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# Evolution of disassortative and assortative mating preferences based on imprinting

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**Abstract**

A two-locus haploid model of sexual selection is investigated to explore evolution of disassortative and assortative mating preferences based on imprinting. In this model, individuals imprint on a genetically transmitted trait during early ontogeny and choosy females later use those parental images as a criterion of mate choice. It is assumed that the presence or absence of the female preference is determined by a genetic locus. In order to incorporate such mechanisms as inbreeding depression and heterozygous advantage into our haploid framework, we assume that same-type matings are less fertile than different-type mating. The model suggests that: if all the females have a disassortative mating preference a viability-reducing trait may be maintained even without the fertility cost of same-type matings; a disassortative mating preference can be established even if it is initially rare, when there is a fertility cost of same-type matings. Further, an assortative mating preference is less likely to evolve than a disassortative mating preference. The model may be applicable to the evolution of MHC-disassortative mating preferences documented in house mice and humans.



*Keywords:* Female preference; Genetic polymorphism; Heterozygous advantage; Inbreeding avoidance; Kin recognition; Mate choice; MHC; Negative assortative mating; Sexual selection; Sexual imprinting

## 1. Introduction

Numerous models of sexual selection have been developed to explore evolution of female mating preferences for males exhibiting viability-reducing traits (e.g., Lande, 1981; Kirkpatrick, 1982; Pomiankowski, 1987; Kirkpatrick et al., 1990; Otto, 1991; Pomiankowski et al., 1991; Iwasa et al., 1991; Ihara and Aoki, 1999). Although most of these models assume genetic transmission of the female preference, some researchers have recently investigated models in which female preferences are acquired by cultural transmission (Richerson and Boyd, 1989; Laland, 1994a; Nakajima and Aoki, 2002; Ihara et al., 2003), including mate-choice copying (Kirkpatrick and Dugatkin, 1994; Servedio and Kirkpatrick, 1996).

In some species, individuals acquire their mating preferences through the process called sexual imprinting, in which individuals learn, or imprint on, certain characteristics of other individuals during early ontogeny and later use them as a criterion of mate choice (Lorenz, 1935; Immelmann, 1972; ten Cate and Vos, 1999). Sexual imprinting is particularly well known in various species of birds. Since individuals of these species usually imprint on characteristics of their immediate kin, sexual imprinting is likely to result in acquisition of assortative or disassortative mating preferences with respect to those characteristics. Traditionally, sexual imprinting has been regarded as a mechanism that is involved in species recognition (ten Cate and Vos, 1999) and thus more attention has been paid to assortative, rather than disassortative, mating preferences. Besides species recognition, however, sexual imprinting may also facilitate inbreeding avoidance. Japanese quails, *Coturnix coturnix japonica*, for example, imprint on their kin early in life and later prefer to mate with an individual that is slightly different (but not too different) from them (Bateson, 1978, 1982; see also ten Cate and Bateson, 1988). With regards to within-species variation, therefore, sexual imprinting may also give rise to disassortative mating preferences.

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Major histocompatibility complex (MHC) genotypes may provide a stimulus for such sexual imprinting that results in disassortative mating. Although the principal function of MHC molecules is to present antigens to T cells to initiate an immune response (Klein, 1986), many studies have been published showing that house mice, *Mus musculus domesticus*, prefer mates dissimilar, rather than similar, to themselves at MHC loci (Yamazaki et al., 1976, 1978; Egid and Brown, 1989; Potts et al., 1991; reviewed in Penn and Potts, 1999) and that such MHC-disassortative mating preference is mediated by olfaction (Yamazaki et al., 1979; Egid and Brown, 1989). Cross-fostering experiments have revealed that in fact mice learn the MHC identity of their family early in life and use it as a referent with which they compare the MHC type of potential mates (Yamazaki et al., 1988; Penn and Potts, 1998). Note that MHC-dependent mate choice has been also documented in fish (Landry et al., 2001).

Also in humans, Ober et al. (1997) reported fewer matches for MHC haplotypes between spouses than expected from random marriage in the Hutterite population, although studies on South Amerindians or Japanese couples did not find such a tendency (Hedrick and Black, 1997; Ihara et al., 2000). Such marriage preferences, if they exist, may be mediated by odor preference, which, it has been suggested, is associated with MHC type (Wedekind et al., 1995; Wedekind and Füri, 1997; see also Milinski and Wedekind, 2001; Jacob et al., 2002). In the Hutterites, when spouses share an MHC haplotype, the matched haplotype is more likely to be inherited from fathers than from mothers, suggesting greater avoidance of maternally than paternally derived haplotypes (Ober et al., 1997). This is consistent with the hypothesis that MHC-disassortative mating preference in humans is acquired through familial imprinting, given the greater involvement of women in child rearing (see Boyd and Richerson, 1985).

Laland (1994a,b) has developed diploid major gene models of sexual selection in which individuals acquire parental images of a genetically transmitted trait and females use them as a referent when they choose their mates. He investigated whether such sexual imprinting can increase the likelihood of a novel adaptive trait to spread, generate sexual selection for a viability-reducing trait, and/or lead to reproductive isolation between populations (see also O'Donald, 1960; Kalmus and Maynard Smith, 1966; Seiger, 1967; Karlin, 1968; Matessi and Scudo, 1975). Aoki et al. (2001) also analyzed a quantitative genetic model of sexual selection in which females choose their mates based on the parental images they have acquired. They examined the possibility that sexual imprinting can displace the mean trait value away from the viability optimum. Both of these studies, however, concentrate on assortative, rather than disassortative, mating preferences as a result of sexual imprinting (but see Matessi and Scudo, 1975). Furthermore, they assume that all (or none) of the females innately show preferences for certain males based on the parental images they have acquired; in other words, the presence (or absence) of the mating preference is given and its evolution is not considered.

In this paper, we develop a simple haploid genetic model to investigate evolution of mating preferences based on imprinting. Both disassortative and assortative mating preferences are considered. The model suggests that: first, if females have disassortative mating preferences as a result of sexual imprinting, a viability-reducing trait can be maintained even without a fertility cost of same-type matings; second, a disassortative mating preference based on imprinting can be established even if it is initially rare, given that there is a cost of same-type matings; and third, assortative mating preferences based on imprinting are less likely to evolve compared to disassortative mating preferences.

## 2. Model

We choose a simple haploid model for mathematical convenience. This enables us to analyze the model more thoroughly than is possible for the diploid counterpart. Following Kirkpatrick's (1982) model of sexual selection, we assume two autosomal diallelic loci. The first locus, $T$, with alleles $T_1$ and $T_2$, governs a trait that affects the viability of individuals: a $T_2$ individual is $1-s$ times less likely to survive to adulthood ($0<s<1$) compared with a $T_1$ individual. We denote the frequencies of $T_1$ and $T_2$ by $1-t$ and $t$. Juveniles learn the phenotype (i.e., $T_1$ or $T_2$) of one of their parents, which may be used as a referent when they choose their mates later in life. The second locus, $P$, with alleles $P_1$ and $P_2$, is expressed only in females and determines the presence or absence of a mating preference: $P_2$ females have a mating preference so that they are $a$ times less (or more when $a>1$) likely to mate with a male whose phenotype (i.e., $T_1$ or $T_2$) is the same as their parental image acquired by imprinting than with a male who has the other phenotype ($a>0$), while $P_1$ females do not have such a mating preference and thus mate at random. The frequencies of $P_1$ and $P_2$ are $1-p$ and $p$.

The life history is as follows. First, juveniles imprint on the phenotype of their mother with probability $b$ and that of their father with $1-b$ ($0<b<1$). Through this process, each individual acquires the parental image $X$, with two alternative states $X_1$ and $X_2$, which correspond to those individuals who are imprinted on $T_1$ and $T_2$, respectively. There are eight possible combinations of phenotype and genotype, or phenogenotypes, $T_1P_1X_1$, $T_1P_1X_2$, $T_1P_2X_1$, $T_1P_2X_2$, $T_2P_1X_1$, $T_2P_1X_2$, $T_2P_2X_1$, and $T_2P_2X_2$, which are represented by $U_1$, $U_2$, $U_3$, $U_4$, $U_5$, $U_6$, $U_7$, and $U_8$, respectively. Let $u_i$ denote the

frequency of $U_i$ at this stage. Second, viability selection acts on both males and females. The phenogenotype frequencies after viability selection are denoted by $u_i^*$. Third, polygamous matings occur during which females choose their mates according to their preferences, if any. Finally, fertility selection takes place. Disassortative mating may be evolutionarily advantageous if it produces more viable offspring than does random mating, due to such mechanisms as inbreeding avoidance and heterozygous advantage. In order to incorporate this into our haploid framework, we simply assume that the fertility of "same-type matings" (i.e., mating types $T_1-T_1$ and $T_2-T_2$) is reduced by the factor $1-d$ $(0<d<1)$ relative to "different-type matings" (i.e., $T_1-T_2$ and $T_2-T_1$). We also discuss the case when $d<0$ (see discussion).

Assuming that the population is large, the sex ratio is unity, generations are discrete, and there is no age structure, we derive the phenogenotype frequencies in the next generation, $u_i'$:

$$u_i' = \frac{1}{\overline{w}} \sum_{j,k} u_j u_k A^i_{jk}, \tag{1}$$

where

$$\overline{w} = \sum_{i,j,k} u_j u_k A^i_{jk}. \tag{2}$$

The matrix $\mathbf{A}^i$, whose $jk$th element is $A^i_{jk}$, is given by the Schur product of the matrices $\mathbf{V}$, $\mathbf{M}$, $\mathbf{F}$, $\mathbf{G}^i$, and $\mathbf{I}^i$ (see Kumm et al., 1994), which describe viability selection, selective mating, fertility selection, genetic inheritance, and imprinting, respectively (see Appendix A):

$$\mathbf{A}^i = \mathbf{V} \circ \mathbf{M} \circ \mathbf{F} \circ \mathbf{G}^i \circ \mathbf{I}^i. \tag{3}$$

Note that reproduction is sexual and there is recombination between the two loci at the rate $r$ $(0 \leqslant r \leqslant 1/2)$. Since behavior of $P_1$ individuals is not affected by their parental image, we need only six variables, $v_1$, $v_2$, $u_3$, $u_4$, $u_7$, and $u_8$, where $v_1 = u_1 + u_2$ $(T_1P_1)$ and $v_2 = u_5 + u_6$ $(T_2P_1)$. The frequency of $P_2$ individuals that are imprinted on $T_2$ (i.e., $T_1P_2X_2$ and $T_2P_2X_2$) is denoted by $x$ $(= u_4 + u_8)$ $(0<x<p)$.

*Case* 1: *No mating preference*. Let us begin with the simplest case when allele $P_1$ is fixed (i.e., $u_3 = u_4 = u_7 = u_8 = 0$). In this case we have only one independent variable, $t$ $(= v_2)$. Per generation change in $t$ is given by

$$\Delta t = \frac{t(1-t)}{\overline{w}(1-st)^2} \{[(1-d)s^2 + 2ds - 2d]t + d - s\}, \tag{4}$$

where

$$\overline{w} = 1 - \frac{(1-s)^2t^2 + (1-t)^2}{(1-st)^2} d. \tag{5}$$

Hence $\Delta t = 0$ if and only if $t = 0$, 1, or

$$t = \frac{s-d}{(1-d)s^2 + 2ds - 2d} \equiv f(s,d). \tag{6}$$

If $s>d$, it can be shown that $f(s,d)$ is either smaller than 0 or larger than 1. Hence there are only two equilibria: $t=0$ and 1. In this case $t$ always decreases and converges to zero unless $t=1$. If $s<d$, on the other hand, since $0<f(s,d)<1$ there are three equilibria: $t=0$, 1, and $f(s,d)$. When $0<t<f(s,d)$, $t$ increases, while $t$ decreases when $f(s,d)<t<1$. Hence $t=f(s,d)$ is globally stable. In the absence of the mating preference, therefore, the viability-reducing trait can be maintained at a polymorphic state only if its viability cost is small relative to the fertility cost of same-type matings.

*Case* 2: *Mating preference fixed*. As a next step, consider the case when all the females have the mating preference, that is, allele $P_2$ is fixed (i.e., $v_1 = v_2 = 0$). There are three independent variables, $t, x$, and $D_{TX}$, where, $t = u_7 + u_8$, $x = u_4 + u_8$, and $D_{TX} = u_3u_8 - u_4u_7$. Two equilibrium points $(\hat{t}, \hat{x}, \hat{D}_{XT})$ are observed: $(0,0,0)$ (i.e., $\hat{u}_3 = 1$) is locally stable if

$$1 - s < \frac{2a(1-d)}{1+a}, \tag{7}$$

and $(1,1,0)$ (i.e., $\hat{u}_8 = 1$) is locally stable if

$$1 - s > \frac{1+a}{2a(1-d)}. \tag{8}$$

If (7) does not hold, (8) is never satisfied so that neither of the above equilibria is stable.

In addition to the above monomorphic equilibria, our numerical analysis suggests that the population will converge to a polymorphic equilibrium whenever (7) is violated. In contrast to case 1, therefore, even in the absence of the fertility cost of same-type matings (i.e., $d=0$), the viability-reducing trait can be maintained at a polymorphic state if $1-s>2a/(1+a)$, which requires $a<1$.

*Case* 3: *Evolution of disassortative mating preference*. Now, we allow for the evolution of the mating preference. In this section, we focus on the case when $P_2$ females have a disassortative mating preference (i.e., $a<1$). There are five independent variables, $t, p, x, D_{TP}$, and $D_{TX}$, where $t = v_2 + u_7 + u_8$, $p = u_3 + u_4 + u_7 + u_8$, $x = u_4 + u_8$, $D_{TP} = v_1(u_7 + u_8) - v_2(u_3 + u_4)$, and $D_{TX} = u_3u_8 - u_4u_7$.

Three sets of equilibria $(\hat{t}, \hat{p}, \hat{x}, \hat{D}_{XT}, \hat{D}_{XP})$ are found analytically. First, the set of points $E_0$ given by $(0,p,0,0,0)$, $0 \leqslant p \leqslant 1$ form a line of equilibria, whose local stability is as follows: the line is neutrally stable (i.e., the leading eigenvalue is unity) if

$$0 < 1 - s < \frac{2a(1-d)}{1+a}, \tag{9}$$

the line is partially stable, that is, the segment of the line $p<K_0$ is neutrally stable, where $K_0 = 2a(s-d)/[(1-a)(1-s)]$, while the other part of the line is unstable, if

$$\frac{2a(1-d)}{1+a} < 1 - s < 1 - d, \tag{10}$$

and the line is unstable if

$$1-d<1-s<1. \tag{11}$$

Second, the set of points $E_1$ given by $(1,p,p,0,0)$, $0\leqslant p\leqslant 1$ form a line of equilibria, which is always unstable. Third, the equilibrium point $E_2$ given by $(f(s,d),0,0,0,0)$ exists if (11) holds (see (6) for the definition of $f(s,d)$). Numerical analysis suggests that this is always unstable when it exists.

In addition to the above three equilibria, we found by numerical iteration that a locally stable equilibrium point, $E_3$, at which $p=1$ and $D_{TP}=0$, also exists whenever (10) or (11) is satisfied.

When (9) is met, the viability-reducing trait never evolves and thus the female preference becomes evolutionarily neutral (Fig. 1A). However, if the mating preference is stronger (i.e., $a$ is smaller) or the viability selection is weaker (i.e., $s$ is smaller) so that (10) is satisfied, $E_3$ may be reached, at which the female preference is fixed and the viability-reducing trait is maintained at a polymorphic state, depending on the initial state (Fig. 1B). Furthermore, if $s$ is small enough for (11) to hold, $E_3$ is always reached irrespective of the initial state (Fig. 1C). In sum, evolution of disassortative mating preference can occur when (10) is satisfied and is most likely to occur when (11) is satisfied.

*Case* 4: *Evolution of assortative mating preference*. Finally, let us consider the case when $P_2$ females have an assortative mating preference (i.e., $a>1$). As in case 3, we observe three sets of equilibria, $E_0$, $E_1$, and $E_2$. First, local stability of the line of equilibria $E_0$ is as follows: the line is neutrally stable if

$$0<1-s<1-d, \tag{12}$$

the line is partially stable, that is, the segment of the line $p>K_0$ is neutrally stable while the other part is unstable if

$$1-d<1-s<\frac{2a(1-d)}{1+a}, \tag{13}$$

and the line is unstable if

$$\frac{2a(1-d)}{1+a}<1-s<1. \tag{14}$$

Second, the line of equilibria $E_1$ is partially stable, that is, only the segment $p>K_1$ is neutrally stable, where $K_1=2a[1-(1-d)(1-s)]/(a-1)$, if

$$\frac{1+a}{2a(1-d)}<1-s<1, \tag{15}$$

otherwise the line is unstable. Third, the equilibrium point $E_2$ exists if (13) or (14) holds and, from a numerical analysis, is locally stable whenever it exists.

When (12) holds, the viability-reducing trait will always be lost from the population unless (15) is satisfied, and thus the female preference will become evolutionarily neutral (see Fig. 1A). If $s$ is smaller or $d$ is larger so that (13) is satisfied, $E_2$ may be reached, at which the female preference is lost and the viability-reducing trait is maintained at a polymorphic state, depending on the initial state (Fig. 1D). When $s$ is so small that (14) is satisfied, $E_2$ is always reached (Fig. 1E). When (15) is met, which requires $a(1-2d)>1$, the viability-reducing trait can either be lost (i.e., $E_0$), fixed (i.e., $E_1$), or maintained at a polymorphic state (i.e., $E_2$), while the female preference is either lost (i.e., $E_2$) or maintained as a neutral trait (i.e., $E_0$ or $E_1$) (Fig. 1F). Taken together, equilibria where both the viability-reducing trait and the assortative mating preference are maintained (i.e., $E_1$) can be (neutrally) stable only if (15) holds. Even in this case, however, $E_1$ can be attained from fairly restricted sets of initial values (see Fig. 1F). Moreover, since there is no force to increase the frequency of the preference once $E_1$ (or $E_0$) is reached, random genetic drift may cause the population to move away from $E_1$ (or $E_0$) toward $E_2$. Therefore, the model suggests that assortative mating preferences are less likely to evolve than disassortative mating preferences.

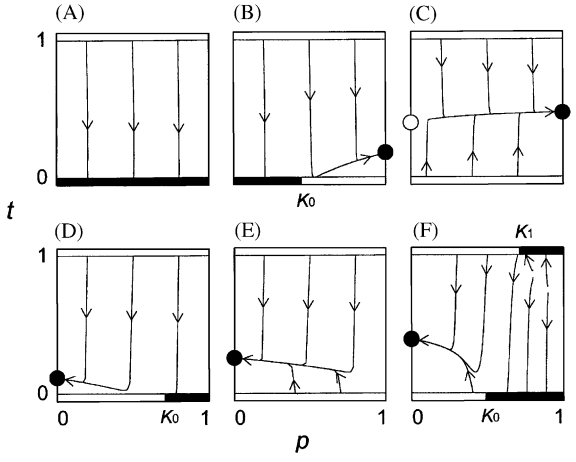


Fig. 1. Sample trajectories and equilibria. The five-dimensional space is projected onto the $pt$-plane. The arrows represent sample trajectories from various initial values of $p$ and $t$ (other initial values are: $x=D_{TP}=D_{TX}=0$). The thick lines on the lower boundary ($E_0$) and the upper boundary ($E_1$) represent the lines of equilibria, the filled segments of which are neutrally stable while the empty segments are unstable. The filled circles indicate locally stable equilibrium points whereas the empty circle is an unstable equilibrium point ($E_2$ and $E_3$). (A) $a=0.8$, $d=0.05$, $s=0.20$; (B) $a=0.8$, $d=0.05$, $s=0.10$; (C) $a=0.8$, $d=0.05$, $s=0.01$; (D) $a=1.2$, $d=0.2$, $s=0.30$; (E) $a=1.2$, $d=0.2$, $s=0.15$; and (F) $a=1.2$, $d=0.05$, $s=0.01$. Other parameter values are: $b=0.5$, $r=0.5$.

## 3. Discussion

We investigated a haploid model for evolution of mating preferences in which females choose their mates

based on the parental images of a genetically transmitted trait acquired by imprinting. We assume that the presence or absence of a female mating preference is determined by a genetic locus; choosy females are less (or more) likely to mate with a male whose phenotype is similar to their parents than with a male whose phenotype is dissimilar to the parents; and the fertility of same-type matings is reduced relative to that of different-type matings due to such mechanisms as inbreeding depression and heterozygous advantage. The model suggests that if females mate disassortatively as a result of sexual imprinting, a viability-reducing trait may be maintained even without the fertility cost of same-type matings; a disassortative mating preference can evolve even if it is initially rare when there is a fertility cost of same-type matings; and an assortative mating preference based on imprinting is less likely to evolve than a disassortative mating preference. These results are not affected by whether juveniles are imprinted on their mothers or fathers.

If none of the females uses its parental images acquired by imprinting as a criterion of mate choice (case 1), the viability-reducing trait will be lost unless its viability cost is small relative to the fertility cost of same-type matings. On the other hand, if all the females choose their mates according to their parental images (case 2), the viability-reducing trait may be maintained at a polymorphic state, which holds true even without the cost of same-type matings given that the mating preference is disassortative (i.e., $a<1$). When we allow for the evolution of mating preferences, the outcome of the model depends heavily on whether the preference is disassortative (i.e., $a<1$) or assortative (i.e., $a>1$). A disassortative mating preference can go to fixation even if it is initially rare (case 3). For a novel disassortative mating preference to increase the viability cost of the trait has to be small relative to the fertility cost of same-type matings. An assortative mating preference, on the other hand, is unlikely to evolve (case 4). If it is rare it will always be lost from the population.

MHC-disassortative mating preferences observed in house mice and perhaps in humans may have coevolved with a genetic trait that causes heterozygous advantage and/or whose phenotypic similarity between individuals is correlated with genetic relatedness (see Fig. 1C). Moreover, once such a disassortative mating preference is established and this preference is general enough to give rise to disassortative mating with respect to other traits, it may facilitate maintenance of genetic polymorphism at other loci that do not render same-type matings costly (see Fig. 1B). This may in part explain the high degree of polymorphism at MHC loci (see Hedrick, 1994).

Our model indicates that the coevolution of a viability-reducing trait and an assortative mating preference with respect to the trait acquired through imprinting is unlikely to occur (case 4). An assortative mating preference may be advantageous if it results in avoidance of matings with individuals of other species. To take this into account, we consider the case when $d<0$, that is, same-type matings are on average more fertile than different-type matings, as would be expected if the different-type matings were actually heterospecific. In this case, the whole line of equilibria $E_1$ is neutrally stable if $1-d>1/(1-s)$. Even in this case, however, since $E_0$ is neutrally stable as a whole whenever $d<0$, the viability-reducing trait cannot increase at a geometric rate when it is rare. For example, a numerical analysis with the parameter values $a=1.2$, $b=0.5$, $d=-0.05$, $r=0.5$, and $s=0.01$ reveals that the initial frequency of $T_2$ must exceed 0.55 for the viability-reducing trait to be eventually fixed.

Given a cost of different-type mating, assortative mating may facilitate reproductive isolation between subpopulations. Suppose that a population is geographically divided into two parts and that $T_1$ and $T_2$ are locally adaptive in the two different environments, respectively (i.e., $s>0$ in one subpopulation and $s<0$ in the other). Servedio (2000), using two- and continent-island models, showed that an allele for assortative mating can spread due to its genetic association with the locally adaptive allele in each subpopulation (see also references in Servedio, 2000). In the case of $d<0$ in our model, however, $P_2$ becomes evolutionarily neutral at equilibrium (i.e., $E_0$ or $E_1$) rather than going to fixation. This may be because in our model the genetic variation of the trait is quickly lost and assortative mating ceases to operate. In Servedio's models, the genetic variation of the trait is maintained by migration between subpopulations.

As suggested by ten Cate and Bateson (1988), a viability-reducing trait may be able to evolve if the mating preference deviates asymmetrically from the familiar. This contention is supported by Laland (1994b) and Aoki et al. (2001), both of which found that viability may not be optimized if females have certain asymmetrical preferences. There is no study so far that considers both the evolution of mating preferences and a perceptual bias that leads to such asymmetrical preferences. Further study along these lines is clearly needed.

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## Appendix A

### A.1. Viability selection

A $2 \times 2$ matrix can describe viability selection. Kroenecker multiplication with a $4 \times 4$ matrix of ones creates the matrix $\mathbf{V}$:

$$\mathbf{V} = \frac{1}{(1-st)^2}\begin{pmatrix} 1 & 1-s \\ 1-s & (1-s)^2 \end{pmatrix} \otimes \begin{pmatrix} 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \end{pmatrix}, \tag{A.1}$$

where the product of $u_j, u_k$, and the $jk$th element of $\mathbf{V}$ gives the product of the frequencies of $U_j$ and $U_k$ after viability selection, or $u_j^* u_k^*$.

### A.2. Selective mating

Selective mating is described by a $4 \times 2$ matrix. Kroenecker multiplication again creates the matrix $\mathbf{M}$:

$$\mathbf{M} = \begin{pmatrix} 1 \\ 1 \end{pmatrix} \otimes \begin{pmatrix} 1 & 1 \\ 1 & 1 \\ a/z_1 & 1/z_1 \\ 1/z_2 & a/z_2 \end{pmatrix} \otimes (1 \quad 1 \quad 1 \quad 1), \tag{A.2}$$

where $z_1 = a(u_1^* + u_2^* + u_3^* + u_4^*) + u_5^* + u_6^* + u_7^* + u_8^*$, and $z_2 = u_1^* + u_2^* + u_3^* + u_4^* + a(u_5^* + u_6^* + u_7^* + u_8^*)$. The product of $u_j^* u_k^*$ and the $jk$th element of $\mathbf{M}$ gives the frequency of matings between $U_j$ females and $U_k$ males (i.e., $U_j - U_k$ matings).

### A.3. Fertility selection

A $2 \times 2$ matrix describes fertility selection. The matrix $\mathbf{F}$ is given by

$$\mathbf{F} = \begin{pmatrix} 1-d & 1 \\ 1 & 1-d \end{pmatrix} \otimes \begin{pmatrix} 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \end{pmatrix}, \tag{A.3}$$

where the $jk$th element of $\mathbf{F}$ is the relative number of offspring from a $U_j - U_k$ mating.

### A.4. Genetic inheritance

For each genotype a $4 \times 4$ matrix is needed to describe genetic inheritance. The matrices $\mathbf{G}^i$ are

$$\mathbf{G}^1 = \mathbf{G}^2 = \begin{pmatrix} 1 & 1/2 & 1/2 & (1-r)/2 \\ 1/2 & 0 & r/2 & 0 \\ 1/2 & r/2 & 0 & 0 \\ (1-r)/2 & 0 & 0 & 0 \end{pmatrix} \otimes \begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix}, \tag{A.4}$$

$$\mathbf{G}^3 = \mathbf{G}^4 = \begin{pmatrix} 0 & 1/2 & 0 & r/2 \\ 1/2 & 1 & (1-r)/2 & 1/2 \\ 0 & (1-r)/2 & 0 & 0 \\ r/2 & 1/2 & 0 & 0 \end{pmatrix} \otimes \begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix}, \tag{A.5}$$

$$\mathbf{G}^5 = \mathbf{G}^6 = \begin{pmatrix} 0 & 0 & 1/2 & r/2 \\ 0 & 0 & (1-r)/2 & 0 \\ 1/2 & (1-r)/2 & 1 & 1/2 \\ r/2 & 0 & 1/2 & 0 \end{pmatrix} \otimes \begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix}, \tag{A.6}$$

and

$$\mathbf{G}^7 = \mathbf{G}^8 = \begin{pmatrix} 0 & 0 & 0 & (1-r)/2 \\ 0 & 0 & r/2 & 1/2 \\ 0 & r/2 & 0 & 1/2 \\ (1-r)/2 & 1/2 & 1/2 & 1 \end{pmatrix} \otimes \begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix}, \tag{A.7}$$

where $r$ is the recombination fraction between $T$ and $P$ $(0 \leqslant r \leqslant 1/2)$. The $jk$th element of $\mathbf{G}^i$ is the probability that a $U_j - U_k$ mating produces offspring whose genotype is identical to that of $U_i$ individuals.

### A.5. Imprinting

A $2 \times 2$ matrix is sufficient to describe imprinting. The matrices $\mathbf{I}^i$ are created as follows:

$$\mathbf{I}^1 = \mathbf{I}^3 = \mathbf{I}^5 = \mathbf{I}^7 = \begin{pmatrix} 1 & b \\ 1-b & 0 \end{pmatrix} \otimes \begin{pmatrix} 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \end{pmatrix} \tag{A.8}$$

and

$$\mathbf{I}^2 = \mathbf{I}^4 = \mathbf{I}^6 = \mathbf{I}^8 = \begin{pmatrix} 0 & 1-b \\ b & 1 \end{pmatrix} \otimes \begin{pmatrix} 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \end{pmatrix}, \tag{A.9}$$

where the $jk$th element of $\mathbf{I}^i$ gives the probability that offspring of a $U_j - U_k$ mating is imprinted on $T_1$ when $i$ is odd, and $T_2$ when $i$ is even.

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