  column headings refer to X-Y sex determination. In the case of Z-W sex determination, the headings should be switched. Calculations use results from Lemmon and Kirkpatrick (2006).

Preference	Incompatibility	$F_p I_f$	$(1 - F_p) I_m$	$F_p I_f + (1 - F_p) I_m$
Additive case				
A	A, A	$\frac{4}{3} s_{02}$	$\frac{4}{3} s_{02}$	$2.67 s_{02}$
A	A, X or Z	$\frac{4}{3} s_{02}$	$\frac{4}{3} s_{02}$	$2.67 s_{02}$
X or Z	A, A	$\frac{16}{9} s_{02}$	$\frac{4}{9} s_{02}$	$2.22 s_{02}$
X or Z	A, X or Z	$\frac{30}{13} s_{02}$	$\frac{65}{78} s_{02}$	$3.14 s_{02}$
Continental alleles dominant				
A	A, A	$\frac{4}{3} s_{02}$	$\frac{4}{3} s_{02}$	$2.67 s_{02}$
A	A, X or Z	$\frac{4}{3} s_{02}$	$\frac{5}{3} s_{02}$	$3.0 s_{02}$
X or Z	A, A	$\frac{16}{9} s_{02}$	$\frac{4}{9} s_{02}$	$2.22 s_{02}$
X or Z	A, X or Z	$\frac{100}{39} s_{02}$	$\frac{15}{26} s_{02}$	$3.14 s_{02}$
Island alleles dominant				
A	A, A	0	0	0
A	A, X or Z	0	$s_{02}$	$s_{02}$
X or Z	A, A	0	0	0
X or Z	A, X or Z	0	$\frac{65}{78} s_{02}$	$0.83 s_{02}$