Reinforcement and the genetics of hybrid incompatibilities

Online supplementary materials

Alan R. Lemmon and Mark Kirkpatrick
INTRODUCTION

We begin by deriving a model of reinforcement that is general with regards to the form of selection against hybrids. We then apply the general model to specific types of hybrid incompatibility in order to determine how the pattern of sex linkage of female preference and hybrid incompatibility genes affects the potential for reinforcement.

The methods and notation follow Kirkpatrick et al. (2002; hereafter KJB), which can be consulted for further details. We say that genes carried by an individual occupy positions, with two positions at each locus. At locus $i$, for example, the gene carried by a female and inherited from a female (the individual's mother) is denoted $i_ff$, while the gene she inherited from a male (her father) is written $i_fm$. The sets of all positions that affect the female preference, male trait, and hybrid incompatibility are denoted $\mathbb{P}$, $\mathbb{T}$, and $\mathbb{H}$, respectively. The entire genome is denoted $\mathbb{W}$. The set of all positions in females that affect the preference is written $\mathbb{P}_f$; with $n$ autosomal loci, there are $2^n$ positions in this set. On the island, the frequency of allele 1 at position $i$ (where $i$ could represent $i_ff$, $i_fm$, $i_ft$, or $i_mn$) is denoted $p_i$, with $q_i = 1 - p_i$. The notation is summarized in the appendix of the manuscript.

Central to our analysis is the "quasi-linkage equilibrium", or QLE, approximation that was introduced by Barton and Turelli (1991). When selection acting on individual loci and groups of loci is weak relative to rates of recombination, the associations (linkage disequilibrium) between loci will rapidly evolve to values that are small relative to their maximum possible values.
THE GENERAL MODEL

We make the assumption that preference genes have additive effects (that is, that they show no dominance or epistasis) and no imprinting (that is, alleles inherited from mothers and fathers are expressed equally). Without making any further assumptions, we can then write the preference for an individual as

\[ P = \bar{P} + \sum_{i \in P_i} b_i \zeta_i, \]  

where \( \bar{P} \) is the mean preference among female zygotes, \( b_i \) is the difference in the preference caused by carrying allele 1 rather than allele 0 at locus \( i \), and \( \zeta_i = q_i \) if the female carries allele 1 at position \( i \) 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

\[ \Delta \bar{P} = \sum_{i \in P_i} b_i \Delta p_i \]  

where \( \Delta p_i \) is the change in allele frequency at position \( i \) from the start of one generation to the start of the next. This change is caused by forces acting within a generation, i.e. migration and selection, and by transmission between generations. Note that transmission can cause a change even at equilibrium.
For example, when there is no selection acting on one sex, allele frequencies after selection are
different in males and females, and thus they change during transmission.

We assume a life cycle that begins with selection on hybrid incompatibility, followed by
migration, followed by selection on the male trait. Assuming selection on hybrid incompatibility
precedes migration is biologically plausible and produces simpler equations than assuming selection on
hybrid incompatibility follows migration. Qualitative results are similar under the second assumption.
In what follows, we use primes to denote the stage of the life cycle, with no primes denoting the start
of the generation, one denoting just after selection on hybrid incompatibility, two denoting just after
migration, three denoting just after natural and sexual selection on the male trait, and four denoting just
after transmission. We assume no direct selection on the female preference loci.

We are seeking the equilibrium for the mean preference. We first note that assuming no
meiotic drive, one can show that the allele frequency change is asymptotically equal for all the
positions at a locus. Further, the rate of change is equal to the change within a generation averaged
over all the positions at that locus. Thus for locus $j$,

\[
\Delta \bar{p}_i = \frac{1}{n_i} \sum_{j: j = i} (p_j^m - p_j),
\]

(3)

where $n_i$ is the number of positions at locus $i$ (e.g. $n_i = 4$ for an autosomal locus in a diploid dioecious
population) and tildas denote values at QLE. The summation is over all positions $j$ that are at the same
locus as position $i$. The proof of (3) is given in Appendix A below. The change in allele frequencies due to migration and selection within a generation is

$$p_j - p_j = \sum_{A \in H} a_A D_{A_j} + m(p_j^C - p_j') + \sum_{A \subseteq J} a_A D_{A_j},$$

where $m$ is proportion of newly arrived migrants, $p_j^C$ is the allele frequency among migrants from the continent, $a_A$ is the selection coefficient on positions in set $A$, and $D_{A_j}$ is the association (linkage disequilibrium) among positions in the set $A_j$.

The $a_A$ are coefficients for selection (both natural and sexual) as defined by KJB (their equation 7). Key to our approach is the fact that these coefficients can describe any form of selection, including arbitrary patterns of dominance and multilocus epistasis. We can use this result, therefore, to study any specific type of hybrid incompatibility, and in a later section we calculate their values for several specific types of hybrid incompatibility. To make further progress on the general model we assume at this point that the $a$ are much smaller than 1, meaning that the force of selection on individual loci and sets of loci is weak relative to rates of recombination. Under these conditions, the associations rapidly evolve to values that are of order $a$. Further, it is possible to derive simple approximations for them that are accurate to order $a$, and we will do that below. We therefore replace $D_{A_j}$ in (4) by $\tilde{D}_{A_j} + O(a^2)$, where a tilda denotes a QLE approximation.
We can now find the asymptotic rate of change in the mean preference by substituting these results into (2), which with some minor rearrangement gives

\[ \Delta \bar{P} = m \sum_{i \in P_i} \sum_{j: j = i} \frac{1}{n_i} b_i (p'_j - p_j) \]

\[ + \sum_{i \in P_i} \sum_{j: j = i} \sum_{A \subseteq H} \frac{1}{n_i} b_i a_A \bar{D}_{Aj} \]

\[ + \sum_{i \in P_i} \sum_{j: j = i} \sum_{A \subseteq H} \frac{1}{n_i} b_i a_A \bar{D}_{A''} + O(a^3). \] (5)

The three terms on the right represent, respectively, migration, the effects of selection on hybrid incompatibility, and selection on the male trait. Consider the first term. Differences between the allele frequencies at positions at the same locus are \( O(a) \), and so we can write \( p'_j = p_j + O(a) \), where \( p_j \) is the average of the allele frequencies at locus \( j \). Likewise, since the changes in allele frequencies due to selection against hybridization are \( O(a) \), we can write \( p'_j = p_j + O(a) \). The inner summation then causes the term corresponding to a given preference position in a female to be summed \( n_i \) times.

Considering the second and third terms, we can replace the two outer summations by a single summation over all positions in set \( P \) (including those in males and females) if each term in the sum is multiplied by \( n_i \), the number of positions at locus \( i \) carried by females.

We now assume that all preference positions have the same mode of inheritance, and that migration is much weaker than selection (specifically, that \( m \) is \( O(a^2) \)). This gives
\[
\Delta \bar{P} = m \sum_{i \in P} b_i (p_i^c - \bar{p}_i) + \sum_{i \in P} \frac{n_i}{n} b_i \sum_{A \subseteq H} a_A \bar{D}_{A|i}
\]

\[
+ \sum_{i \in P} \frac{n_i}{n} b_i \sum_{A \subseteq I} a_A \bar{D}_{A|i} + O(a^3)
\]

\[
= m (P^c - \bar{P}) + F_p \sum_{i \in P} b_i \sum_{A \subseteq H} a_A \bar{D}_{A|i}
\]

\[
+ F_p \sum_{i \in P} b_i \sum_{A \subseteq I} a_A \bar{D}_{A|i} + O(a^3),
\]

where \(P^c\) is the mean female preference on the continent, and \(F_p\) is the fraction of preference positions carried by females (e.g., 1/2 for autosomal preferences, 2/3 for X-linked preferences).

Setting \(\Delta \bar{P}\) to zero and rearranging, we find at equilibrium that the amount of reinforcement is

\[
\hat{P} - P^c = \frac{F_p}{m} \left( \sum_{i \in P} b_i \sum_{A \subseteq H} a_A \bar{D}_{A|i} + \sum_{i \in P} b_i \sum_{A \subseteq H} a_A \bar{D}_{A|i} \right)
\]

\[
+ \frac{F_p}{m} \sum_{i \in P} b_i \sum_{A \subseteq I} a_A \bar{D}_{A|i} + O(a).
\]

where \(\hat{P}\) is the mean preference at equilibrium. Here we have split up the sum corresponding to selection on hybrid incompatibility into two terms, one reflecting selection on females and the second
selection on males. We are able split the sum because \( \bar{D}_{Ai} = 0 \) whenever \( Ai \) contains more than one sex of carrier.

Hybrid incompatibility drives evolution of the preference through the genetic associations between incompatibility alleles and preference alleles, which appear as \( \bar{D}_{Ai} \) in equation (7). These associations are generated by admixture (that is, migration or hybridization). As we show in Appendix B, when there is a lack of pleiotropy between the male trait and the hybrid incompatibility the QLE values for the associations among positions are of the form

\[
\bar{D}_{Ai} = m d_{Ai} \phi_{Ai},
\]

where

\[
d_{Ai} = (p_C^i - p_i) \prod_{j \in A} (p_C^j - p_j),
\]

and \( \phi_{Ai} \) is a constant factor that depends on the mode of inheritance for the preference position \( i \) and the incompatibility positions in the set \( A \), as well as the probabilities of recombination in males and females breaking up loci in the set \( Ai \). Appendix B shows how to compute \( \phi_{Ai} \) for any mode of inheritance for the preference and incompatibility loci.
In order to simplify (7) further, however, we need an expression for \( \phi_{A_i} \) that is independent of the preference position \( i \). \( \phi_{A_i} \) is independent of \( i \) when all loci affecting the preference have the same mode of inheritance and the probability of recombination breaking up the set \( Ai \) in each sex is the same for all preference loci. This condition is met, for example, when there is only one loci affects the preference or when all of the preference loci are unlinked to the incompatibility loci when possible.

We assume that the latter case is true. This means that when the preference is autosomal,

\[
(1 - r_{Ai}^f) = \frac{1}{2} (1 - r_{Ai}^f) \quad \text{and} \quad (1 - r_{Ai}^m) = \frac{1}{2} (1 - r_{Ai}^m),
\]

where the superscript denotes whether recombination is occurring in females (f) or males (m). When the preference and one or more of the incompatibility loci are X-linked, however,

\[
(1 - r_{Ai}^f) = \frac{1}{2} (1 - r_{Ai}^f) \quad \text{and} \quad (1 - r_{Ai}^m) = (1 - r_{Ai}^m).
\]

With this assumption we can write (8) as

\[
\bar{D}_{(A \delta)_{i_{f}}} = m d_{Ai} \phi_{A_{i_{f}}}^f \quad \text{and} \quad \bar{D}_{(A \delta)_{i_{m}}} = m d_{Ai} \phi_{A_{i_{m}}}^m.
\]

(10)

The values of the \( \phi_{A}^f \) and \( \phi_{A}^m \) are given in Table 3, Appendix B. Equation (10) shows that the associations between the preference and incompatibility loci are generated by introgression, and are proportional to its rate (represented by \( m \)). These are the associations that link selection against hybrids to reinforcement of the preference. Now we can write
\[
\hat{P} - P^C = F_P \left( \sum_{i \in P_f} b_i \sum_{A \subseteq H_f} a_A d_A \phi_A^f + \sum_{i \in P_m} b_i \sum_{A \subseteq H_m} d_A \phi_A^m \right)
\]

\[
+ \frac{1}{m} F_P \sum_{i \in P} b_i \sum_{A \subseteq I} a_A \bar{D}^A_i + O(a)
\]

\[
= (\hat{P} - P^C) \left[ F_P I_f + (1 - F_P) I_m \right] + M + O(a).
\]

Here,

\[
I_f = - \sum_{A \subseteq H_f} a_A d_A \phi_A^f \quad \text{and} \quad I_m = - \sum_{A \subseteq H_m} a_A d_A \phi_A^m
\]

represent the effects on the preference of selection on hybrid incompatibility acting on females and males, respectively, and

\[
M = \frac{F_P}{m} \sum_{i \in P} b_i \sum_{A \subseteq I} a_A \bar{D}^A_i
\]

represents the effects on the preference of natural and sexual selection on the male display.

Rearranging finally gives us an expression for the amount of reinforcement that is general to all forms of inheritance for the hybrid incompatibility:
\[ \hat{P} - P^C = \frac{M}{1 - T} + O(a), \]  

(14)

where

\[ I = F_p I_f + (1 - F_p) I_m. \]  

(15)

Written this way, we have partly isolated the effects of the modes of inheritance of the display trait loci from the those of the hybrid incompatibility loci. The modes of inheritance of hybrid incompatibility affect \( I_f \) and \( I_m \), but it is plausible that (at least to a first approximation) they will not change \( M \).

Likewise, the mode of inheritance of the display trait loci will only affect \( M \). Since our focus of this paper is on how inheritance of hybrid incompatibility affects speciation, we will simplify our analysis by treating \( M \) as a fixed entity. It is possible that reinforcement will cause the male trait to evolve in a way that causes \( M \) to vary depending on the strength of selection on hybrid incompatibility. Lastly, note that the mode of inheritance of the preference will affect \( M, F_p, I_f, \) and \( I_m \).
We can see from (14) that the approximation becomes less accurate as the force of selection against hybrids increases (the denominator approaches zero as $I$ approaches 1). A second approximation that will be more accurate for values of $I$ close to 1 can be obtained using a Taylor approximation. Multiplying the numerator and denominator of (14) by $1 + I$ and neglecting the $I^2$ that appears in the denominator, we obtain

$$\hat{P} - P^C = M(1 + I) + O(a).$$

Equation (16) has a simple and intuitive interpretation. Selection on the male trait is sufficient to cause reinforcement, even without additional selection on the incompatibility loci (in which case $I = 0$). Selection against hybrid incompatibilities further amplifies the amount of reinforcement. We will now see how different forms of hybrid incompatibility affect reinforcement.
ONE- AND TWO-LOCUS INCOMPATIBILITIES

In the previous section we derived equations describing the effect of selection against hybrid incompatibility on the amount of reinforcement. As (12) shows, this effect depends on the values of three terms: $a_A$, $d_A$, and $f_A$. Values for $f_A$, derived in Appendix B, depend on how the preference and incompatibility loci are inherited and on the rates of recombination breaking them up.

The value of $a_A$ depends on the intensity and pattern of selection on the hybrid incompatibility loci. Here we study one- and two-locus incompatibilities. We allow each incompatibility locus to be either autosomal, X-linked, Y-linked, Z-linked, or W-linked. Our notation for the strengths of selection against different genotypes at the hybrid incompatibility loci are given in the manuscript Figure 1. We assign the island genotype, defined to be homozygous/hemizygous for the 1 allele at all loci, a fitness of one and other genotypes a fitness relative to that of the island genotype. Using this notation we show in Appendix C how to derive expressions for the $a_A$ found in (12) in terms of the selection coefficients given in Figure 1 of the manuscript. Table 4 of Appendix C presents those expressions for all types of one- and two-locus incompatibilities.

The value of $d_A$ depends on the amount of divergence between the island and continent at the hybrid incompatibility loci. The value of $d_A$ turns out to be quite simple since we are assuming that migration is much weaker than selection (i.e. $m = O(s^2)$). This assumption is reasonable because when migration is not relatively weak, the continent and island cannot maintain a polymorphism at the incompatibility loci and reinforcement cannot occur. One can easily show that under this assumption,
\( p_j^C - p_j = -1 + O(s) \) for any locus \( j \). This fact allows us to use the following \( O(s) \) approximation for \( d_A \):

\[
d_A = (-1)^n + O(s),
\]

where \( n \) is the number of elements in \( A \). This result holds regardless of the number of loci in \( A \) or the pattern of inheritance of those loci.

Now that we have expressions for \( a_A, d_A, \) and \( \phi_A \) we can compute \( I_f \) and \( I_m \) for any type of one- or two-locus incompatibility by plugging values from Tables 3-4 and equation (17) into (12).

Before we give the results, we summarize the assumptions required to arrive at the results, which are:

1) QLE (selection is weak relative to rates of recombination)
2) preference genes have additive effects
3) no imprinting
4) two alleles per locus
5) selection against hybrid incompatibility happens before migration
6) selection on the male trait happens after migration
7) no direct selection on the female preference
8) no meiotic drive
9) all preference positions have the same mode of inheritance
10) migration is weak relative to the strength of selection
11) no pleiotropy (each locus affects only the incompatibility, the male trait, or the preference)

12) preference positions are unlinked to the incompatibility loci when possible

The effects of selection against hybrids on the amount of reinforcement ($I_f$ and $I_m$) are presented in the following table. A, X, and Y indicate that all loci are autosomally inherited, X-linked, and Y-linked, respectively. A-A, A-X, A-Y, X-X, and X-Y denote autosome-autosome, autosome-X, autosome-Y, X-X, and X-Y incompatibilities, respectively. Equations pertaining to a Z-W system of sex-determination are identical, except with $f$ and $m$ subscripts interchanged.
Table 1. The effect of selection against male ($I_f$) and female ($I_m$) hybrids on reinforcement.

**Autosomal preference**

<table>
<thead>
<tr>
<th></th>
<th>$I_f$</th>
<th>$I_m$</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>$4 s_{1f}$</td>
<td>$4 s_{1m}$</td>
</tr>
<tr>
<td>X</td>
<td>$4 s_{1f}$</td>
<td>$2 s_{0m}$</td>
</tr>
<tr>
<td>Y</td>
<td>0</td>
<td>$2 s_{0m}$</td>
</tr>
<tr>
<td>A-A</td>
<td>$4 (s_{12f} + s_{21f}) + 8 \frac{8 s_{11f} - s_{12f} - s_{21f}}{2 + r_{d1}^2 + r_{d2}^2}$</td>
<td>$4 (s_{12m} + s_{21m}) + 8 \frac{8 s_{11m} - s_{12m} - s_{21m}}{2 + r_{d1}^2 + r_{d2}^2}$</td>
</tr>
<tr>
<td>A-X</td>
<td>$\frac{8}{3} s_{11f} + \frac{4}{3} s_{12f} + \frac{4}{3} s_{21f}$</td>
<td>$\frac{4}{3} s_{10m} + \frac{8}{3} s_{12m} + \frac{2}{3} s_{20m}$</td>
</tr>
<tr>
<td>A-Y</td>
<td>0</td>
<td>$\frac{4}{3} s_{10m} + \frac{8}{3} s_{12m} + \frac{2}{3} s_{20m}$</td>
</tr>
<tr>
<td>X-X</td>
<td>$2 (s_{12f} + s_{21f}) + 20 \frac{8 s_{11f} - s_{12f} - s_{21f}}{5 + 3 r_{d1}^2}$</td>
<td>$2 (s_{02m} + s_{20m}) + 2 \frac{8 (5 - r_{d1}^2) s_{00m} - s_{02m} - s_{20m}}{5 + 3 r_{d1}^2}$</td>
</tr>
<tr>
<td>X-Y</td>
<td>0</td>
<td>$2 (s_{02m} + s_{20m})$</td>
</tr>
</tbody>
</table>
X-linked preference

\[ I_f \]

A \( 4 s_{1f} \)

X \( 6 s_{1f} \)

Y \( 0 \)

A-A \( 4 (s_{12f} + s_{21f}) + 4 \frac{(5 - r_{il}^2)(s_{11f} - s_{12f} - s_{21f})}{5 + r_{il}^2(3 - r_{il}^2) + r_{il}^4} \)

A-X \( \frac{40}{13} s_{11f} + \frac{12}{13} s_{12f} + \frac{38}{13} s_{21f} \)

A-Y \( 0 \)

X-X \( 6 (s_{12f} + s_{21f}) + 6 \frac{s_{11f} - s_{12f} - s_{21f}}{1 + r_{il}^2} \)

X-Y \( 0 \)

\[ I_m \]

\( 2 s_{1m} \)

\( \frac{5}{2} s_{0m} \)

\( 0 \)

\( 0 \)

\( 2 (s_{12m} + s_{21m}) + 2 \frac{(5 - r_{il}^2)(s_{11m} - s_{12m} - s_{21m})}{5 + r_{il}^2(3 - r_{il}^2) + r_{il}^4} \)

\( \frac{18}{13} s_{10m} + \frac{8}{13} s_{12m} + \frac{29}{26} s_{20m} \)

\( 2 s_{12m} \)

\( \frac{5}{2} (s_{02m} + s_{20m}) + \frac{(5 - r_{il}^2)(s_{00m} - s_{02m} - s_{20m})}{2 + 2 r_{il}^2} \)

\( \frac{5}{2} s_{02m} \)
To compute the total contribution to reinforcement, $I$, contributions from females and males are weighted by the proportion of preference genes found in females ($F_P$) and males ($1 - F_P$) as follows:

$$ I = F_P I_f + (1 - F_P) I_m $$

(18)

where $F_P = \frac{1}{2}$ with an autosomal preference and $F_P = \frac{2}{3}$ with an X-linked preference. The following table provides expressions for the total contribution to reinforcement.
Table 2. The total effect of selection against hybrids (I) on reinforcement.

**Autosomal preference**

\[ \begin{align*}
I & \\
A & 2s_{1f} + 2s_{1m} \\
X & 2s_{1f} + s_{0m} \\
Y & s_{0m} \\
A-A & 2(s_{12f} + s_{21f}) + 4 \frac{s_{11f} - s_{12f} - s_{21f}}{2 + r_{d1}^2 + r_{d2}^2} + 2(s_{12m} + s_{21m}) + 4 \frac{s_{11m} - s_{12m} - s_{21m}}{2 + r_{d1}^2 + r_{d2}^2} \\
A-X & \frac{4}{3}s_{11f} + \frac{2}{3}s_{12f} + \frac{2}{3}s_{21f} + \frac{2}{3}s_{10m} + \frac{4}{3}s_{12m} + \frac{1}{3}s_{20m} \\
A-Y & \frac{2}{3}s_{10m} + \frac{4}{3}s_{12m} + \frac{1}{3}s_{20m} \\
X-X & 2(s_{12f} + s_{21f}) + 10 \frac{s_{11f} - s_{12f} - s_{21f}}{5 + 3r_{d1}^2} + (s_{02m} + s_{20m}) + \frac{(5 - r_{d1})(s_{00m} - s_{02m} - s_{20m})}{5 + 3r_{d1}^2} \\
X-Y & s_{02m} + s_{20m}
\end{align*} \]
X-linked preference

\[ I \]

\[ A \quad \frac{8}{3} s_{1f} + \frac{2}{3} s_{1m} \]

\[ X \quad 4 s_{1f} + \frac{5}{6} s_{0m} \]

\[ Y \quad 0 \]

\[ A-A \quad \frac{8}{3} (s_{12f} + s_{21f}) + \frac{8}{3} \left( \frac{5 - r_{3l}^{ij}}{5 + r_{3l}^{ij}} \right) (s_{11f} - s_{12f} - s_{21f}) + \frac{2}{3} (s_{12m} + s_{21m}) + \frac{2}{3} \left( \frac{5 - r_{3l}^{ij}}{5 + r_{3l}^{ij}} \right) (s_{11m} - s_{12m} - s_{21m}) \]

\[ A-X \quad \frac{80}{39} s_{11f} + \frac{24}{39} s_{12f} + \frac{76}{39} s_{21f} + \frac{18}{39} s_{10m} + \frac{8}{39} s_{12m} + \frac{29}{78} s_{20m} \]

\[ A-Y \quad \frac{2}{3} s_{12m} \]

\[ X-X \quad 4 (s_{12f} + s_{21f}) + 4 \left( \frac{s_{11f} - s_{12f} - s_{21f}}{1 + r_{3l}^{ij}} \right) + \frac{5}{6} (s_{02m} + s_{20m}) + \frac{1}{6} \left( \frac{5 - r_{3l}^{ij}}{1 + r_{3l}^{ij}} \right) (s_{00m} - s_{02m} - s_{20m}) \]

\[ X-Y \quad \frac{5}{6} s_{02m} \]
ECOLOGICAL INCOMPATIBILITIES

Here we answer the question: how does selection against ecologically-inferior hybrids favor reinforcement of prezygotic isolation? Here we study a model in which genes contribute additively to a quantitative trait, such as body size or bill length. In this model, hybrids are unfit because they have intermediate phenotypes that are selected against. We'll assume that in the absence of hybridization, the island and the continent species would be fixed for a set of loci that have additive effects on the ecological trait. It turns out to simplify things substantially if we assume that the \( n \) diploid loci influencing the trait are interchangeable: then they have equal allele frequencies and equal effects on the trait. Without loss of generality, we can define the scale of measurement for the ecological trait such that \( Z = 0 \) when all the loci are fixed for the favored allele (allele 0). The mean of the continent is denoted \( Z^C \).

**Selection coefficients:** We can approximate the fitness function of an individual in the vicinity of \( Z = 0 \) by a quadratic:

\[
W = 1 + \beta Z + \Gamma Z^2. \tag{19}
\]

Here, fitness is a function of the directional selection gradient \( \beta \) and the stabilizing selection gradient \( \Gamma \) acting on the ecological trait. (Negative values of \( \Gamma \) correspond to stabilizing selection, and positive values to disruptive selection.) The values of the selection gradients depend on the fitness function for
the ecological trait and also on the distribution of that trait in the island population. That distribution evolves in response to selection and migration, which causes the values of the selection gradients to change. The $\beta$ and $\Gamma$ in the expressions that follow refer to the equilibrium values for the gradients. See Lande and Arnold (1993) and Kirkpatrick (2001) for more details.

Using our usual notation, the phenotype of an individual can be written

$$ Z = \bar{Z} + \sum_{i \in \mathbb{I}} b_i \xi_i, $$  \hspace{1cm} (20)  

where mean phenotype is

$$ \bar{Z} = 2np_i b_i. $$  \hspace{1cm} (21)  

Recall that $p_i$ is the frequency of the $1$ allele. Under our assumptions, when $p_i = 1$ the mean phenotype is $Z^C$. That means $b_i = \frac{Z^C}{2n}$, and so

$$ \bar{Z} = 2n p_i \left( \frac{Z^C}{2n} \right) = p_i Z^C. $$  \hspace{1cm} (22)  

The fitness function needed to calculate the $a$s is

$$ \frac{W}{W'} \approx 1 + \beta (p_i Z^C + \sum_{i \in \mathbb{I}} b_i \xi_i) + \Gamma (p_i Z^C + \sum_{i \in \mathbb{I}} b_i \xi_i)^2 $$  \hspace{1cm} (23)  

The approximation assumes that all individuals in the population are near $Z = 0$. This is consistent with our assumption that the hybridization rate is very small, and so the frequencies of alleles from the continent are very small. Picking out the appropriate coefficients of the $\zeta$s shows that the selection coefficients are

$$a_i = \frac{1}{2n} \beta Z^C + \frac{1}{n} \Gamma Z^{C^2} p_i,$$

(24)

and

$$a_{ij} = \frac{1}{4n^2} \Gamma Z^{C^2}.$$

(25)

Assuming selection is much stronger than hybridization, the equilibrium value for the allele frequencies for the ecological trait are:

$$p_i \approx \frac{m}{\beta b_i} \approx \frac{2mn}{\beta Z^C},$$

(26)

which completes the calculation for the selection coefficients:
\[ a_i = \frac{1}{2\pi} \beta Z^C + \frac{2}{\beta} m \Gamma Z^C. \] (27)

**The effect of ecological selection:** Now we derive an expression for \( I \) using the selection coefficients derived above. We will assume that females and males with the same value of \( Z \) have equal fitness. Under this assumption, \( I_f = I_m \). From the derivation of the \( a_i \)s above, we know that there are two types of \( a_i \)s, those that involve one position and those that involve two positions.

Separating the sum into two parts yields

\[
I = -\sum_{i \in H} a_i d_i \phi_i - \sum_{i \in H} \sum_{j \neq i} a_{ij} d_{ij} \phi_{ij}.
\] (28)

Since we are assuming that the continent and island are nearly fixed for alternative alleles, \( d_i \approx -1 \) and \( d_{ij} \approx 1 \). Now we have

\[
I = \sum_{i \in H} a_i \phi_i - \sum_{i \in H} \sum_{j \neq i} a_{ij} \phi_{ij}.
\] (29)

Plugging in the values for the \( a_i \)s yields

\[
I = \sum_{i \in H} \left( \frac{1}{2\pi} \beta Z^C + \frac{2}{\beta} m \Gamma Z^C \right) \phi_i - \sum_{i \in H} \sum_{j \neq i} \left( \frac{1}{4\pi^2} \Gamma Z^C \right)^2 \phi_{ij}
\]
\[
I = \left( \frac{1}{2n} \beta Z^C + \frac{2}{\beta} m \Gamma Z^C \right) \sum_{i \in H} \phi_i - \left( \frac{1}{4n^2} \Gamma Z^C^2 \right) \sum_{i \in H} \sum_{j \neq i} \phi_{ij}.
\]

If we assume that \( n \) is large, then \( n^2 \) is very large and the right term is nearly zero so

\[
I \approx \left( \frac{1}{2n} \beta Z^C + \frac{2}{\beta} m \Gamma Z^C \right) \sum_{i \in H} \phi_i.
\]  
(31)

The summation in equation (31) adds up the contributions to reinforcement for all positions affecting the ecological trait. Using \( n \bar{\phi} = \sum_{i \in H} \phi_i \), where \( \bar{\phi} \) is the average contribution of a position to reinforcement, we have

\[
I \approx \left( \frac{1}{2n} \beta Z^C + \frac{2}{\beta} m \Gamma Z^C \right) n \bar{\phi}
\]

(32)

\[
= \left( \frac{1}{2} \beta Z^C + \frac{2n}{\beta} m \Gamma Z^C \right) \bar{\phi}.
\]

Using the fact that \( mn / \beta = Z^C p_i / 2 \), we substitute to obtain

\[
I \approx \left( \frac{1}{2} \beta Z^C + \Gamma Z^C^2 p_i \right) \bar{\phi}.
\]  
(33)
Since we are assuming that \( p_i \approx 1 \) for all \( i \),

\[
I \approx (\frac{1}{2} \beta Z^C + \Gamma Z^C^2) \bar{\phi}.
\]  

(34)

Since we have defined \( Z \) to be in the vicinity of zero at equilibrium, we can replace

\[
Z^C = Z^C - \hat{Z} = |\hat{Z} - Z^C|.
\]

Our final result for the effect of ecological selection on the amount of reinforcement is

\[
I \approx \bar{\phi}(\frac{1}{2} \beta |\hat{Z} - Z^C| + \Gamma (\hat{Z} - Z^C)^2).
\]  

(35)

To study the affect of sex linkage, we define \( \pi_A, \pi_X, \) and \( \pi_Y \) to be the proportions of the ecological trait loci that are autosomally inherited, X-linked, and Y-linked, respectively. Using this notation, results from Table 3, and the fact that \( r_{kl} = 0 \) when \( \phi_A \) contains one position, one can show that \( \bar{\phi} = 8 \pi_A + 6 \pi_X + 2 \pi_Y \) when the preference is autosomally inherited and \( \bar{\phi} = 6 \pi_A + \frac{17}{2} \pi_X \) when the preference is X-linked.
LITERATURE CITED


APPENDIX A: The asymptotic change in allele frequencies among positions at a locus

Here we show that after a short period, the allele frequencies of all the positions at a locus evolve at the same rate. This rate is equal to the change within a generation averaged over all the positions at that locus. Begin by writing the initial frequencies of the alleles at a locus as the vector $\mathbf{p}_0$.

After one generation,

$$
\mathbf{p}_1 = \mathbf{T} (\mathbf{p}_0 + \mathbf{\Delta}),
$$

where $\mathbf{T}$ is a matrix of transmission coefficients and $\mathbf{\Delta}$ is the vector of changes in allele frequencies within a generation caused by selection and migration. At QLE, $\mathbf{\Delta}$ is constant. After two generations of QLE, we have

$$
\mathbf{p}_2 = \mathbf{T}(\mathbf{p}_1 + \mathbf{\Delta}) = \mathbf{T}^2 \mathbf{p}_0 + \mathbf{T}^2 \mathbf{\Delta} + \mathbf{T} \mathbf{\Delta},
$$

and after $t$ generations,

$$
\mathbf{p}_t = \mathbf{T}^t \mathbf{p}_0 + (\sum_{i=1}^{t} \mathbf{T}^i) \mathbf{\Delta}.
$$

Thus the vector of changes in allele frequencies at generation $t$ is

$$
\mathbf{\Delta} \mathbf{p}_t = \mathbf{p}_{t+1} - \mathbf{p}_t = (\mathbf{T}^{t+1} - \mathbf{T}^t) \mathbf{p}_0 + \mathbf{T}^t \mathbf{\Delta}.
$$

Since $\mathbf{T}$ is a stochastic matrix, for $t$ large we have $\mathbf{T}^{t+1} - \mathbf{T}^t \rightarrow 0$ as $t \rightarrow \infty$. Thus asymptotically the allele frequency change is

$$
\mathbf{\Delta} \mathbf{\hat{p}} = \mathbf{T}^t \mathbf{\Delta}.
$$
This implies that, for large $t$, the vector of allele frequency change $\Delta \hat{p}$ is proportional to the leading eigenvector of $T$.

We assume that meiosis is normal in the sense that there is no meiotic drive. In that case, transmission is conservative, meaning that all positions at a locus are transmitted with equal probability. This implies that the rows as well as the columns of $T$ sum to unity, that is, the matrix is "doubly-stochastic". In that case, the leading eigenvector is $\{1/n, 1/n, \ldots\}^T$ (Karlin & Taylor 1975), implying that

$$\Delta \hat{p} = \{1/n, 1/n, \ldots\}^T \vec{\Delta},$$

(41)

where $\vec{\Delta}$ is simply the mean allele frequency change within a generation among all the positions at the locus (that is, the mean of the elements of $\Delta$).

To sum up, at QLE and in the absence of meiotic drive, the change in allele frequency at position $i$ is equal to the average change at all the positions at that locus within a generation:

$$\Delta \hat{p}_i = \frac{1}{n_i} \sum_{j: j = i} (p^m_j - p^L_j),$$

(42)

where $n_i$ is the number of positions at locus $i$ and the summation is over all positions at locus $i$. 
APPENDIX B: Associations between preference and incompatibility positions at QLE

Here we find the QLE approximations for the $\bar{D}_{\mathcal{A}i}$, the associations between preference and incompatibility positions that appear in (7). To do so, we derive a recursion for their evolution. Because we are interested in the affect of hybrid incompatibility on reinforcement, we assume that there is a lack of pleiotropy between the hybrid incompatibility and the male trait, that is $\mathcal{H} \cap \mathcal{T} = \emptyset$. Under this assumption, selection on the male trait loci will not affect the associations between the preference and incompatibility positions.

It is convenient to work backwards, starting with the associations in zygotes at the beginning of the next generation, which we denote as $\bar{D}_{\mathcal{A}i}$, and we assume that the life cycle begins with selection against incompatibilities, followed by migration, followed by mating and transmission. The associations in zygotes can be written in terms of the associations among mated adults of the current generation:

\[
\bar{D}_{\mathcal{A}i} = \sum_{j : \mathcal{A}i \cap \mathcal{U}j \neq \emptyset} \sum_{\mathcal{U}j : U = A} t_{\mathcal{A}i - \mathcal{U}j} \bar{D}_{\mathcal{U}j},
\]

(43)

where $t_{\mathcal{A}i - \mathcal{U}j}$ is a transmission coefficient, defined as the probability that the positions in set $\mathcal{A}i$ were inherited from those in set $\mathcal{U}j$, and $\bar{D}_{\mathcal{U}j}$ is the association between positions in set $\mathcal{U}j$ in the current generation after selection and migration (see KJB equation 12). Since selection on the male trait will
not affect the associations between the preference and incompatibility loci, \( D_{\mathcal{U}j}^m = D_{\mathcal{U}j}^n \), so we can rewrite (43) as

\[
D_{\mathcal{A}i}^m = \sum_{j:j=i} \sum_{U:U=A} t_{\mathcal{A}i-Uj} D_{\mathcal{U}j}^n.
\]  

(44)

The associations after migration, in turn, can be written in terms of the associations before migration but after selection on the hybrid incompatibility. We assume that migration is weak \((m << 1)\), an assumption required both by our QLE approximation and to prevent swamping of the locally-adapted allele in the island population. Then when all positions in the set \( \mathcal{U}j \) have the same sex-of-carrier,

\[
D_{\mathcal{U}j}^n = D_{\mathcal{U}j}^m + m d_{\mathcal{U}j},
\]  

(45)

where

\[
d_{\mathcal{U}j} = (p_i^c - p_j) \prod_{i \in \mathcal{U}} (p_i^c - p_i).
\]  

(46)
and a single prime denotes a value after selection but before migration (see KJB equation 34). When \( \cup_j \) involves positions with both sexes-of-carrier, \( D''_{\cup_j} = D'_{\cup_j} \). At QLE, the differences in allele frequencies among different positions at the same locus are \( O(a) \). This fact allows us to rewrite \( d_{\cup_j} \) as

\[
d_{\cup_j} = (p^C_j - p_j) \prod_{i \in U} (p^C_i - p_i)^{n_{ij}} + O(a)
\]  

(47)

where \( n_{ij} \) is defined to be the number of positions in \( \cup \) that are at the locus \( i \) and \( p_i \) is the allele frequency at locus \( i \), averaged across all positions at that locus. This expression simplifies nicely when no two positions in \( \cup \) are at the same locus (i.e. \( n_{ij} = 1 \) for all \( \cup i \)), which is true when all positions in \( \cup \) have the same sex of carrier and the same sex of origin. When this is true we can replace \( d_{\cup_j} \) with

\[
d_{\cup_j} + O(a), \text{ where } d_{\cup_j} \text{ is defined as}
\]

\[
d_{\cup_j} = (p^C_j - p_j) \prod_{i \in U} (p^C_i - p_i).
\]  

(48)

To complete the life cycle, we write the associations after selection in terms of those in zygotes. Since \( j \) represents a preference position, and since we assume that the preference is free of direct selection, the change in associations between \( j \) and incompatibility positions caused by selection is \( O(a^2) \). Thus we can write
\[ D_{ij}^1 = D_{ij} + O(a^2). \] (49)

We can now find the QLE approximation for the associations. We set the values of the associations at the beginning of successive generations equal, \( D_{Ai} = D_{Ai} = D_{Ai}, \) and drop terms \( O(a^2) \). Substituting equations (45) and (49) into (44) shows that when the positions in set \( Ai \) include both sexes of origin, then \( D_{Ai} = 0 \). When they all have a single sex-of-origin,

\[
D_{Ai} = \sum_{j: j = i} \sum_{U: U = A} \ t_{Ai - Uj} (D_{ij} + m \ d_{ij})
\]

\[
= m \ d_{Ai} + \sum_{j: j = i} \sum_{U: U = A} \ t_{Ai - Uj} \ D_{ij}
\] (50)

Expression (50) represents a linear system of equations that can always be solved to give the QLE approximations for the associations under any kind of inheritance, which is specified by the transmission coefficients. We could, for example, study a case in which some preference genes are autosomal while others are cytoplasmic, and hybrid incompatibilities involving autosome-X epistatic interactions. The number of associations described by equation (50) depends on the mode of inheritance. For example, if preference locus \( i \) and all the hybrid incompatibility loci \( A \) are autosomal, then there are four kinds of associations: \( D_{(Ai)}^1, D_{(A)}^1, D_{(Ai)}^m, \) and \( D_{(A)}^m \). On the other hand, if \( A \) and \( i \) are all X-linked, then there are only three kinds of these associations: \( D_{(Ai)}^1, D_{(A)}^1, \) and \( D_{(A)}^m \).
Given any particular form of inheritance, we can solve for these associations by first writing them as a vector \( \hat{D} \) (where the order of the elements is arbitrary). We can then write equation (50) in matrix form as

\[
\hat{D} = T \hat{D} + m d_{Ai} \mathbf{1},
\]

(51)

where \( T \) is a matrix of transmission coefficients and \( \mathbf{1} \) is a vector of 1s. The solution for the associations is therefore

\[
\hat{D} = m d_{Ai} (I - T)^{-1} \mathbf{1},
\]

(52)

where \( I \) is the identity matrix.

To make the calculation clear, take the example where set \( A_i \) consists of a mixture of autosomal and X-linked loci. Then the QLE values for the associations given by equation (50) are
\[
\begin{pmatrix}
D_{(Ai)_{it}} \\
\bar{D}_{(Ai)_{itm}} \\
\bar{D}_{(Ai)_{mf}}
\end{pmatrix}
= m d_{ik} \begin{pmatrix}
1 - t_{(Ai)_{it} \leftarrow (Ai)_{in}} & - t_{(Ai)_{it} \leftarrow (Ai)_{im}} & - t_{(Ai)_{it} \leftarrow (Ai)_{mf}} \\
- t_{(Ai)_{itm} \leftarrow (Ai)_{it}} & 1 - t_{(Ai)_{itm} \leftarrow (Ai)_{im}} & - t_{(Ai)_{itm} \leftarrow (Ai)_{mf}} \\
- t_{(Ai)_{imf} \leftarrow (Ai)_{it}} & - t_{(Ai)_{imf} \leftarrow (Ai)_{itm}} & 1 - t_{(Ai)_{imf} \leftarrow (Ai)_{imf}}
\end{pmatrix}^{-1}
\]

\[
= m d_{ik} \begin{pmatrix}
1 - \frac{1}{2} (1 - r_{Ai}^{f}) & - \frac{1}{2} (1 - r_{Ai}^{f}) & 0 \\
0 & 1 & - \frac{1}{2} (1 - r_{Ai}^{m}) \\
- \frac{1}{2} (1 - r_{Ai}^{f}) & - \frac{1}{2} (1 - r_{Ai}^{f}) & 1
\end{pmatrix}^{-1}
\]

\[
= m d_{Ai} \begin{pmatrix}
\frac{3 - r_{Ai}^{f}}{r_{Ai}^{f} (2 - r_{Ai}^{m}) + r_{Ai}^{m}} \\
\frac{3 + r_{Ai}^{f} - 2 r_{Ai}^{m}}{r_{Ai}^{f} (2 - r_{Ai}^{m}) + r_{Ai}^{m}} \\
\frac{3 - r_{Ai}^{f}}{r_{Ai}^{f} (2 - r_{Ai}^{m}) + r_{Ai}^{m}}
\end{pmatrix},
\]

where \( r_{Ai}^{f} \) is the probability that a recombination event occurs somewhere among the loci in set \( Ai \) in females, and \( r_{Ai}^{m} \) is the corresponding rate in males. These results show that for loose linkage (which is consistent with the assumptions of the approximation), the magnitudes of the associations are greater when recombination rates between the preference locus \( i \) and the incompatibility loci \( A \) are smaller.

These results allow us to work out the associations needed to calculate the strength of reinforcement for any mixture of modes of inheritance for the preference and incompatibility loci. The results simplify greatly, however, if all the preference loci have the same recombination rates with all the incompatibility loci. This happens in two situations: when there is just a single preference locus,
or when the recombination rates $r_{Ai}^f$ and $r_{Ai}^m$ are the same for all preference loci $i$. That happens when the preference loci are autosomally inherited, and unlinked to any incompatibility loci. This is a biologically plausible situation, and so we will make that assumption in what follows. In this case, a transmission coefficient involving a preference locus $i$ can be written

$$t_{A_i, x, y, z} = \frac{1}{2} t_{A, x, y, z}. \quad (54)$$

where $x$, $y$, and $z$ can take the values $m$ and $f$. Substituting that into equation (50) gives the associations when the preference is autosomal and unlinked to the incompatibility loci, which themselves are X-linked or a mixture of X-linked and autosomal:

$$\left( \begin{array}{c} \bar{D}_{(A_i)_{xt}} \\
\bar{D}_{(A_i)_{tm}} \\
\bar{D}_{(A_i)_{mf}} \end{array} \right) = 2 m d_{A_i} \begin{pmatrix} \frac{5 - r_{Ai}^f}{5 + r_{Ai}^f (3 - r_{Ai}^m) + r_{Ai}^m} \\
\frac{5 + r_{Ai}^f - 2 r_{Ai}^m}{5 + r_{Ai}^f (3 - r_{Ai}^m) + r_{Ai}^m} \\
\frac{5 - r_{Ai}^m}{5 + r_{Ai}^f (3 - r_{Ai}^m) + r_{Ai}^m} \end{pmatrix}. \quad (55)$$

All other forms of inheritance can be worked out in the same way.

We can finally write the associations needed in (7) for the case of autosomal preferences. For a preference position $i$ and a set of incompatibility positions $A$,
\[ \tilde{D}_{\mathbf{A}_i} = m d_{\mathbf{A}_i} \phi_{\mathbf{A}} \]  

(56)

where \( \phi_{\mathbf{A}} = 0 \) if \( \mathbf{A} \) contains both sexes of origin or both sexes of carrier. When \( \mathbf{A}_i \) contains only one sex of carrier and only one sex of origin, the value of \( \phi_{\mathbf{A}} \) depends on the mode of inheritance of the preference and the incompatibility loci. Values for \( \phi_{\mathbf{A}} \) assuming autosomal preference and values assuming X-linked preference are given in Table 3 below. In the table, A indicates that all loci are autosomally inherited, X indicates that all loci are X-linked, Y indicates that all loci are Y-linked, A-X indicates that one or more locus is autosomally inherited and one or more locus is X-linked, and A-Y indicates that one or more locus is autosomally inherited and one or more locus is Y-linked.
Table 3. The effect of recombination and sex linkage ($\phi_A$) on reinforcement.

**Autosomal preference**

<table>
<thead>
<tr>
<th></th>
<th>$\phi_{(A)_{hf}}$</th>
<th>$\phi_{(A)_{lm}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>$\frac{4 - r^H \alpha + r^H \beta}{2 + r^H \alpha + r^H \beta}$</td>
<td>$\frac{4 + r^H \alpha - r^H \beta}{2 + r^H \alpha + r^H \beta}$</td>
</tr>
<tr>
<td>X</td>
<td>$\frac{2 (5 - r^H \gamma)}{5 + 3 r^H \gamma}$</td>
<td>$\frac{2 (5 - r^H \gamma)}{5 + 3 r^H \gamma}$</td>
</tr>
<tr>
<td>Y</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>A-X</td>
<td>$\frac{36 - 4 r^H \gamma (1 - r^H \gamma) - 4 r^H \gamma}{27 + r^H \gamma (1 - r^H \gamma) (5 - r^H \gamma) + r^H \gamma (5 - r^H \gamma) + r^H \gamma}$</td>
<td>$\frac{4 (9 + r^H \gamma - r^H \gamma (1 - r^H \gamma) (5 - r^H \gamma) + r^H \gamma (5 - r^H \gamma) + r^H \gamma)}{27 + r^H \gamma (1 - r^H \gamma) (5 - r^H \gamma) + r^H \gamma (5 - r^H \gamma) + r^H \gamma}$</td>
</tr>
<tr>
<td>A-Y</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>X-Y</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
\[
\phi_{\text{inf}}(A) = \frac{4 - r_{dA}^4 + r_{dA}^6}{2 + r_{dA}^4 + r_{dA}^6}
\]
\[
\phi_{\text{num}}(A) = \frac{4 + r_{dA}^4 - r_{dA}^6}{2 + r_{dA}^4 + r_{dA}^6}
\]

\[
A = \frac{2(5 - r_{dA}^4)}{5 + 3 r_{dA}^4}
\]

\[
X = 0
\]

\[
Y = 2
\]

\[
A - X = \frac{36 - 4 r_{dA}^4 (1 - r_{dA}^4) - 4 r_{dA}^4}{27 + r_{dA}^4 (1 - r_{dA}^4) (5 - r_{dA}^4) + r_{dA}^4 (5 - r_{dA}^4) + r_{dA}^4}
\]

\[
A - Y = 0
\]

\[
X - Y = 0
\]

\[
27 + r_{dA}^4 (1 - r_{dA}^4) (5 - r_{dA}^4) + r_{dA}^4 (5 - r_{dA}^4) + r_{dA}^4
\]

\[
3 + r_{dA}^4
\]
X-linked preference

\[
\phi(A)_H = \frac{2(5 - r_{AH}^2)}{5 - r_{AH}^2 (3 - r_{AH}^2) + r_{AH}^4} \\
\phi(A)_L = \frac{2(5 + r_{AH}^2 - 2 r_{AH}^4)}{5 + r_{AH}^2 (3 - r_{AH}^2) + r_{AH}^4}
\]

\[
X = \frac{5 - r_{AX}^2}{2 + 2 r_{AX}^2} \\
Y = 0
\]

\[
A-X = \frac{18 - 2 r_{AX}^2 (1 - r_{AX}^2) - 2 r_{AX}^4}{13 + r_{AX}^2 (1 - r_{AX}^2) (3 - r_{AX}^2) + r_{AX}^4 (3 - r_{AX}^2) + r_{AX}^6} \\
A-Y = 0
\]

\[
X-Y = 0
\]
\[
\begin{align*}
\phi_{(A)_{\text{in}}} &= \frac{2 (5 - r_{SA}^3)}{5 + r_{SA}^3 (3 - r_{dA}^3) + r_{dA}^3} \\
0 &= 0 \\
\phi_{(A)_{\text{num}}} &= 0
\end{align*}
\]

\[
\begin{align*}
A &= \frac{5 - r_{SA}^3}{2 + 2 r_{dA}^3} \\
0 &= 0 \\
X &= 0 \\
0 &= 0
\end{align*}
\]

\[
\begin{align*}
Y &= 0 \\
0 &= 0 \\
A-X &= \frac{18 - 2 r_{SA}^3 (1 - r_{SA}^3) - 2 r_{dA}^3}{13 + r_{dA}^3 (1 - r_{dA}^3) (3 - r_{dA}^3) + r_{dA}^3 (3 - r_{dA}^3) + r_{dA}^3} \\
0 &= 0 \\
A-Y &= 0 \\
0 &= 0 \\
X-Y &= 0 \\
0 &= 0
\end{align*}
\]

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APPENDIX C: Expressions for $a_A$ for one- and two-locus incompatibilities

Here we present $O(a)$ approximations for the selection coefficients (the $a_A$) that appear in equation (12) under a variety of assumptions about how the hybrid incompatibility genes are inherited. The general procedure for deriving the selection coefficients is given in KJB. In the next section we give, as an example, the derivation for the case when hybrid incompatibilities are caused by two autosomal loci. The results for the selection coefficients for other types of hybrid incompatibilities, derived in a similar fashion, are summarized below in Table 4.

**Deriving selection coefficients for an autosome-autosome incompatibility:** Assuming that interactions between alleles at two autosomal loci, $k$ and $l$, contribute to decreased hybrid fitness, our notation for the selection coefficients is given in the bottom left corner of Figure 1 of the manuscript. We allow females and males to have different fitnesses, so we use the subscripts $f$ and $m$ to denote selection coefficients pertaining to females and males, respectively. Given this notation we can write the general fitness functions as
\[ W_f = 1 - s_{00f}((1 - X_{k_{lf}})(1 - X_{k_{lf}})) - s_{01f}((1 - X_{k_{lf}})(1 - X_{k_{lf}})X_{l_{lf}}(1 - X_{l_{lf}})) - s_{02f}((1 - X_{k_{lf}})(1 - X_{k_{lf}})X_{l_{lf}}X_{l_{lf}}) - s_{11f}((1 - X_{k_{lf}})X_{k_{lf}}X_{l_{lf}}(1 - X_{l_{lf}})) - s_{12f}((1 - X_{k_{lf}})X_{k_{lf}}X_{l_{lf}}X_{l_{lf}}) - s_{10f}((1 - X_{k_{lf}})X_{k_{lf}}(1 - X_{l_{lf}})(1 - X_{l_{lf}})) - s_{11f}(X_{k_{lf}}(1 - X_{k_{lf}})X_{l_{lf}}X_{l_{lf}}) - s_{12f}(X_{k_{lf}}(1 - X_{k_{lf}})X_{l_{lf}}X_{l_{lf}}) - s_{20f}(X_{k_{lf}}X_{k_{lf}}(1 - X_{l_{lf}})(1 - X_{l_{lf}})) - s_{21f}(X_{k_{lf}}X_{k_{lf}}X_{l_{lf}}(1 - X_{l_{lf}})) \]

(57)

\[
W_m = 1 - s_{00m}((1 - X_{k_{luf}})(1 - X_{k_{luf}})(1 - X_{l_{luf}})) - s_{01m}((1 - X_{k_{luf}})(1 - X_{k_{luf}})(1 - X_{l_{luf}})X_{l_{luf}}) - s_{02m}((1 - X_{k_{luf}})(1 - X_{k_{luf}})X_{l_{luf}}X_{l_{luf}}) - s_{11m}((1 - X_{k_{luf}})X_{k_{luf}}X_{l_{luf}}X_{l_{luf}}) - s_{12m}((1 - X_{k_{luf}})X_{k_{luf}}X_{l_{luf}}X_{l_{luf}}) - s_{10m}(X_{k_{luf}}(1 - X_{k_{luf}})(1 - X_{l_{luf}})(1 - X_{l_{luf}})) - s_{11m}(X_{k_{luf}}(1 - X_{k_{luf}})(1 - X_{l_{luf}})X_{l_{luf}}X_{l_{luf}}) - s_{12m}(X_{k_{luf}}(1 - X_{k_{luf}})X_{l_{luf}}X_{l_{luf}}) - s_{10m}(X_{k_{luf}}X_{k_{luf}}(1 - X_{l_{luf}})(1 - X_{l_{luf}})) - s_{11m}(X_{k_{luf}}X_{k_{luf}}X_{l_{luf}}X_{l_{luf}}) - s_{12m}(X_{k_{luf}}X_{k_{luf}}X_{l_{luf}}X_{l_{luf}}) - s_{20m}(X_{k_{luf}}X_{k_{luf}}(1 - X_{l_{luf}})(1 - X_{l_{luf}})) - s_{21m}(X_{k_{luf}}X_{k_{luf}}X_{l_{luf}}X_{l_{luf}}) - s_{20m}(X_{k_{luf}}X_{k_{luf}}X_{l_{luf}}X_{l_{luf}}) - s_{21m}(X_{k_{luf}}X_{k_{luf}}X_{l_{luf}}X_{l_{luf}}) \]

(58)

where \( W_f \) is the fitness function for the females and \( W_m \) is the fitness function for the males. \( X_i \) takes the value 1 when the genotype of interest contains the position \( i \) and takes the value 0 when it does not.

Replacing the \( X \)'s using \( \zeta_k = X_k - p_k \approx X_k - 1 + O(s) \approx X_k - 1 \) yields
\[ W_f = 1 - s_{00} \zeta_{la} \zeta_{la} \zeta_{la} \zeta_{la} + s_{10} (1 + \zeta_{la}) \zeta_{la} \zeta_{la} \zeta_{la} + s_{10} \zeta_{la} (1 + \zeta_{la}) \zeta_{la} \zeta_{la} - s_{20} (1 + \zeta_{la}) (1 + \zeta_{la}) \zeta_{la} \zeta_{la} + s_{01} \zeta_{la} \zeta_{la} \zeta_{la} \zeta_{la} - s_{11} (1 + \zeta_{la}) (1 + \zeta_{la}) \zeta_{la} \zeta_{la} + \]

\[ s_{21} (1 + \zeta_{la}) (1 + \zeta_{la}) \zeta_{la} \zeta_{la} - s_{02} \zeta_{la} \zeta_{la} \zeta_{la} \zeta_{la} + s_{12} \zeta_{la} (1 + \zeta_{la}) \zeta_{la} \zeta_{la} \zeta_{la} + \]

\[ (59) \]

\[ W_m = 1 - s_{00} \zeta_{ma} \zeta_{ma} \zeta_{ma} \zeta_{ma} + s_{10} \zeta_{ma} \zeta_{ma} \zeta_{ma} \zeta_{ma} + s_{10} \zeta_{ma} \zeta_{ma} \zeta_{ma} \zeta_{ma} + s_{11} \zeta_{ma} \zeta_{ma} \zeta_{ma} \zeta_{ma} - s_{20} \zeta_{ma} \zeta_{ma} \zeta_{ma} \zeta_{ma} + s_{01} \zeta_{ma} \zeta_{ma} \zeta_{ma} \zeta_{ma} - s_{11} \zeta_{ma} \zeta_{ma} \zeta_{ma} \zeta_{ma} + s_{21} \zeta_{ma} \zeta_{ma} \zeta_{ma} \zeta_{ma} - s_{02} \zeta_{ma} \zeta_{ma} \zeta_{ma} \zeta_{ma} + s_{12} \zeta_{ma} \zeta_{ma} \zeta_{ma} \zeta_{ma} \]

\[ (60) \]

Lastly, we determine the selection coefficients by looking for the coefficients of the \( \zeta \) terms who's subscript matches that of the \( a \) that we desire, which are the \( a \) containing one position or two positions with the same sex-of-carrier and sex-of-origin. The \( a's \) are given in Table 4 for the case of two autosomal loci, as well as for all other combinations assuming X-Y or Z-W sex determination.
Table 4. Selection coefficients ($a_A$).

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<th>$a_{k_{mf}}$</th>
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APPENDIX D: The effect of sex linkage of two-locus incompatibilities on reinforcement

In the main manuscript, Figure 2, we compare the amount of reinforcement for A-A, A-X and X-X incompatibilities. The following figure also presents the comparisons involving A-Y and X-Y incompatibilities. The main conclusion that we can draw from this figure is that when the preference is X-linked, reinforcement is expected to be much stronger when the incompatibility is a function of interactions involving autosomal and/or X-linked genes only, rather than interactions involving one or more Y-linked genes.
FIGURE 1. – The effect of sex-linkage on reinforcement for five types of hybrid incompatibility. The five matrices in the top row denote five types of hybrid incompatibility at two loci, \( k \) and \( l \). Values in the center and bottom rows indicate the relative amounts of reinforcement due to A-A, A-X, A-Y, X-X, and X-Y incompatibilities. The amount of reinforcement for the pattern of sex linkage indicated to the left of the value is divided by that for the pattern indicated above the value. For example, the value 0.2 found in the lower left most square indicates that an A-A incompatibility is expected to produce 5 times more reinforcement than an X-Y incompatibility when the preference is X-linked. Values greater than one before rounding are shaded.
To study the robustness of our conclusions in a more thorough fashion, we generalized two of the patterns of selection (D and E) from Figure 1 above. The generalized patterns are given below in Figures 2 and 3 (in the upper left corner), where the pattern of dominance and epistasis is a function of two parameters, $a$ and $b$. We varied these two parameters independently and computed the amount of reinforcement for A-A, A-X, A-Y, X-X, and X-Y incompatibilities. To visualize the results, we constructed contour plots, where the elevation represents the amount of reinforcement for one pattern of sex linkage relative to a second pattern of sex linkage (see the figure caption for more details). Two conclusions can be drawn from Figures 2 and 3. First, for most comparisons involving A-A, A-X, and X-X incompatibilities, the relative amount of reinforcement is fairly insensitive to the exact values of $a$ and $b$. This suggests that our qualitative conclusions regarding the effect of X-linkage are robust. For most of the comparisons involving A-Y and X-Y incompatibilities, however, the particular values of $a$ and $b$ have a much larger effect. This is evidenced by the fact that many contour lines are present. Any conclusions we might make regarding the importance of Y-linkage, therefore, will be sensitive to the pattern of selection we assume.
Figure 2. – The effect of dominance and epistasis on the contribution to reinforcement for five two-locus incompatibilities that may have evolved by drift. The type of selection assumed is indicated in the matrix located in the upper left corner of the figure, where the pattern of dominance and epistasis is a function of \( a \) and \( b \). Each graph is a contour plot showing the expected amount of reinforcement for the type of incompatibility labeled to the left/right of the graph relative to the amount for the type labeled above/below the graph. A bold line indicates that the amount of reinforcement is equal for the two types of incompatibility being compared in
the graph. Values in the corners of each graph indicate the relative amounts of reinforcement at those points in parameter space. For example, the value 1.0 seen in the upper right corner of the figure indicates that A-A and X-Y incompatibilities are expected to produce equal amounts of reinforcement when \( a = 4 \) and \( b = 8 \). The presence of many contour lines indicates that conclusions about the relative amount of reinforcement are sensitive to the specific pattern of dominance and epistasis, whereas the presence of fewer lines indicates that conclusions are more robust.
FIGURE 3. – The effect of dominance and epistasis on the contribution to reinforcement for five two-locus incompatibilities that may have evolved by selection. This figure is analogous to Figure 2.