

Selection and Segregation Distortion in a Sex-Differentiated Population

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We extend the classical model for selection at an autosomal locus in a sex-differentiated population to include segregation distortion. The equations remain the same, but the fitness parameters are interpreted differently and refer to alleles instead of genotypes. We derive conditions for internal and external stability of the equilibria, i.e., stability with respect to perturbations of alleles that are already present at equilibrium and stability with respect to invasion attempts by newly arising alleles. We show that, in a sex-differentiated population, external stability of an equilibrium can be judged on the basis of Shaw–Mohler criteria. Throughout, we compare the situation in populations with and without sex differentiation. Interestingly, internal stability is more difficult to achieve in a population without sex differentiation than in a population in which selection and segregation distortion are restricted to one sex. In a companion paper we show how the general results of the present paper can lead to new insights into specific systems such as the *t* complex of the house mouse. © 2001 Elsevier Science

Key Words: segregation distortion; meiotic drive; mathematical model; internal and external stability; replicator dynamics; evolutionary stability; *t* complex; *SD* complex.

INTRODUCTION

The Mendelian rule of equal segregation is one of the basic principles of biology that is ordinarily taken for granted. There are, however, genes that cheat against this rule by biasing segregation in their favor. The existence of such meiotic drive genes or segregation distorters has raised questions concerning the stability and evolution of Mendelian segregation (Sandler and Novitski, 1957). Indeed, any gene that manages to become overrepre-

sented in the gametes that make up the next generation is selectively favored and should spread in the population (e.g., Liberman, 1976; Eshel, 1985; Lessard, 1985; Hatcher, 2000).

Most models on general aspects of segregation distortion, in particular models aiming at the evolutionary stability of Mendelian segregation, focus on populations without sex differentiation, i.e., on populations with one sex or with no differences between the sexes. The one-sex approach has the obvious advantage of analytical

tractability (e.g., Cannings, 1969; Liberman, 1976, 1991; Nagylaki, 1983; Eshel, 1985; Lessard, 1985). It is important to notice, however, that these conceptual models do not properly represent real-world systems such as the *SD* complex of *Drosophila melanogaster* or the *t* complex of the house mouse. In these empirical systems, segregation distortion is restricted to one sex, a fact that is hardly surprising in view of the fundamental differences between spermatogenesis and oogenesis. Since sex specificity is a prominent feature of most, if not all, real-world segregation distorters, the analysis of sex-differentiated populations is required to judge the robustness and empirical relevance of predictions derived from the earlier one-sex models.

In contrast to the more general models mentioned above, sex differentiation is taken into account in many models aiming at specific segregation distortion systems (Feldman and Otto, 1991, and references therein). However, most of these specific models make rather restrictive assumptions from the beginning (e.g., extreme fitness effects such as sterility or lethality), making it difficult to extrapolate their results. For instance, the model of Bruck (1957) was specifically tailored for a so-called “lethal” *t* allele that induces lethality in both sexes when homozygous, and Dunn and Levene (1961) treated the case of a “sterile” *t* allele that leads to homozygous male sterility. Moreover, with a few notable exceptions (e.g., Hartl, 1970c; Nagylaki, 1983; Liberman, 1990, 1991; Stadler, 1996), these models focus on the interaction between two alleles, the wildtype and a single distorter. In contrast, well-known systems such as the *SD* complex and the *t* complex are characterized by a broad spectrum of distorter alleles. This finding is in line with the predictions of our earlier models that a high degree of polymorphism is to be expected in segregation distortion systems (van Boven *et al.*, 1996; van Boven and Weissing 1998, 2000, 2001). It is therefore desirable to develop a more general, coherent theory for the interaction of selection and segregation distortion in a sex-differentiated population.

The present paper is a step in this direction. We extend the classical model for selection at an autosomal locus in a sex-differentiated population to include segregation distortion. The resulting dynamics has been derived before (Karlín, 1978; Karlín and Lessard, 1986; Nagylaki, 1992), but it has been analyzed only for rather specific parameter configurations. We characterize the equilibria, derive conditions for stability of the equilibria, and investigate the relation between models with and without sex differentiation. In essence, the present paper reviews and develops the theory needed to study the competition between segregation distorter alleles in a

sex-differentiated population. In a companion paper we show how the general results can be put to good use to obtain new insights into specific segregation distortion systems.

The paper is structured as follows. To introduce our method, we first consider selection and segregation distortion in a population without sex differentiation. The main consequence of the inclusion of segregation distortion in the classical Haldane–Fisher–Wright selection model is that the two alleles within an individual do not necessarily share a common interest. As a consequence, fitness has to be viewed from the perspective of the allele rather than the genotype. Formally, this implies that the fitness matrix is no longer symmetric, leading to a model structure that is equivalent to the discrete replicator dynamics. This dynamics has been intensely studied in various contexts (e.g., Hofbauer and Sigmund, 1998). Accordingly, selection and segregation distortion in a one-sex population is rather well understood. In a sex-differentiated population, the dynamics of selection and segregation distortion is inherently more complex because allele and genotype frequencies differ between the sexes. We characterize the equilibria and notice that their calculation, which is straightforward in the one-sex case, can be quite complicated when the allele frequencies differ between the sexes (see Lewontin (1968) for the difficulties already encountered in simple examples). Next, we derive conditions for internal stability (i.e., stability with respect to perturbations involving only those alleles that are already present at equilibrium) and external stability (i.e., stability with respect to invasion attempts by newly arising alleles). In general, external stability is much easier to check than internal stability. In fact, Lessard’s (1989) extension of the classical Shaw–Mohler criterion for the invasion prospects of a rare allele generalizes to the context of segregation distortion. We also derive a second, equivalent invasion criterion that is often easier to apply in practical applications.

Throughout, we discuss the special properties of two extremes: selection in the absence of segregation distortion and segregation distortion in the absence of selection. Both cases have special symmetry properties that facilitate the analysis significantly. We also investigate the relation between populations with and without sex differentiation. Motivated by practical applications (see the companion paper), we focus on the special case in which the strength but not the direction of selection and segregation distortion differs between the sexes. Interestingly, the equilibria of one-sex populations are inherently less stable than those of a corresponding two-sex population in which selection and segregation distortion are restricted to one of the sexes.

Notational Conventions

Throughout, boldface characters such as \mathbf{p} and \mathbf{q} denote (column) vectors with elements p_i and q_i . Specifically, \mathbf{u} is the vector of units, $\mathbf{u} = (1\dots 1)^T$, where T denotes transposition. Boldface capitals such as \mathbf{A} or \mathbf{W} denote matrices with elements a_{ij} and w_{ij} . $\mathbf{I} = (\delta_{ij})$ represents the identity matrix, where δ_{ij} is the Kronecker delta ($\delta_{ij} = 1$ if $i = j$ and $\delta_{ij} = 0$ if $i \neq j$). \mathbf{U} denotes the matrix of units; i.e., $u_{ij} = 1$ for all i and j . The action of a matrix \mathbf{W} on a vector \mathbf{p} results in a vector with elements $(\mathbf{W}\mathbf{p})_i = \sum_j w_{ij} p_j$. The inner product of two vectors \mathbf{a} and \mathbf{b} is denoted by $\langle \mathbf{a}, \mathbf{b} \rangle = \sum_i a_i b_i$, while the Schur product $\mathbf{a} \circ \mathbf{b}$ is the vector with elements $(\mathbf{a} \circ \mathbf{b})_i = a_i b_i$. Finally, the spectral radius of a matrix \mathbf{A} , i.e., the absolute value of its dominant eigenvalue, will be denoted by $\rho(\mathbf{A})$.

A POPULATION WITHOUT SEX DIFFERENTIATION

The Model

Let us first consider an infinite population without sex differentiation. Generations are discrete and non-overlapping and mating occurs at random. We consider a single autosomal locus with alleles A_i ($i = 1, 2, \dots, n$). Let p_i represent the relative frequency of allele A_i in the gametes (after segregation distortion has taken place). Since random mating is in our case equivalent to the random union of gametes (Karlin, 1978), the ordered genotype frequencies at the zygote stage are given by $p_i p_j$.

The viability and fertility of $A_i A_j$ individuals will be denoted by v_{ij} and ϕ_{ij} , respectively ($v_{ij} = v_{ji} \geq 0$ and $\phi_{ij} = \phi_{ji} \geq 0$). We assume that fertilities are multiplicative; i.e., the fertility of the mating pair $A_{ij} \times A_{kl}$ is given by the product $\phi_{ij} \phi_{kl}$. The segregation ratio or fraction of A_i gametes contributed by $A_i A_j$ individuals is given by σ_{ij} ($\sigma_{ij} \geq 0$, $\sigma_{ij} + \sigma_{ji} = 1$). We define the fitness w_{ij} of *allele* $A_i A_j$ individual as the product of the viability v_{ij} , the fertility ϕ_{ij} , and the segregation ratio σ_{ij} ; i.e.,

$$w_{ij} = v_{ij} \phi_{ij} \sigma_{ij}. \quad (1)$$

With this notation, the representation of allele A_i in the gamete pool of the next generation is given by (e.g., Liberman, 1991)

$$p'_i = p_i \frac{w_i(\mathbf{p})}{\bar{w}(\mathbf{p})}, \quad (2)$$

where

$$w_i(\mathbf{p}) = (\mathbf{W}\mathbf{p})_i = \sum_l w_{il} p_l \quad (3)$$

represents the marginal fitness of allele A_i , while

$$\bar{w}(\mathbf{p}) = \sum_k p_k w_k(\mathbf{p}) = \frac{1}{2} \sum_{k,l} p_k v_{kl} \phi_{kl} p_l \quad (4)$$

denotes the mean fitness of the population. Notice that $\bar{w}(\mathbf{p})$ does not depend on the segregation parameters σ_{ij} . The dynamics (2) can be written more compactly using the Schur product as follows:

$$\mathbf{p}' = \frac{\mathbf{p} \circ \mathbf{W}\mathbf{p}}{\langle \mathbf{p}, \mathbf{W}\mathbf{p} \rangle}. \quad (5)$$

As was noticed by Nagylaki (1983) and Liberman (1991), Eq. (5) corresponds to the discrete replicator dynamics that is widely used in evolutionary game theory to describe the dynamics of evolutionary games with payoff matrix \mathbf{W} (e.g., Taylor and Jonker, 1978; Weissing, 1991). If segregation is Mendelian (i.e., $\sigma_{ij} = \sigma_{ji} = \frac{1}{2}$ for all i and j), the fitness matrix $\mathbf{W} = (w_{ij})$ is symmetric and (5) boils down to the classical selection equation of Haldane, Fisher, and Wright that has been extensively studied (e.g., Kingman, 1961; Cannings, 1969; reviewed in Karlin, 1978; Nagylaki, 1992). In game theoretical terms, a symmetric fitness matrix represents a “partnership game” (Hofbauer and Sigmund, 1998), i.e., a game in which the interests of both players coincide. In fact, in the absence of segregation distortion, both alleles A_i and A_j have the same “interest” in the survival and reproduction of individuals of genotype $A_i A_j$.

In the absence of selection ($w_{ij} = \sigma_{ij}$), the fitness matrix satisfies $\mathbf{W} + \mathbf{W}^T = \mathbf{U}$; i.e., \mathbf{W} is skew-symmetric up to the matrix of units \mathbf{U} . In game theoretical terms, such a matrix represents a “constant-sum game,” i.e., a strictly competitive game in which the two players have opposed interests. As with partnership games, the special structure of constant-sum games facilitates the analysis considerably (Nagylaki, 1983; Akin and Losert, 1984; Weissing, 1991; Hofbauer and Sigmund, 1998).

In this paper, we will focus on the interaction of selection and segregation distortion, which is harder to analyze and less well understood (e.g., Taylor and Jonker, 1978; Weissing, 1991; Hofbauer and Sigmund, 1998). In this case, w_{ij} should be interpreted as the fitness of an individual of genotype $A_i A_j$ viewed from the perspective of allele A_i . Hence, our model explicitly takes the point of view of the allele instead of that of the genotype.

Equilibria

The equilibrium points \mathbf{p}^* of (5) are characterized by

$$w_i(\mathbf{p}^*) = \bar{w}(\mathbf{p}^*) \quad \text{unless } p_i^* = 0 \quad (6)$$

for all i . Hence, at equilibrium, either the frequency of allele A_i is zero or its marginal fitness equals the mean fitness of the population. At times we will also use the shorter notation $w_i^* = w_i(\mathbf{p}^*)$ and $\bar{w}^* = \bar{w}(\mathbf{p}^*)$.

Calculation of the equilibria is straightforward (e.g., Cannings, 1969). For example, a fully polymorphic equilibrium (i.e., $p_i^* > 0$ for all i) is a positive solution of the vector equation $\mathbf{W}\mathbf{p}^* = \bar{w}^*\mathbf{u}$. In the special cases $\mathbf{W} = \mathbf{W}^T$ (no segregation distortion) and $\mathbf{W} + \mathbf{W}^T = \mathbf{U}$ (no selection), a fully polymorphic equilibrium also satisfies $\mathbf{W}^T\mathbf{p}^* = \bar{w}^*\mathbf{u}$, a fact that simplifies the stability analysis considerably.

Linearization

To investigate the stability of an equilibrium, we consider the linear approximation of the allele frequency dynamics (5) at \mathbf{p}^* . This is given by $\mathbf{x}' = \mathbf{J}_W\mathbf{x}$, where \mathbf{J}_W denotes the Jacobian matrix evaluated at equilibrium, and $\mathbf{x} = \mathbf{p} - \mathbf{p}^*$ is the vector of deviations from equilibrium. The Jacobian is given by

$$\mathbf{J}_W = \left(\left. \frac{\partial p_i'}{\partial p_j} \right|_{\mathbf{p}^*} \right) = \left(\left. \frac{\partial}{\partial p_j} \frac{p_i w_i(\mathbf{p})}{\bar{w}(\mathbf{p})} \right|_{\mathbf{p}^*} \right), \quad (7)$$

where the notation indicates that the derivatives are evaluated at equilibrium. A straightforward calculation shows that the elements of the Jacobian are given by

$$a_{ij} = \delta_{ij} \frac{w_i^*}{\bar{w}^*} + \frac{p_i^*}{\bar{w}^*} \left(w_{ij} - w_j^* - \sum_k p_k^* w_{kj} \right). \quad (8)$$

In matrix notation, the action of \mathbf{J}_W is given by

$$\mathbf{J}_W\mathbf{x} = \frac{1}{\bar{w}^*} [\mathbf{x} \circ \mathbf{W}\mathbf{p}^* + \mathbf{p}^* \circ \mathbf{W}\mathbf{x} - \langle \mathbf{x}, (\mathbf{W} + \mathbf{W}^T)\mathbf{p}^* \rangle \mathbf{p}^*]. \quad (9)$$

In the case of a fully polymorphic equilibrium (i.e., $p_i^* > 0$ for all i), the equilibrium condition (6) implies $\mathbf{W}\mathbf{p}^* = \bar{w}^*\mathbf{u}$ and hence $\langle \mathbf{x}, \mathbf{W}\mathbf{p}^* \rangle = 0$. As a result, (9) simplifies to

$$\mathbf{J}_W\mathbf{x} = \mathbf{x} + \frac{1}{\bar{w}^*} [\mathbf{p}^* \circ \mathbf{W}\mathbf{x} - \langle \mathbf{x}, \mathbf{W}^T\mathbf{p}^* \rangle \mathbf{p}^*]. \quad (10)$$

In the two special cases $\mathbf{W} = \mathbf{W}^T$ and $\mathbf{W} + \mathbf{W}^T = \mathbf{U}$, (9) is simplified even further by the fact that $\langle \mathbf{x}, \mathbf{W}^T\mathbf{p}^* \rangle = 0$:

$$\mathbf{J}_W\mathbf{x} = \mathbf{x} + \frac{1}{\bar{w}^*} \mathbf{p}^* \circ \mathbf{W}\mathbf{x}. \quad (11)$$

Stability

Throughout we will consider generic cases only: stability (or instability) should henceforth be interpreted as hyperbolic stability (or instability). \mathbf{p}^* is a (hyperbolically) stable equilibrium if all eigenvalues of the Jacobian are smaller than 1 in absolute value. In other words, \mathbf{p}^* is stable if and only if the spectral radius of the Jacobian is smaller than 1, i.e. iff $\rho(\mathbf{J}_W) < 1$. In the degenerate case $\rho(\mathbf{J}_W) = 1$, the equilibrium may still be stable, but then higher order conditions have to be verified (e.g., Lessard and Karlin, 1982).

Strictly speaking, only those eigenvalues of \mathbf{J}_W that belong to right eigenvectors from the invariant subspace $S_0 = \{\mathbf{x} \mid \sum x_i = 0\}$ which describes the deviations $\mathbf{x} = \mathbf{p} - \mathbf{p}^*$ from equilibrium should be taken into account. However, it is easy to see that the vector of units $\mathbf{u} = (1, \dots, 1)$ is a left eigenvector of \mathbf{J}_W with respect to the eigenvalue 0. As a consequence (e.g., Gantmacher, 1966), all right eigenvectors of \mathbf{J}_W corresponding to nonzero eigenvalues are perpendicular to \mathbf{u} and thus belong to S_0 . In other words, 0 is the only eigenvalue with a right eigenvector not belonging to S_0 , and this eigenvalue does not contribute to the spectral radius.

In selection models, it is useful to distinguish two kinds of stability: internal stability and external stability (Lieberman, 1991). Internal stability of an equilibrium \mathbf{p}^* refers to perturbations which involve only alleles that are already present at equilibrium. In contrast, external stability refers to stability with respect to invasion attempts of rare alleles that are not yet present at equilibrium.

Internal versus External Stability

Consider an equilibrium \mathbf{p}^* with the alleles A_1, \dots, A_m present in positive frequencies ($p_i^* > 0$ for $i = 1, \dots, m$). The internal stability of \mathbf{p}^* can be judged on the basis of the $m \times m$ matrix \mathbf{A}_W which results from \mathbf{J}_W by dropping all rows and columns that do not belong to the support of \mathbf{p}^* (i.e., for which $p_i^* = 0$).

\mathbf{p}^* is (hyperbolically) internally stable if all eigenvalues of the matrix \mathbf{A}_W are smaller than 1 in absolute value, i.e.,

iff $\rho(\mathbf{A}_W) < 1$. In view of the equilibrium condition (6), the matrix elements simplify to (see (10))

$$a_{ij} = \delta_{ij} - p_i^* + \frac{p_i^*}{\bar{w}^*} \left(w_{ij} - \sum_k p_k^* w_{kj} \right).$$

Instead of \mathbf{A}_W we may just as well consider the matrix $\tilde{\mathbf{A}}_W$, given by

$$\tilde{a}_{ij} = \delta_{ij} + \frac{p_i^*}{\bar{w}^*} \left(w_{ij} - \sum_k p_k^* w_{kj} \right). \quad (12)$$

In fact, \mathbf{A}_W and $\tilde{\mathbf{A}}_W$ act identically on the invariant subspace S_0 which describes the deviations from equilibrium. The only eigenvector of \mathbf{A}_W and $\tilde{\mathbf{A}}_W$ not belonging to S_0 corresponds to the eigenvalue 0. This eigenvalue does not contribute to the spectral radius of \mathbf{A}_W or $\tilde{\mathbf{A}}_W$: $\rho(\tilde{\mathbf{A}}_W) = \rho(\mathbf{A}_W)$.

In the two special cases $\mathbf{W} = \mathbf{W}^T$ (no segregation distortion) and $\mathbf{W} + \mathbf{W}^T = \mathbf{U}$ (no selection), internal stability can be determined on the basis of the spectral radius of the matrix $\hat{\mathbf{A}}_W = (\hat{a}_{ij})$ (see (11)), where

$$\hat{a}_{ij} = \delta_{ij} + p_i^* \frac{w_{ij}}{\bar{w}^*}.$$

In the special case $\mathbf{W} + \mathbf{W}^T = \mathbf{U}$ (no selection) the analysis is relatively easy. In fact, Liberman (1990) has shown that a polymorphic equilibrium (i.e., $m \geq 2$) can never be internally stable. The other special case, $\mathbf{W} = \mathbf{W}^T$ (no segregation distortion), is more complex, but still amenable to analysis. Selection in the absence of segregation distortion has been studied extensively in the past (e.g., Scheuer and Mandel, 1959; Kingman, 1961), and a number of equivalent criteria for internal stability have been derived (see Karlin, 1978, or Nagylaki, 1992, for a review). Such a classification is still missing in the more difficult general case (e.g., Taylor and Jonker, 1978; Hofbauer and Sigmund, 1998).

Suppose that the equilibrium \mathbf{p}^* is internally stable (i.e., $\rho(\mathbf{A}_W) < 1$), and consider an invasion attempt of a rare mutant allele A_{m+1} . The linear approximation of A_1, \dots, A_{m+1} near \mathbf{p}^* is governed by the recurrence equations

$$\begin{pmatrix} \mathbf{p}' - \mathbf{p}^* \\ p'_{m+1} \end{pmatrix} = \begin{pmatrix} \mathbf{A}_W & \mathbf{B} \\ \mathbf{0} & a_{m+1, m+1} \end{pmatrix} \begin{pmatrix} \mathbf{p} - \mathbf{p}^* \\ p_{m+1} \end{pmatrix}. \quad (13)$$

Here $a_{m+1, m+1}$ is given by (8)

$$a_{m+1, m+1} = \frac{\partial}{\partial p_{m+1}} \frac{p_{m+1} w_{m+1}(\mathbf{p})}{\bar{w}(\mathbf{p})} \Big|_{\mathbf{p}^*} = \frac{w_{m+1}^*}{\bar{w}^*}.$$

The spectral radius of the block matrix in (13) is given by

$$\rho \left[\begin{pmatrix} \mathbf{A}_W & \mathbf{B} \\ \mathbf{0} & a_{m+1, m+1} \end{pmatrix} \right] = \max[\rho(\mathbf{A}_W), a_{m+1, m+1}]. \quad (14)$$

In view of our assumption that the equilibrium \mathbf{p}^* is internally stable we have $\rho(\mathbf{A}_W) < 1$, and (14) implies that \mathbf{p}^* is destabilized by the advent of A_{m+1} if and only if $a_{m+1, m+1} > 1$. In view of the equilibrium condition (6), this implies

Result 1 (Liberman, 1991). An internally stable equilibrium \mathbf{p}^* is unstable against invasion of a rare mutant allele A_{m+1} if and only if the marginal fitness of A_{m+1} at equilibrium is larger than the mean fitness at equilibrium, i.e., iff

$$w_{m+1}^* > \bar{w}^* \quad (15)$$

or equivalently iff

$$w_{m+1}^* > w_i^* \quad \text{for any } i \in \{1, \dots, m\}. \quad (16)$$

Notice that w_i^* is a linear function of the components of \mathbf{p}^* , while \bar{w}^* is a quadratic form. Therefore, the invasion criterion (16) is in practice easier to check than the equivalent criterion (15).

A SEX-DIFFERENTIATED POPULATION

The Model

We now turn to the case of a sex-differentiated population. Again we consider a single autosomal distorter locus in an infinite, randomly mating population with discrete nonoverlapping generations. Let p_i and q_i represent the frequencies of A_i in male and female gametes after segregation distortion has taken place. Random mating is equivalent to the random union of gametes, and the ordered genotype frequencies at the zygote stage are given by $\frac{1}{2}(p_i q_j + q_i p_j)$. Notice that, at the zygote stage, the genotype frequencies do not differ between the sexes.

Let us denote the sex-specific viability of $A_i A_j$ males and females by v_{ij}^m and v_{ij}^f ($v_{ij} = v_{ji} \geq 0$ in both sexes), the sex-specific fertility of $A_i A_j$ males and females by φ_{ij}^m and φ_{ij}^f ($\varphi_{ij} = \varphi_{ji} \geq 0$ in both sexes), and the segregation ratio of A_i in $A_i A_j$ males and females by σ_{ij}^m and σ_{ij}^f ($\sigma_{ij} = 1 - \sigma_{ji} \geq 0$ in both sexes). The fitness of allele A_i in $A_i A_j$ males and females is again defined as the product of the viability, fertility, and segregation ratio and will be denoted by m_{ij} and f_{ij} , respectively:

$$m_{ij} = v_{ij}^m \varphi_{ij}^m \sigma_{ij}^m \quad \text{and} \quad f_{ij} = v_{ij}^f \varphi_{ij}^f \sigma_{ij}^f. \quad (17)$$

As in case of a population without sex differentiation (henceforth called one-sex population), the fitness measure proposed here explicitly takes the point of view of the allele rather than that of the genotype. In the absence of segregation distortion the fitness matrices of males or females are symmetric; i.e., $\mathbf{M} = \mathbf{M}^T$ or $\mathbf{F} = \mathbf{F}^T$. In the absence of selection the fitness matrices are skew-symmetric up to the constant matrix \mathbf{U} ; i.e., $\mathbf{M} + \mathbf{M}^T = \mathbf{U}$ or $\mathbf{F} + \mathbf{F}^T = \mathbf{U}$. In most—if not all—empirical examples, e.g., the t complex of the house mouse (Silver, 1993) or the SD complex of *D. melanogaster* (Temin *et al.*, 1991), segregation distortion takes place in one sex only, often the males. As a consequence, $\mathbf{F} = \mathbf{F}^T$. Sometimes, females are not even affected by selection. In this case, the female fitness matrix simplifies further to $\mathbf{F} = \mathbf{F}^T = \frac{1}{2} \mathbf{U}$. We will demonstrate below and in the companion paper that such special forms of the fitness matrices \mathbf{F} simplify the analysis considerably.

The allele frequency dynamics of the two-sex model is given by (e.g., Karlin, 1978)

$$\begin{aligned} p'_i &= \frac{M_i(\mathbf{p}, \mathbf{q})}{\bar{m}(\mathbf{p}, \mathbf{q})} \\ q'_i &= \frac{F_i(\mathbf{p}, \mathbf{q})}{\bar{f}(\mathbf{p}, \mathbf{q})}, \end{aligned} \quad (18)$$

where

$$M_i(\mathbf{p}, \mathbf{q}) = \frac{1}{2} (p_i(\mathbf{M}\mathbf{q})_i + q_i(\mathbf{M}\mathbf{p})_i)$$

and

$$F_i(\mathbf{p}, \mathbf{q}) = \frac{1}{2} (p_i(\mathbf{F}\mathbf{q})_i + q_i(\mathbf{F}\mathbf{p})_i)$$

correspond to $p_i w_i(\mathbf{p})$, the product of the allele frequency and the marginal fitness in the one-sex model (2), while

$$\bar{m}(\mathbf{p}, \mathbf{q}) = \sum_k M_k(\mathbf{p}, \mathbf{q}) = \frac{1}{2} \sum_{kl} p_k v_{kl}^m \varphi_{kl}^m q_l \quad (19)$$

and

$$\bar{f}(\mathbf{p}, \mathbf{q}) = \sum_k F_k(\mathbf{p}, \mathbf{q}) = \frac{1}{2} \sum_{kl} p_k v_{kl}^f \varphi_{kl}^f q_l$$

represent the mean fitness of the male and female subpopulation, respectively. Notice that the mean fitness of males and females is again independent of the segregation parameters σ_{ij}^m and σ_{ij}^f .

In compact matrix notation, the allele frequency dynamics is given by (see (5))

$$\begin{aligned} \mathbf{p}' &= \frac{\mathbf{p} \circ \mathbf{M}\mathbf{q} + \mathbf{q} \circ \mathbf{M}\mathbf{p}}{\langle \mathbf{p}, \mathbf{M}\mathbf{q} \rangle + \langle \mathbf{q}, \mathbf{M}\mathbf{p} \rangle} \\ \mathbf{q}' &= \frac{\mathbf{p} \circ \mathbf{F}\mathbf{q} + \mathbf{q} \circ \mathbf{F}\mathbf{p}}{\langle \mathbf{p}, \mathbf{F}\mathbf{q} \rangle + \langle \mathbf{q}, \mathbf{F}\mathbf{p} \rangle}. \end{aligned} \quad (20)$$

This dynamics has been derived before by Karlin (1978) (see also Karlin and Lessard, 1986; Nagylaki, 1992), but it has been analyzed for some specific cases only. Karlin (1978) and Lessard (1989) treat the special case $\mathbf{M} = \mathbf{M}^T$ and $\mathbf{F} = \mathbf{F}^T$ (i.e., absence of segregation distortion in both sexes), while Liberman (1990) considers the case $\mathbf{M} + \mathbf{M}^T = \mathbf{U}$ and $\mathbf{F} + \mathbf{F}^T = \mathbf{U}$ (i.e., absence of selection in both sexes).

Equilibria

The characterization of the equilibria and the determination of their stability is much harder than in the case of a population without sex differentiation, and only partial results exist even for the case of Mendelian segregation (Cannings, 1969; Karlin, 1978). Already in low-dimensional cases (e.g., two alleles) the equilibrium conditions

$$\begin{aligned} 2\bar{m}^* \mathbf{p}^* &= \mathbf{p}^* \circ \mathbf{M}\mathbf{q}^* + \mathbf{q}^* \circ \mathbf{M}\mathbf{p}^* \\ 2\bar{f}^* \mathbf{q}^* &= \mathbf{p}^* \circ \mathbf{F}\mathbf{q}^* + \mathbf{q}^* \circ \mathbf{F}\mathbf{p}^* \end{aligned} \quad (21)$$

often lead to intricate polynomial equations that can be solved only numerically (e.g., Lewontin, 1968; Hartl, 1970a, b). This is illustrated in the companion paper by means of some simple but realistic examples.

Linearization

The stability of an equilibrium $(\mathbf{p}^*, \mathbf{q}^*)$ is again determined by the linear approximation of the allele

frequency dynamics at $(\mathbf{p}^*, \mathbf{q}^*)$. The Jacobian matrix \mathbf{J}_{MF} is a block-matrix of the form

$$\mathbf{J}_{\text{MF}} = \begin{pmatrix} \mathbf{P} & \mathbf{Q} \\ \mathbf{R} & \mathbf{S} \end{pmatrix} = \begin{pmatrix} \frac{\partial p'_i}{\partial p_j} & \frac{\partial p'_i}{\partial q_j} \\ \frac{\partial q'_i}{\partial p_j} & \frac{\partial q'_i}{\partial q_j} \end{pmatrix} \Bigg|_{(\mathbf{p}^*, \mathbf{q}^*)}, \quad (22)$$

where \mathbf{P} , \mathbf{Q} , \mathbf{R} , and \mathbf{S} are $n \times n$ matrices of the derivatives of the allele frequency dynamics, evaluated at equilibrium. A straightforward calculation shows that the elements of \mathbf{J}_{MF} are given by

$$\begin{aligned} P_{ij} &= \frac{\partial p'_i}{\partial p_j} \Bigg|_{(\mathbf{p}^*, \mathbf{q}^*)} = \frac{1}{2\bar{m}^*} (\delta_{ij}(\mathbf{M}\mathbf{q}^*)_i + q_i^* m_{ij} - p_i^*(\mathbf{M}\mathbf{q}^*)_j - p_i^*(\mathbf{M}^T\mathbf{q}^*)_j) \\ Q_{ij} &= \frac{\partial p'_i}{\partial q_j} \Bigg|_{(\mathbf{p}^*, \mathbf{q}^*)} = \frac{1}{2\bar{m}^*} (\delta_{ij}(\mathbf{M}\mathbf{p}^*)_i + p_i^* m_{ij} - p_i^*(\mathbf{M}\mathbf{p}^*)_j - p_i^*(\mathbf{M}^T\mathbf{p}^*)_j) \\ R_{ij} &= \frac{\partial q'_i}{\partial p_j} \Bigg|_{(\mathbf{p}^*, \mathbf{q}^*)} = \frac{1}{2\bar{f}^*} (\delta_{ij}(\mathbf{F}\mathbf{q}^*)_i + q_i^* f_{ij} - q_i^*(\mathbf{F}\mathbf{q}^*)_j - q_i^*(\mathbf{F}^T\mathbf{q}^*)_j) \\ S_{ij} &= \frac{\partial q'_i}{\partial q_j} \Bigg|_{(\mathbf{p}^*, \mathbf{q}^*)} = \frac{1}{2\bar{f}^*} (\delta_{ij}(\mathbf{F}\mathbf{p}^*)_i + p_i^* f_{ij} - q_i^*(\mathbf{F}\mathbf{p}^*)_j - q_i^*(\mathbf{F}^T\mathbf{p}^*)_j), \end{aligned} \quad (23)$$

where $\bar{m}^* = \bar{m}(\mathbf{p}^*, \mathbf{q}^*)$ and $\bar{f}^* = \bar{f}(\mathbf{p}^*, \mathbf{q}^*)$.

The action of \mathbf{J}_{MF} can therefore be described by

$$\mathbf{J}_{\text{MF}} \begin{pmatrix} \mathbf{x} \\ \mathbf{y} \end{pmatrix} = \begin{pmatrix} \mathbf{P}\mathbf{x} + \mathbf{Q}\mathbf{y} \\ \mathbf{R}\mathbf{x} + \mathbf{S}\mathbf{y} \end{pmatrix}, \quad (24)$$

where

$$\begin{aligned} \mathbf{P}\mathbf{x} &= \frac{1}{2\bar{m}^*} [\mathbf{x} \circ \mathbf{M}\mathbf{q}^* + \mathbf{q}^* \circ \mathbf{M}\mathbf{x} - \langle \mathbf{x}, (\mathbf{M} + \mathbf{M}^T)\mathbf{q}^* \rangle \mathbf{p}^*] \\ \mathbf{Q}\mathbf{y} &= \frac{1}{2\bar{m}^*} [\mathbf{y} \circ \mathbf{M}\mathbf{p}^* + \mathbf{p}^* \circ \mathbf{M}\mathbf{y} - \langle \mathbf{y}, (\mathbf{M} + \mathbf{M}^T)\mathbf{p}^* \rangle \mathbf{p}^*] \\ \mathbf{R}\mathbf{x} &= \frac{1}{2\bar{f}^*} [\mathbf{x} \circ \mathbf{F}\mathbf{q}^* + \mathbf{q}^* \circ \mathbf{F}\mathbf{x} - \langle \mathbf{x}, (\mathbf{F} + \mathbf{F}^T)\mathbf{q}^* \rangle \mathbf{q}^*] \\ \mathbf{S}\mathbf{y} &= \frac{1}{2\bar{f}^*} [\mathbf{y} \circ \mathbf{F}\mathbf{p}^* + \mathbf{p}^* \circ \mathbf{F}\mathbf{y} - \langle \mathbf{y}, (\mathbf{F} + \mathbf{F}^T)\mathbf{p}^* \rangle \mathbf{q}^*]. \end{aligned} \quad (25)$$

Notice that in the special case $\mathbf{M} + \mathbf{M}^T = \mathbf{U}$ and $\mathbf{F} + \mathbf{F}^T = \mathbf{U}$ (i.e., absence of selection in both sexes) considered by Liberman (1990), the Jacobian is simplified considerably since $\bar{m}^* = \bar{f}^* = \frac{1}{2}$, and the last terms in (25) vanish (e.g., $\langle \mathbf{x}, (\mathbf{M} + \mathbf{M}^T)\mathbf{q}^* \rangle = 0$).

The equilibrium $(\mathbf{p}^*, \mathbf{q}^*)$ is (hyperbolically) stable if and only if all eigenvalues of \mathbf{J}_{MF} are smaller than 1 in absolute value: $\rho(\mathbf{J}_{\text{MF}}) < 1$. Strictly speaking, one has, as in the one-sex model, to consider only the action of \mathbf{J}_{MF} on the invariant subspace $S_{0,0} = \{(\mathbf{x}, \mathbf{y}) \mid \sum_i x_i = \sum_i y_i = 0\}$ which includes the deviations $(\mathbf{x}, \mathbf{y}) = (\mathbf{p} - \mathbf{p}^*, \mathbf{q} - \mathbf{q}^*)$ from equilibrium. However, eigenvalues belonging to right eigenvectors not belonging to the invariant subspace $S_{0,0}$ are zero and therefore do not contribute to the spectral radius of \mathbf{J}_{MF} . In fact, it is readily verified that the vectors $\mathbf{z}_1 = (1, \dots, 1, 0, \dots, 0)$ and $\mathbf{z}_2 = (0, \dots, 0, 1, \dots, 1)$ consisting of n zero entries and n entries of ones are left eigenvectors with respect to the eigenvalue 0. As a consequence, all right eigenvectors of \mathbf{J}_{MF} corresponding to nonzero eigenvalues are perpendicular to \mathbf{z}_1 and \mathbf{z}_2 , and they belong to $S_{0,0}$. In other words, 0 is the only eigenvalue with right eigenvectors not belonging to $S_{0,0}$, and this eigenvalue does not contribute to the spectral radius.

Internal versus External Stability

Consider an equilibrium $(\mathbf{p}^*, \mathbf{q}^*)$ where the alleles A_1, \dots, A_m are present in positive frequencies ($p_i^* > 0$ or $q_i^* > 0$ for $1 \leq i \leq m$). The internal stability of $(\mathbf{p}^*, \mathbf{q}^*)$ is again determined by the spectral radius of the matrix \mathbf{A}_{MF} which results from \mathbf{J}_{MF} by deleting all rows and columns corresponding to alleles A_k ($k > m$) not present at equilibrium. $(\mathbf{p}^*, \mathbf{q}^*)$ is internally stable if and only if

$$\rho(\mathbf{A}_{\text{MF}}) < 1. \quad (26)$$

Now suppose that (26) is satisfied and that a new allele A_{m+1} is introduced in low frequency. Following Lessard (1989), the first-order approximation of the augmented system A_1, \dots, A_{m+1} near $(\mathbf{p}^*, \mathbf{q}^*)$ can be written as

$$\begin{pmatrix} \mathbf{p}' - \mathbf{p}^* \\ \mathbf{q}' - \mathbf{q}^* \\ p'_{m+1} \\ q'_{m+1} \end{pmatrix} = \begin{pmatrix} \mathbf{A}_{\text{MF}} & \mathbf{B} \\ \mathbf{0} & \mathbf{C}_{m+1} \end{pmatrix} \begin{pmatrix} \mathbf{p} - \mathbf{p}^* \\ \mathbf{q} - \mathbf{q}^* \\ p_{m+1} \\ q_{m+1} \end{pmatrix}, \quad (27)$$

where the 2×2 ‘‘invasion matrix’’ C_{m+1} is of the form (see (23))

$$C_{m+1} = \begin{pmatrix} \frac{\partial p'_{m+1}}{\partial p_{m+1}} & \frac{\partial p'_{m+1}}{\partial q_{m+1}} \\ \frac{\partial q'_{m+1}}{\partial p_{m+1}} & \frac{\partial q'_{m+1}}{\partial q_{m+1}} \end{pmatrix} \Bigg|_{(p^*, q^*)} = \begin{pmatrix} \frac{(\mathbf{Mq}^*)_{m+1}}{2\bar{m}^*} & \frac{(\mathbf{Mp}^*)_{m+1}}{2\bar{m}^*} \\ \frac{(\mathbf{Fq}^*)_{m+1}}{2\bar{f}^*} & \frac{(\mathbf{Fp}^*)_{m+1}}{2\bar{f}^*} \end{pmatrix}. \tag{28}$$

The spectral radius of the block matrix in (27) is given by (cf. (14))

$$\rho \left[\begin{pmatrix} \mathbf{A}_{MF} & \mathbf{B} \\ \mathbf{0} & C_{m+1} \end{pmatrix} \right] = \max[\rho(\mathbf{A}_{MF}), \rho(C_{m+1})]. \tag{29}$$

The equilibrium (p^*, q^*) is externally stable against invasion by a rare mutant allele A_{m+1} iff $\rho(C_{m+1}) < 1$. In contrast, the rare allele A_{m+1} will spread (at a geometric rate) iff $\rho(C_{m+1}) > 1$. For a 2×2 matrix C , $\rho(C) < 1$ is equivalent to $|\text{tr}(C)| < 1 + \det(C) < 2$ (e.g., Edelstein–Keshet, 1988). In our case, the trace of C_{m+1} is positive. Hence, we arrive at

Result 2. The invasion prospects of a rare mutant allele A_{m+1} of the two-sex dynamics (20) can be deduced from the invasion matrix C_{m+1} (28). A_{m+1} will successfully invade an internally stable equilibrium (p^*, q^*) if and only if

$$\det(C_{m+1}) > 1 \quad \text{or} \quad \text{tr}(C_{m+1}) > 1 + \det(C_{m+1}). \tag{30}$$

Lessard (1989) takes a different approach to judge the invasion prospects of a rare allele. Although his analysis was originally intended for the symmetric case $\mathbf{M} = \mathbf{M}^T$ and $\mathbf{F} = \mathbf{F}^T$, the analysis extends to the general case since it does not depend on symmetry considerations. Lessard (1989) shows that $\rho(C_{m+1})$ is given by

$$\rho(C_{m+1}) = \frac{1}{2} \left(\frac{m^*_{m+1}}{\bar{m}^*} + \frac{f^*_{m+1}}{\bar{f}^*} \right),$$

where

$$\begin{aligned} m^*_{m+1} &= \zeta(\mathbf{Mq}^*)_{m+1} + (1 - \zeta)(\mathbf{Mp}^*)_{m+1} \\ f^*_{m+1} &= \zeta(\mathbf{Fq}^*)_{m+1} + (1 - \zeta)(\mathbf{Fp}^*)_{m+1} \end{aligned} \tag{31}$$

denote the marginal male and female fitness of A_{m+1} at equilibrium. The weighing factor ζ corresponds to the relative asymptotic frequency of A_{m+1} in males; i.e., $(\zeta, 1 - \zeta)$ is the normalized dominant right eigenvector of C_{m+1} . Hence, we obtain a Shaw–Mohler criterion (Shaw and Mohler, 1953) for the invasion prospects of a rare allele A_{m+1} :

Result 3 (Lessard, 1989). A rare mutant allele A_{m+1} of the two-sex dynamics (20) will successfully invade an internally stable equilibrium (p^*, q^*) if and only if the average of the marginal fitness of the mutant in males and females compared to the mean fitness in males and females exceeds one:

$$\frac{1}{2} \left(\frac{m^*_{m+1}}{\bar{m}^*} + \frac{f^*_{m+1}}{\bar{f}^*} \right) > 1. \tag{32}$$

Here the marginal fitness of A_{m+1} in males and females is given by (31).

Lessard’s approach has the advantage that (32) makes it quite transparent and intuitively plausible when and why a new allele can spread in a population. It has, however, the disadvantage that the weighing factor ζ in (31) and, hence, the marginal fitness values of A_{m+1} are difficult to calculate. In practical applications (see the companion paper), the invasion criterion (30) is usually checked more easily than the Shaw–Mohler criterion (32).

Symmetric Equilibria

The analysis is simplified considerably in the case of a ‘‘symmetric’’ equilibrium (p^*, p^*) , i.e., an equilibrium with identical allele frequencies in male and female gametes are identical. In the case of a symmetric equilibrium, the equilibrium conditions (21) reduce to

$$\begin{aligned} (\mathbf{Mp}^*)_i &= \bar{m}^* \\ (\mathbf{Fp}^*)_i &= \bar{f}^*, \end{aligned} \tag{33}$$

unless $p_i^* = 0$.

Symmetric equilibria occur only under rather special restrictions on the matrices \mathbf{M} and \mathbf{F} . To see this, consider a fully polymorphic equilibrium $p^* > 0$, which is given by $\mathbf{Mp}^* = \bar{m}^* \mathbf{u}$ and $\mathbf{Fp}^* = \bar{f}^* \mathbf{u}$. As a consequence, the vectors $\mathbf{M}^{-1} \mathbf{u}$ and $\mathbf{F}^{-1} \mathbf{u}$ have to be collinear, a condition that will hold only for rather specific relations between \mathbf{M} and \mathbf{F} . Nevertheless, symmetric equilibria play an important role in practical applications, as will be demonstrated below and in the companion paper.

Insertion of $\mathbf{q}^* = \mathbf{p}^*$ into (23) and comparison of the result with (25) shows that the Jacobian matrix \mathbf{J}_{MF} is of the form

$$\mathbf{J}_{\text{MF}} = \frac{1}{2} \begin{pmatrix} \mathbf{J}_{\text{M}} & \mathbf{J}_{\text{M}} \\ \mathbf{J}_{\text{F}} & \mathbf{J}_{\text{F}} \end{pmatrix}, \quad (34)$$

where \mathbf{J}_{M} and \mathbf{J}_{F} are the Jacobians at the equilibrium \mathbf{p}^* of the two one-sex dynamics induced by the fitness matrices $\mathbf{W} = \mathbf{M}$ and $\mathbf{W} = \mathbf{F}$, respectively. In Appendix A it is shown that the spectral radius of this $2n \times 2n$ matrix is the same as the spectral radius of the $n \times n$ matrix $\frac{1}{2}(\mathbf{J}_{\text{M}} + \mathbf{J}_{\text{F}})$:

$$\rho(\mathbf{J}_{\text{MF}}) = \rho\left(\frac{1}{2}(\mathbf{J}_{\text{M}} + \mathbf{J}_{\text{F}})\right). \quad (35)$$

Hence, we obtain

Result 4. A symmetric equilibrium $(\mathbf{p}^*, \mathbf{p}^*)$ of the two-sex dynamics (20) is (internally and externally) stable if and only if

$$\rho\left[\frac{1}{2}(\mathbf{J}_{\text{M}} + \mathbf{J}_{\text{F}})\right] < 1, \quad (36)$$

where \mathbf{J}_{M} and \mathbf{J}_{F} denote the Jacobians of the one-sex dynamics induced by \mathbf{M} and \mathbf{F} .

As a consequence, the condition for internal stability can now be checked by replacing \mathbf{J}_{M} and \mathbf{J}_{F} in (36) by \mathbf{A}_{M} and \mathbf{A}_{F} , i.e., by dropping all rows and columns that belong to alleles not present at equilibrium. Furthermore, the criterion (32) for external instability is easy to check, because the marginal fitnesses at equilibrium are now given by

$$m_i^* = (\mathbf{M}\mathbf{p}^*)_i \quad \text{and} \quad f_i^* = (\mathbf{F}\mathbf{p}^*)_i.$$

In view of this, and the equilibrium conditions (33), we arrive at

Result 5. A rare mutant allele A_{m+1} will successfully invade an internally stable equilibrium $(\mathbf{p}^*, \mathbf{p}^*)$ of the two-sex dynamics (20) if and only if

$$\frac{1}{2} \left(\frac{(\mathbf{M}\mathbf{p}^*)_{m+1}}{(\mathbf{M}\mathbf{p}^*)_i} + \frac{(\mathbf{F}\mathbf{p}^*)_{m+1}}{(\mathbf{F}\mathbf{p}^*)_i} \right) > 1 \quad \text{for any } i \in \{1, \dots, m\}, \quad (37)$$

i.e., if and only if the relative fitness of A_{m+1} in males and females is, on average, larger than 1.

POPULATIONS WITH AND WITHOUT SEX DIFFERENTIATION: A COMPARISON

The Model

Most studies of segregation distortion are based on the one-sex model (5) or extensions thereof. The two-sex model (20) is much harder to analyze but more realistic since segregation distortion typically differs between the sexes. It is therefore interesting to consider those cases where both models are comparable and to investigate whether the insights obtained from the one-sex model also apply in the two-sex context. To this end, we will consider the special case where only the strength but not the direction of selection and segregation distortion differs between the sexes. More precisely, we assume that the male and female fitness parameters are of the form

$$\mathbf{M} = \mathbf{W} \quad \text{and} \quad \mathbf{F} = a\mathbf{W} + b\mathbf{U}; \quad (38)$$

i.e., $m_{ij} = w_{ij}$ and $f_{ij} = aw_{ij} + b$. The parameters a and b are assumed to be nonnegative: $a, b \geq 0$.

Insertion of (38) in (20) shows that the allele frequency dynamics is given by

$$\begin{aligned} \mathbf{p}' &= \frac{\mathbf{p} \circ \mathbf{W}\mathbf{q} + \mathbf{q} \circ \mathbf{W}\mathbf{p}}{\langle \mathbf{p}, \mathbf{W}\mathbf{q} \rangle + \langle \mathbf{q}, \mathbf{W}\mathbf{p} \rangle} \\ \mathbf{q}' &= \frac{a[\mathbf{p} \circ \mathbf{W}\mathbf{q} + \mathbf{q} \circ \mathbf{W}\mathbf{p}] + b(\mathbf{p} + \mathbf{q})}{a[\langle \mathbf{p}, \mathbf{W}\mathbf{q} \rangle + \langle \mathbf{q}, \mathbf{W}\mathbf{p} \rangle + 2b]}. \end{aligned} \quad (39)$$

Let us for a moment consider the special case $b = 0$, i.e., selection and segregation distortion the same in both sexes. In this case, $\mathbf{q}' = \mathbf{p}'$; i.e., the allele frequencies are the same in males and females after one generation. From then on, the dynamics is given by

$$\mathbf{p}' = \frac{\mathbf{p} \circ \mathbf{W}\mathbf{p}}{\langle \mathbf{p}, \mathbf{W}\mathbf{p} \rangle},$$

i.e., by the one-sex dynamics induced by \mathbf{W} .

The other special case $a = 0$, i.e., no selection and segregation distortion in females, (39) reduces to

$$\begin{aligned} \mathbf{p}' &= \frac{\mathbf{p} \circ \mathbf{W}\mathbf{q} + \mathbf{q} \circ \mathbf{W}\mathbf{p}}{\langle \mathbf{p}, \mathbf{W}\mathbf{q} \rangle + \langle \mathbf{q}, \mathbf{W}\mathbf{p} \rangle} \\ \mathbf{q}' &= \frac{1}{2}(\mathbf{p} + \mathbf{q}). \end{aligned} \quad (40)$$

Notice that this is in contrast with the claim of Karlin and Lessard (1986, p. 65) that $\mathbf{q}' = \mathbf{p}$.

Equilibria

The equilibrium points $(\mathbf{p}^*, \mathbf{q}^*)$ of (39) are characterized by the relations

$$\begin{aligned} 2\bar{w}^* \mathbf{p}^* &= \mathbf{p}^* \circ \mathbf{W}\mathbf{q}^* + \mathbf{q}^* \circ \mathbf{W}\mathbf{p}^* \\ 2(a\bar{w}^* + b) \mathbf{q}^* &= a(\mathbf{p}^* \circ \mathbf{W}\mathbf{q}^* + \mathbf{q}^* \circ \mathbf{W}\mathbf{p}^*) \\ &\quad + b(\mathbf{p}^* + \mathbf{q}^*), \end{aligned} \tag{41}$$

where $2\bar{w}^* = \langle \mathbf{p}^*, \mathbf{W}\mathbf{q}^* \rangle + \langle \mathbf{q}^*, \mathbf{W}\mathbf{p}^* \rangle$. Insertion of the first line of (41) into the second line yields

$$(2a\bar{w}^* + b) \mathbf{q}^* = (2a\bar{w}^* + b) \mathbf{p}^*,$$

implying that $\mathbf{q}^* = \mathbf{p}^*$ (unless $2a\bar{w}^* + b = 0$). In other words, all equilibrium points are symmetric and given by the equilibrium conditions for a population without sex differentiation. Hence, we arrive at our next result:

Result 6. All equilibria of the two-sex dynamics generated by $\mathbf{M} = \mathbf{W}$ and $\mathbf{F} = a\mathbf{W} + b\mathbf{U}$ are symmetric. There is a one-to-one correspondence between the symmetric equilibria $(\mathbf{p}^*, \mathbf{p}^*)$ of the two-sex dynamics and the equilibria \mathbf{p}^* of the one-sex dynamics generated by \mathbf{W} .

Stability

Consider an equilibrium \mathbf{p}^* of the one-sex dynamics and the corresponding equilibrium $(\mathbf{p}^*, \mathbf{p}^*)$ of the two-sex dynamics. The natural question to ask is whether \mathbf{p}^* and $(\mathbf{p}^*, \mathbf{p}^*)$ have the same stability properties. With respect to external stability, the answer is simple: the one- and two-sex dynamics are fully congruent. This can be seen as follows. In view of Result 5, a rare mutant allele A_{m+1} will invade the internally stable equilibrium $(\mathbf{p}^*, \mathbf{p}^*)$ if and only if

$$\frac{1}{2} \left(\frac{w_{m+1}^*}{\bar{w}^*} + \frac{aw_{m+1}^* + b}{a\bar{w}^* + b} \right) > 1.$$

It is easy to see that this inequality is equivalent to $w_{m+1}^* > \bar{w}^*$, the criterion for the spread of A_{m+1} with respect to the one-sex dynamics (Result 1). Hence, we obtain

Result 7. An internally stable equilibrium $(\mathbf{p}^*, \mathbf{p}^*)$ of the two-sex dynamics induced by $\mathbf{M} = \mathbf{W}$ and $\mathbf{F} = a\mathbf{W} + b\mathbf{U}$ is externally stable against invasion by a rare mutant

allele A_{m+1} if and only if the equilibrium \mathbf{p}^* of the one-sex dynamics induced by \mathbf{W} is externally stable against invasion by A_{m+1} as well.

Karlin and Lessard (1986) give a proof of Result 7 for the special case of a symmetric matrix \mathbf{W} (see their discussion preceding Theorem 7.2). Although their proof is rather indirect, it is in principle also applicable in the present context since the conditions for external stability are not affected by symmetry considerations.

With respect to internal stability, the relation between the one-sex and the two-sex dynamics is less clear. As shown earlier (Result 4), the (internal) stability of $(\mathbf{p}^*, \mathbf{p}^*)$ depends on the location of the eigenvalues of $\frac{1}{2}(\mathbf{J}_M + \mathbf{J}_F)$. In Appendix B it is shown that on the invariant subspace S_0 , the Jacobian $\mathbf{J}_F = \mathbf{J}_{a\mathbf{W} + b\mathbf{U}}$ is given by

$$\mathbf{J}_{a\mathbf{W} + b\mathbf{U}} = \frac{a\bar{w}^*}{a\bar{w}^* + b} \mathbf{J}_W + \frac{b}{a\bar{w}^* + b} \mathbf{I}. \tag{42}$$

Hence, $\frac{1}{2}(\mathbf{J}_M + \mathbf{J}_F)$ is of the form

$$\frac{1}{2}(\mathbf{J}_M + \mathbf{J}_F) = \xi \mathbf{J}_W + (1 - \xi) \mathbf{I}, \tag{43}$$

where

$$\xi = \frac{1}{2} \left(1 + \frac{a\bar{w}^*}{a\bar{w}^* + b} \right). \tag{44}$$

Notice that $\frac{1}{2} \leq \xi \leq 1$.

To obtain the one-sex dynamics that corresponds to the two-sex dynamics generated by $\mathbf{M} = \mathbf{W}$ and $\mathbf{F} = a\mathbf{W} + b\mathbf{U}$, one may argue as follows (S. P. Otto, personal communication): Since males and females contribute genetically to offspring in equal proportions, the marginal fitness of an allele is simply the arithmetic average of its fitness in males and females when these are standardized to have the same mean fitness. To standardize fitnesses in the two-sex population male fitness should be divided by \bar{w}^* (mean male fitness at equilibrium), while female fitness should be divided by $a\bar{w}^* + b$ (mean female fitness at equilibrium). Hence, the one-sex fitness matrix $\tilde{\mathbf{W}}$ corresponding to the two-sex population induced by $\mathbf{M} = \mathbf{W}$ and $\mathbf{F} = a\mathbf{W} + b\mathbf{U}$ is given by

$$\tilde{\mathbf{W}} = \frac{1}{2} \left(\frac{\mathbf{W}}{\bar{w}^*} + \frac{a\mathbf{W} + b\mathbf{U}}{a\bar{w}^* + b} \right) = \frac{\xi}{\bar{w}^*} \mathbf{W} + (1 - \xi) \mathbf{U}. \tag{45}$$

It is not difficult to see that the equilibrium \mathbf{p}^* of $\tilde{\mathbf{W}}$ has the same stability properties as the equilibrium $(\mathbf{p}^*, \mathbf{p}^*)$ of the two-sex dynamics generated by $\mathbf{M} = \mathbf{W}$ and $\mathbf{F} = a\mathbf{W} + b\mathbf{U}$, since (42) applied to $\tilde{\mathbf{W}}$ yields

$$\mathbf{J}_{\tilde{\mathbf{W}}} = \xi \mathbf{J}_{\mathbf{W}} + (1 - \xi) \mathbf{I} = \frac{1}{2} (\mathbf{J}_{\mathbf{M}} + \mathbf{J}_{\mathbf{F}}). \quad (46)$$

Result 8. The symmetric equilibrium $(\mathbf{p}^*, \mathbf{p}^*)$ of the two-sex dynamics generated by $\mathbf{M} = \mathbf{W}$ and $\mathbf{F} = a\mathbf{W} + b\mathbf{U}$ is (internally and externally) stable if and only if \mathbf{p}^* is stable with respect to the one-sex dynamics generated by $\tilde{\mathbf{W}}$ (45).

The two-sex population therefore corresponds to a one-sex population with fitness matrix $\tilde{\mathbf{W}}$, where—due to the term $(1 - \xi)\mathbf{U}$ —the combined action of selection and segregation distortion is weaker than in a one-sex population with fitness matrix \mathbf{W} . It is known (Weissing, 1991) that weaker selection and segregation distortion prevent overshooting and therefore tend to stabilize the system. Accordingly, symmetric equilibria have a higher degree of stability than the corresponding one-sex equilibria, since weaker selection in one sex ($b > 0$) leads to weaker selection in the overall population, and weaker selection has a dampening effect. In fact:

Result 9. If the equilibrium \mathbf{p}^* of the one-sex dynamics induced by \mathbf{W} is (internally and/or externally) stable, then the corresponding symmetric equilibrium $(\mathbf{p}^*, \mathbf{p}^*)$ of the two-sex dynamics generated by $\mathbf{M} = \mathbf{W}$ and $\mathbf{F} = a\mathbf{W} + b\mathbf{U}$ is stable as well. In contrast, the stability of $(\mathbf{p}^*, \mathbf{p}^*)$ does not necessarily imply the stability of \mathbf{p}^* .

The proof is easy: In view of (43), the eigenvalues $\lambda_{\mathbf{MF}}$ of $\frac{1}{2}(\mathbf{J}_{\mathbf{M}} + \mathbf{J}_{\mathbf{F}})$ are of the form

$$\lambda_{\mathbf{MF}} = \xi \lambda_{\mathbf{W}} + (1 - \xi), \quad (47)$$

where $\lambda_{\mathbf{W}}$ is an eigenvalue of $\mathbf{J}_{\mathbf{W}}$. It is easy to see that $|\lambda_{\mathbf{W}}| < 1$ implies that $|\lambda_{\mathbf{MF}}| < 1$. In fact, $0 \leq \xi \leq 1$ and $\lambda \mapsto \xi\lambda + 1 - \xi$ maps the open unit disk D_1 onto an open disk D_ξ with radius ξ around the point $1 - \xi$ (see Fig. 1). It is obvious that the latter disk is contained in the open unit disk. That the converse is not true in general can be seen as follows. Consider the case where selection and segregation distortion is acting only in males: $\mathbf{M} = \mathbf{W}$ and $\mathbf{F} = b\mathbf{U}$. In this case, $\xi = \frac{1}{2}$, and it is conceivable that $\lambda \mapsto \xi\lambda + 1 - \xi$ maps values of λ ($= \lambda_{\mathbf{W}}$) from outside the open unit disk to values ($= \lambda_{\mathbf{MF}}$) inside the open unit disk.

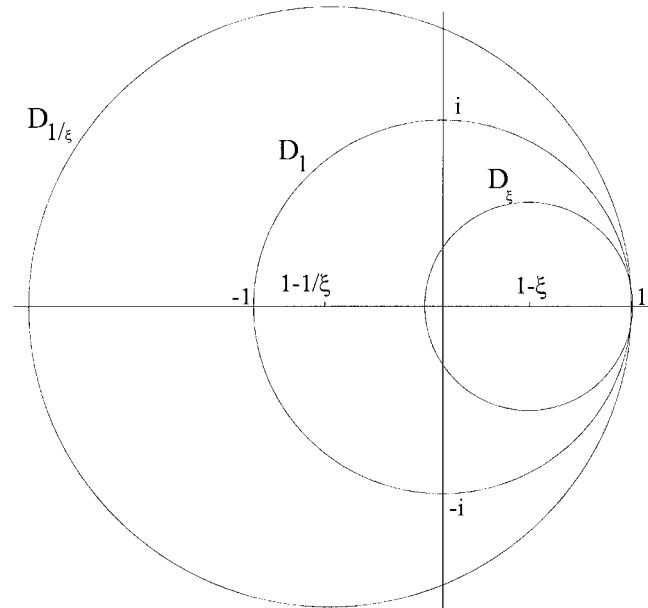


FIG. 1. The function $\varphi_\xi: \lambda \mapsto \xi\lambda + 1 - \xi$ maps the eigenvalues $\lambda_{\mathbf{W}}$ with respect to the one-sex dynamics to the eigenvalues of the two-sex dynamics. φ_ξ maps the complex unit disk D_1 onto the disk D_ξ , which is centered at $1 - \xi$ and which has radius ξ . Since $0 \leq \xi \leq 1$, D_ξ is contained in D_1 and $\lambda_{\mathbf{W}} \in D_1$ implies $\varphi_\xi(\lambda_{\mathbf{W}}) \in D_\xi \subseteq D_1$. The disk $D_{1/\xi}$ is centered at $1 - \frac{1}{\xi}$ and has radius $\frac{1}{\xi}$. This disk contains all λ which are mapped by φ_ξ onto the unit disk: $\varphi_\xi(\lambda) \in D_1 \Leftrightarrow \lambda \in D_{1/\xi}$.

To give an example, set $b = 1$ and take the fitness matrix

$$\mathbf{W} = \begin{pmatrix} 1 & \alpha(1 - \sigma) & \alpha(1 + \sigma) \\ \alpha(1 + \sigma) & 1 & \alpha(1 - \sigma) \\ \alpha(1 - \sigma) & \alpha(1 + \sigma) & 1 \end{pmatrix} \quad (48)$$

considered by Liberman (1991). Here σ ($0 \leq \sigma \leq 1$) is a distortion parameter (so that no segregation distortion occurs if $\sigma = 0$) and α is a selection parameter (so that if $\alpha < 1$ there is underdominance, while for $\alpha > 1$ there is some form of overdominance). Figure 2 shows that an equilibrium \mathbf{p}^* of the one-sex dynamics may be internally unstable (Fig. 2A), whereas if selection and segregation distortion act in one sex only, the corresponding equilibrium $(\mathbf{p}^*, \mathbf{p}^*)$ of the two-sex dynamics is internally stable (Fig. 2B).

The example shows that already in the simple and rather special case of selection and segregation distortion acting in one sex (i.e., $\alpha = 0$ and the dynamics given by (40)), the stability of \mathbf{p}^* is not necessarily implied by the

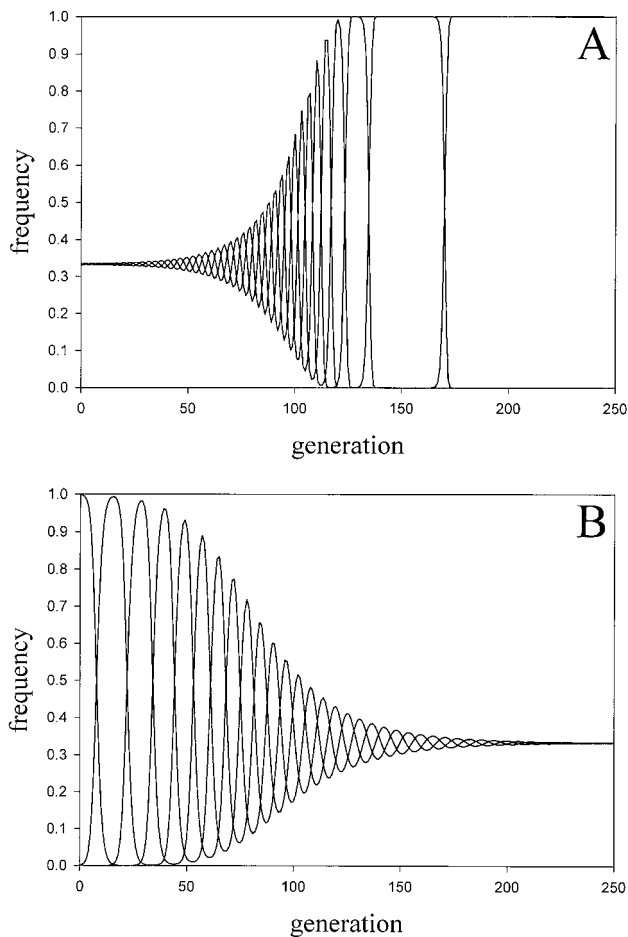


FIG. 2. Different outcomes of selection and segregation distortion in (A) a one-sex population with fitness matrix \mathbf{W} , and (B) a two-sex population with selection and segregation distortion in only one sex ($\mathbf{M} = \mathbf{W}$, $\mathbf{F} = \mathbf{U}$). The matrix \mathbf{W} is given by (48) with $\alpha = 2$ and $s = 1$. The central equilibrium is a global attractor for the two-sex dynamics, but a global repeller for the one-sex dynamics (see Weissing, 1991).

stability of $(\mathbf{p}^*, \mathbf{p}^*)$. On the other hand, the stability criteria for \mathbf{p}^* and $(\mathbf{p}^*, \mathbf{p}^*)$ coincide for the other special case $b = 0$ (i.e., $\mathbf{M} = \mathbf{W}$ and $\mathbf{F} = a\mathbf{W}$), since in this case the two-sex dynamics (39) essentially reduces to the one-sex dynamics after one generation.

There are two other exceptions to the rule that stability with respect to the one-sex dynamics is more difficult to achieve than stability with respect to the two-sex dynamics. If only two alleles are present at equilibrium, the state space of the one-sex dynamics (5) is one dimensional. Since the one-sex dynamics is a diffeomorphism (Akin and Losert, 1984), it follows that (5) is a monotone mapping. This implies that the only relevant eigenvalue is a positive real number, but for a real positive eigenvalue

$\lambda_{\mathbf{W}}$, (47) implies that $\lambda_{\mathbf{W}} < 1$ if and only if $\lambda_{\mathbf{MF}} < 1$. Hence, we are led to

Result 10. If only two alleles are present at equilibrium, \mathbf{p}^* is (internally and/or externally) stable with respect to the one-sex dynamics induced by \mathbf{W} if and only if $(\mathbf{p}^*, \mathbf{p}^*)$ is stable with respect to the two-sex dynamics induced by $\mathbf{M} = \mathbf{W}$ and $\mathbf{F} = a\mathbf{W} + b\mathbf{U}$.

The second exception is less obvious and, in fact, claims to the contrary can be found in the early literature (Cannings, 1969; Karlin, 1978):

Result 11. In the absence of segregation distortion (i.e., \mathbf{W} is a symmetric matrix), \mathbf{p}^* is an (internally and/or externally) stable equilibrium of the one-sex dynamics induced by \mathbf{W} if and only if $(\mathbf{p}^*, \mathbf{p}^*)$ is an internally stable equilibrium of the two-sex dynamics induced by $\mathbf{M} = \mathbf{W}$ and $\mathbf{F} = a\mathbf{U} + b\mathbf{W}$.

This result was noticed earlier by Karlin and Lessard (1986, p. 223). Here we give a simple proof that makes use of the fact that mean fitness is a Lyapunov function when the fitness matrix \mathbf{W} is symmetric (e.g., Nagylaki, 1992): In view of Result 8, $(\mathbf{p}^*, \mathbf{p}^*)$ is stable with respect to the one-sex dynamics induced by the (symmetric) fitness matrix $\tilde{\mathbf{W}}$ (45). As well known from classical selection theory, the latter condition is equivalent to mean fitness $\bar{w}_{\xi}(\mathbf{p}) = \frac{\xi}{\bar{w}^*} \sum_{kl} p_k w_{kl} p_l + 1 - \xi$ being maximized at $\mathbf{p} = \mathbf{p}^*$. But \mathbf{p}^* maximizes $\bar{w}_{\xi}(\mathbf{p})$ if and only if it maximizes $\bar{w}_1(\mathbf{p})$, and the latter is equivalent to \mathbf{p}^* being an internally stable equilibrium with respect to the fitness matrix \mathbf{W} .

CONCLUSIONS

Our study was motivated by the question whether and when several segregation distorter alleles can stably coexist. The obvious approach would be to characterize all equilibrium points and to investigate their stability. However, this approach seems feasible only for specific cases (the one-sex model, the two-sex model with selection and segregation distortion identical in both sexes, or the two-sex model with selection and segregation distortion in one sex only). In essence, a complete analysis of the two-sex model seems possible only in those cases for which the equilibria are symmetric, i.e., if the frequencies in male and female gametes do not differ. In the case of asymmetric equilibria, already the calculation of the interior equilibria is a daunting

task (see Manos *et al.*, 2000, for a specific example). Accordingly, we have little hope that an analytical characterization of the equilibria and their stability can be accomplished.

To obtain at least a partial characterization of the equilibria, the problem of stability of the equilibria is split by separate consideration of the internal and external stabilities. Internal stability refers to stability with respect to perturbations of alleles that are already present at equilibrium. In contrast, external stability refers to stability with respect to invasion attempts of alleles that are not yet present. Hence, internal stability may be thought of as being concerned with the relatively short population dynamical time scale, while external stability deals with the longer, evolutionary time scale on which new mutant alleles may arise. While the problem of internal stability is difficult and cannot be solved in general, we have shown that the determination of the external stability of the equilibria is still manageable. Notice, however, that this conclusion hinges on the assumption that equilibria, if they exist, are internally stable.

It is tempting to speculate that mutual invadability will result in stable coexistence, i.e., that all alleles will stably coexist if they are able to spread when rare. Unfortunately, this is not true in general. Take the one-sex model, which is formally equivalent to the discrete replicator dynamics (Liberman, 1991). For this dynamics it is well known that mutual invadability does not preclude the possibility that the frequency of one or more alleles approaches zero (Hofbauer and Sigmund, 1998). In principle this can already happen in the context of three alleles (Fig. 2A; see also Weissing, 1991; Stadler, 1996).

Nevertheless, in practical applications the situation may not be as grim as sketched above. In practice, the aforementioned problems play a minor role, due to natural restrictions on the fitness matrices \mathbf{M} and/or \mathbf{F} . Take, for instance, the t complex of the house mouse. The so-called t haplotypes strongly distort Mendelian segregation in heterozygous males. Females, however, are unaffected by segregation distortion. As a consequence, the female fitness matrix is symmetric ($\mathbf{F} = \mathbf{F}^T$). Furthermore, certain variants of the t haplotypes induce only male sterility, so that females are unaffected by selection. In this case, the female fitness matrix is simplified even further ($\mathbf{F} = \mathbf{F}^T = \mathbf{U}$). As we have shown, the analysis of these special cases is still within reach. And even the case of a lethal t haplotype that leads to homozygous lethality in both males and females may still be amenable to analysis, as the expression of selection does not differ between the sexes ($\mathbf{M} + \mathbf{M}^T = \mathbf{F} + \mathbf{F}^T$), so that male

fitness equals female fitness. Illustrations that apply to the t complex are given in the companion paper.

APPENDIX A

Stability of a Symmetric Equilibrium

For a symmetric equilibrium (\mathbf{p}^* , \mathbf{p}^*) the Jacobian \mathbf{J}_{MF} is given by the block matrix (34)

$$\mathbf{J}_{\text{MF}} = \frac{1}{2} \begin{pmatrix} \mathbf{J}_{\text{M}} & \mathbf{J}_{\text{M}} \\ \mathbf{J}_{\text{F}} & \mathbf{J}_{\text{F}} \end{pmatrix}.$$

The eigenvalues of \mathbf{J}_{MF} are the roots of the characteristic polynomial $\chi(\lambda)$ of \mathbf{J}_{MF} :

$$\chi(\lambda) = \det \begin{pmatrix} \frac{1}{2} \mathbf{J}_{\text{M}} - \lambda \mathbf{I} & \frac{1}{2} \mathbf{J}_{\text{M}} \\ \frac{1}{2} \mathbf{J}_{\text{F}} & \frac{1}{2} \mathbf{J}_{\text{F}} - \lambda \mathbf{I} \end{pmatrix}. \quad (\text{A1})$$

Since the matrices $\frac{1}{2} \mathbf{J}_{\text{M}} - \lambda \mathbf{I}$ and $\frac{1}{2} \mathbf{J}_{\text{M}}$ commute we may use Schur's formula (e.g., Gantmacher, 1966) to express the characteristic polynomial of \mathbf{J}_{MF} in terms of \mathbf{J}_{M} and \mathbf{J}_{F} :

$$\begin{aligned} \chi(\lambda) &= \det[(\frac{1}{2} \mathbf{J}_{\text{F}} - \lambda \mathbf{I})(\frac{1}{2} \mathbf{J}_{\text{M}} - \lambda \mathbf{I}) - \frac{1}{2} \mathbf{J}_{\text{F}} \frac{1}{2} \mathbf{J}_{\text{M}}] \\ &= \det[-\frac{1}{2} \mathbf{J}_{\text{F}} \lambda \mathbf{I} - \lambda \mathbf{I} \frac{1}{2} \mathbf{J}_{\text{M}} + \lambda^2 \mathbf{I}] \\ &= (-1)^n \det[\frac{1}{2} (\mathbf{J}_{\text{M}} + \mathbf{J}_{\text{F}}) - \lambda \mathbf{I}]. \end{aligned} \quad (\text{A2})$$

Since the second term of (A2) is just the characteristic polynomial of the matrix $\frac{1}{2} (\mathbf{J}_{\text{M}} + \mathbf{J}_{\text{F}})$, it is evident that the eigenvalues of \mathbf{J}_{MF} either are 0 (with multiplicity n) or are equal to the eigenvalues of $\frac{1}{2} (\mathbf{J}_{\text{M}} + \mathbf{J}_{\text{F}})$ (see (35)). This result was derived by Cannings (1969) for some special cases and is stated in general, but without proof, in Karlin (1978).

APPENDIX B

The Relation between \mathbf{J}_{W} and $\mathbf{J}_{a\mathbf{W}+b\mathbf{U}}$

Consider the fitness matrix $\mathbf{F} = a\mathbf{W} + b\mathbf{U}$ and an equilibrium \mathbf{p}^* of the one-sex dynamics induced by \mathbf{F} . The action of the Jacobian $\mathbf{J}_{\text{F}} = \mathbf{J}_{a\mathbf{W}+b\mathbf{U}}$ on the invariant subspace $S_0 = \{\mathbf{p} - \mathbf{p}^* \mid \sum (p_i - p_i^*) = 0\}$ which describes the deviations from equilibrium is given by (9)

$$\begin{aligned} \mathbf{J}_{a\mathbf{W}+b\mathbf{U}} \mathbf{x} &= \frac{1}{a\bar{w}^* + b} [\mathbf{x} \circ \mathbf{F} \mathbf{p}^* + \mathbf{p}^* \circ \mathbf{F} \mathbf{x} \\ &\quad - \langle \mathbf{x}, (\mathbf{F} + \mathbf{F}^T) \mathbf{p}^* \rangle \mathbf{p}^*], \end{aligned} \quad (\text{B1})$$

where $\mathbf{x} \in S_0$. On S_0 we have the identities $\mathbf{U}\mathbf{x} = \mathbf{0}$, $\mathbf{U}\mathbf{p}^* = \mathbf{u}$, and $\langle \mathbf{x}, \mathbf{u} \rangle = 0$ and, as a consequence,

$$\begin{aligned}\mathbf{x} \circ \mathbf{F}\mathbf{p}^* &= a\mathbf{x} \circ \mathbf{W}\mathbf{p}^* + b\mathbf{x} \\ \mathbf{p}^* \circ \mathbf{F}\mathbf{x} &= a\mathbf{p}^* \circ \mathbf{W}\mathbf{x}\end{aligned}\quad (\text{B2})$$

$$\langle \mathbf{x}, (\mathbf{F} + \mathbf{F}^T)\mathbf{p}^* \rangle = a\langle \mathbf{x}, (\mathbf{W} + \mathbf{W}^T)\mathbf{p}^* \rangle.$$

Insertion of (B2) into (B1) and use of (9) yield

$$\mathbf{J}_{a\mathbf{W}+b\mathbf{U}}\mathbf{x} = \left[\frac{a\bar{w}^*}{a\bar{w}^*+b} \mathbf{J}_{\mathbf{W}} + \frac{b}{a\bar{w}^*+b} \mathbf{I} \right] \mathbf{x}. \quad (\text{B3})$$

In other words, the action of $\mathbf{J}_{a\mathbf{W}+b\mathbf{U}}$ on S_0 is identical with the action of $\frac{a\bar{w}^*}{a\bar{w}^*+b} \mathbf{J}_{\mathbf{W}} + \frac{b}{a\bar{w}^*+b} \mathbf{I}$ on S_0 .

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