

## On the optimal sex-ratio: A stability analysis based on a characterization for one-locus multiallele viability models<sup>\*</sup>

Samuel Karlin<sup>1</sup> and Sabin Lessard<sup>2</sup>

<sup>1</sup> Department of Mathematics, Stanford University, Stanford, CA 94305, USA

<sup>2</sup> Département de Mathématiques et de Statistique, Université de Montréal, Montréal, Québec H3C 3J7, Canada

**Abstract.** Theoretical one-locus multiallele sex-determination models are found to admit even sex ratio equilibrium *surfaces* besides the equilibria for corresponding one-locus multiallele viability models. Both types of equilibria can be defined in terms of a single spectral radius function, the former corresponding to level surfaces and the latter to critical points. The stable equilibria in the corresponding viability models are associated with the local maxima, and the equilibrium structures for the sex-determination models can be fully described. Several optimality properties of the even-sex-ratio equilibrium surfaces can be deduced.

**Key words:** Sex ratio — evolutionary stability — optimality — multiallele viability models

### 1. Introduction

Sex-determination governed at an autosomal locus with probabilities of being male or female depending on zygote genotype was first given a theoretical formulation by Shaw (1958). A one-locus two-allele model was studied by Eshel (1975). Variant models (e.g. Nur, 1974; Uyenoyama and Bengtsson, 1979) allowing for maternal (or paternal) genotype control on brood sex ratio led to similar qualitative conclusions in favor of an equal representation of the sexes in panmictic populations. Eshel and Feldman (1982) considered generalizations to multi-allele cases. Two classes of equilibria were pointed out: symmetric equilibrium states exhibiting the same allele frequencies in the male and female populations, and even-sex-ratio equilibria associated with an equal representation of males and females. These authors dealt with conditions for the initial increase of a mutant allele introduced at a symmetric equilibrium state.

In this paper, we present an analysis circumscribing the existence and stability nature of both types of equilibria. Section 2 reviews the formulation of the

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one-locus multiallele sex-determination model and sets forth the recurrence equations. It is observed that a symmetric equilibrium state coincides with an equilibrium for a one-sex one-locus multiallele viability model while even-sex-ratio equilibria correspond to a level surface of a spectral radius functional. In order to fully describe the equilibrium structure for the sex-determination model, we introduce a characterization delineating the existence and stability of equilibria in the viability model in terms of the spectral radius functional (Sect. 3 with proofs of the main results in Section 4). Various optimality properties of the even-sex-ratio equilibrium surfaces are deduced (Sect. 5). Global convergence is ascertained in the case of sex-determination based on heterozygosity versus homozygosity (Sect. 6).

For further results and extensions to several variant models, we refer to Karlin and Lessard (1983, in press).

## 2. A multiallele sex-determination model

### 2.1. Formulation of the model

Consider a bisexual infinite population with  $r$  possible alleles  $A_1, A_2, \dots, A_r$  at an autosomal locus responsible for sex determination. We denote the frequency of genotype  $A_i A_j$  in the female population by  $2p_{ij}$  when  $i \neq j$  and by  $p_{ii}$  when  $i = j$ . The corresponding frequency of allele  $A_i$  is  $p_i = \sum_{j=1}^r p_{ij}$ . The quantities  $2q_{ij}$ ,  $q_{ii}$ , and  $q_i$  are defined analogously with respect to the male population. We assume discrete generations, random mating, Mendelian segregation, and equal fertility for all mating types. Let  $m_{ij}$  be the probability for an  $A_i A_j$  individual to be a male, and concomitantly  $1 - m_{ij}$  that of being a female. Clearly,  $0 \leq m_{ij} = m_{ji} \leq 1$ . We refer to  $M = \|m_{ij}\|_{i,j=1}^r$  as the *sex-determination coefficient matrix*. The case  $0 < m_{ij} < 1$  may reflect the effects of modifier genes coupled to prenatal and/or neonatal interactions. Where  $m_{ij} = 1$  or  $0$ , the sex phenotype is determined such that the collection of all genotypes  $A_i A_j$  partition into two groups,  $\mathcal{A}_M$  and  $\mathcal{A}_F$ , where every individual of type  $\mathcal{A}_M$  and  $\mathcal{A}_F$  is unambiguously male and female, respectively. We refer to this situation as *dichotomous* (or exact) *genotypic sex-determination*.

Under the above assumptions, the genotype frequencies over two successive generations obey the recursion relations

$$\begin{aligned} q'_{ij} &= \frac{m_{ij}(p_i q_j + p_j q_i)}{2w}, \\ p'_{ij} &= \frac{(1 - m_{ij})(p_i q_j + p_j q_i)}{2(1 - w)}, \quad i, j = 1, \dots, r \end{aligned} \tag{2.1}$$

where  $w = \sum_{i,j=1}^r m_{ij} p_i q_j$  is the proportion of males, the *sex-ratio*, in the total population for the given allelic frequency state. It will be convenient for later purposes to employ the Schur product operation of two vectors  $\underline{x} = (x_1, x_2, \dots, x_r)$  and  $\underline{y} = (y_1, y_2, \dots, y_r)$  symbolized by  $\underline{x} \circ \underline{y} = (x_1 y_1, x_2 y_2, \dots, x_r y_r)$ , and the inner product denoted by  $\langle \underline{x}, \underline{y} \rangle = \sum_{i=1}^r x_i y_i$ . Further, if  $M$  is any matrix, the representation  $\underline{x} \circ M$  stands for the matrix product  $D_{\underline{x}} M$  where  $D_{\underline{x}}$  designates the diagonal matrix with entries  $x_1, x_2, \dots, x_r$  down the main diagonal. In this notation, the

above system can be converted into the following recurrence equations for the allelic frequency vectors  $\underline{p} = (p_1, p_2, \dots, p_r)$  and  $\underline{q} = (q_1, q_2, \dots, q_r)$ :

$$\begin{aligned} \underline{q}' &= \frac{\underline{p} \circ M\underline{q} + \underline{q} \circ M\underline{p}}{2w}, \\ \underline{p}' &= \frac{\underline{p} \circ (U - M)\underline{q} + \underline{q} \circ (U - M)\underline{p}}{2(1 - w)} = \frac{\underline{p} + \underline{q} - \underline{p} \circ M\underline{q} - \underline{q} \circ M\underline{p}}{2(1 - w)} \end{aligned} \quad (2.2)$$

where  $w = \langle \underline{p}, M\underline{q} \rangle = \sum_{i=1}^r p_i (M\underline{q})_i = \sum_{i,j=1}^r m_{ij} p_i q_j$  and  $U$  denotes the matrix with all unit entries.

The transformation equations (2.2) represent an important case of the dynamical system describing the allele frequency changes for a two-sex one-locus multi-allele viability model. Formally the sex-determination model where an offspring of genotype  $A_i A_j$  is male (female) with probability  $m_{ij}$  ( $(1 - m_{ij})$ ) is equivalent to a sex differentiated viability model with viability matrices  $M = \|m_{ij}\|$  and  $F = \|1 - m_{ij}\| = U - M$  for males and females, respectively (see, e.g. Karlin, 1978). The fact that  $M$  and  $F = U - M$  are generated from a single matrix  $M$  allows a more tractable analysis of the system at hand.

### 2.2. Identification of the equilibria

An equilibrium of the sex-determination model consists of a pair of frequency vectors  $\{\underline{p}, \underline{q}\}$  having  $\underline{p}' = \underline{p}$  and  $\underline{q}' = \underline{q}$  in (2.2) and therefore satisfying

$$\underline{p} = \frac{\underline{p} + \underline{q} - 2w\underline{q}}{2(1 - w)}, \quad \text{i.e. } (1 - 2w)\underline{q} = (1 - 2w)\underline{p} \quad (2.3)$$

where  $w = \langle \underline{p}, M\underline{q} \rangle$ . Two kinds of equilibria can be distinguished (Eshel and Feldman, 1982): *symmetric equilibria* exhibiting identical allelic frequencies in the male and female populations (i.e. with  $\underline{p} = \underline{q}$ ), and *even-sex-ratio equilibrium states* (i.e. with  $\langle \underline{p}, M\underline{q} \rangle = \frac{1}{2}$ ), that is, with an equal representation of males and females in the population. A symmetric equilibrium  $\{\hat{\underline{p}}, \hat{\underline{p}}\}$  (abbreviated by  $\hat{\underline{p}}$ ) verifies

$$\hat{\underline{p}} = \frac{\hat{\underline{p}} \circ M\hat{\underline{p}}}{\langle \hat{\underline{p}}, M\hat{\underline{p}} \rangle}, \quad (2.4)$$

while an even-sex-ratio equilibrium state  $\{\tilde{\underline{p}}, \tilde{\underline{q}}\}$  is characterized by the relation

$$\tilde{\underline{q}} = \tilde{\underline{p}} \circ M\tilde{\underline{q}} + \tilde{\underline{q}} \circ M\tilde{\underline{p}}. \quad (2.5)$$

Note that the relation (2.5) entails an even-sex-ratio: summing over all coordinates, we have  $1 = 2\langle \tilde{\underline{p}}, M\tilde{\underline{q}} \rangle$  and therefore  $\tilde{w} = \langle \tilde{\underline{p}}, M\tilde{\underline{q}} \rangle = \frac{1}{2}$ . However, the property  $\langle \tilde{\underline{p}}, M\tilde{\underline{q}} \rangle = \frac{1}{2}$  alone is not sufficient to ensure equilibrium.

Equation (2.5) can be viewed in the following manner. For each  $\underline{p}$  in  $\Delta$  (i.e.  $\underline{p} = (p_1, \dots, p_r)$  with  $p_i \geq 0$  and  $\sum_{i=1}^r p_i = 1$ ), we form the matrix

$$B(\underline{p}) = D_p M + D_{M\underline{p}} \quad (2.6)$$

( $D_p$  the diagonal matrix with the components of  $\underline{p}$  down the main diagonal).

If  $\underline{p}$  is in  $\Delta^0$ , the interior of the simplex of frequency vectors  $\Delta$  (i.e. if  $\underline{p}$  is a positive frequency vector in  $\Delta$ ), and  $M$  is a positive matrix, then  $B(\underline{p})$  is a positive

matrix and the Perron-Frobenius theory (see, e.g. Gantmacher, 1959; Lancaster, 1969) affirms that the eigenvalue of largest magnitude for  $B(\underline{p})$  is real and positive admitting a unique (apart from a multiplicative factor) positive right eigenvector. We denote by  $\rho(\underline{p})$  the *spectral radius* of  $B(\underline{p})$ , that is, the eigenvalue of largest magnitude of  $B(\underline{p})$  and normalize the associated positive right-eigenvector  $\underline{y} = (y_1, \dots, y_r)$  to satisfy  $\sum_{i=1}^r y_i = 1$ . Then  $\underline{y} = \underline{y}(\underline{p})$  and  $\rho(\underline{p})$  vary continuously (actually analytically) as a function of  $\underline{p}$ ,  $\underline{p}$  in  $\Delta^0$ . The principal eigenvalue-eigenvector identity is

$$B(\underline{p})\underline{y}(\underline{p}) = \rho(\underline{p})\underline{y}(\underline{p}). \quad (2.7)$$

Comparing with the equilibrium relation (2.5), we note that an even-sex-ratio equilibrium state represented by  $\{\underline{p}, \underline{q}\}$ , both  $\underline{p}$  and  $\underline{q}$  interior to  $\Delta$ , exists if and only if  $\rho(\underline{p}) = 1$  and then the corresponding  $\underline{y}(\underline{p})$  is  $\underline{q}$ . These conditions can be extended by continuity allowing  $\underline{p}$  and  $\underline{q}$  on the same face of  $\Delta$ .

In order to fully describe the equilibrium structure for the sex-determination model (2.2), we will make appeal to a characterization of the symmetric equilibria defined by (2.4) based on the spectral function  $\rho(\underline{p})$ . Since such equilibria correspond to the equilibria for standard one-sex one-locus multiallele viability models (cf. Sect. 3), we will develop conditions for the existence and stability of an equilibrium in those models in terms of  $\rho(\underline{p})$ .

### 3. A characterization for equilibrium and stability in one-locus multiallele viability models

#### 3.1. A review of classical results

The transformation on the allelic frequency vectors  $\underline{p} = (p_1, \dots, p_r)$  for a classical one-locus multiallele viability model with  $M = \|m_{ij}\|$  as a viability matrix is

$$T\underline{p} = \frac{\underline{p} \circ M\underline{p}}{w(\underline{p})} \quad (3.1)$$

where  $w(\underline{p}) = \langle \underline{p}, M\underline{p} \rangle = \sum_{i,j=1}^r m_{ij} p_i p_j$ . In this model, random mating and Mendelian segregation are assumed and the quantity  $m_{ij}$  is interpreted as the relative number of  $A_i A_j$  zygotes that survive to contribute to the next generation. (See, e.g. Kingman, 1961a, b; Crow and Kimura, 1970; Nagylaki, 1977; Karlin, 1978; Ewens, 1979.)

To avoid unimportant technical details we assume henceforth unless stated otherwise that  $M = \|m_{ij}\|$  satisfies the following *genericity conditions*:

- (a)  $0 < m_{ij} < 1$  for all  $i$  and  $j$ ,
- (b) every principal submatrix of  $M$  is nonsingular,
- (c) for any set of indices  $i_1 < i_2 < \dots < i_k$ , the solution of

$$\sum_{\nu=1}^k m_{i_\mu, i_\nu} x_\nu = 1 \quad \text{for } \mu = 1, 2, \dots, k$$

has

$$\sum_{\nu=1}^k m_{i_0, i_\nu} x_\nu \neq 1 \quad \text{for all } i_0 \neq i_\mu. \quad (3.2)$$

Recall the following facts (see loc. cit.).

A polymorphic equilibrium  $\underline{p}^* = (p_1^*, \dots, p_r^*)$  (i.e. with  $p_i^* > 0$  for all  $i$ ) for the system (3.1) exists if and only if

$$\sum_{j=1}^r m_{ij}x_j = 1, \quad i = 1, 2, \dots, r \text{ admits a positive solution,} \quad (3.3)$$

and then  $p_i^* = x_i / \sum_{j=1}^r x_j$ . This polymorphic equilibrium is locally stable if any of the following conditions holds:

(i) The eigenvalues of  $M$ ,  $\lambda_1(M) \geq \lambda_2(M) \geq \dots \geq \lambda_r(M)$ , satisfy

$$\lambda_1(M) > 0 > \lambda_2(M) \geq \dots \geq \lambda_r(M). \quad (3.4)$$

(ii) The mean fitness function  $w(\underline{p}) = \langle \underline{p}, M\underline{p} \rangle$  achieves a strict maximum at  $\underline{p}^*$  with respect to the simplex of frequency vectors  $\Delta$ . (3.5)

(These conditions are necessary and sufficient if  $M$  is nonsingular.) An important fact in the one-locus multiallele viability model is that a locally stable polymorphic equilibrium is globally stable relative to all initial polymorphic states. More precisely, the mean fitness  $w(\underline{p})$  monotonically increases until an equilibrium is reached.

With any number of alleles represented, an equilibrium  $\hat{\underline{p}} = (\hat{p}_1, \dots, \hat{p}_r)$  of (3.1) solves the system of equations

$$(M\hat{\underline{p}})_i = \sum_{j=1}^r m_{ij}\hat{p}_j = w(\hat{\underline{p}}) = \langle \hat{\underline{p}}, M\hat{\underline{p}} \rangle, \quad i \in I^0(\hat{\underline{p}}), \quad (3.6)$$

the equations applying for those indices  $I^0(\hat{\underline{p}})$  where  $\hat{p}_i > 0$ . The equilibrium  $\hat{\underline{p}}$  is internally stable provided the principal submatrix of  $M$  restricted to the indices where  $p_i > 0$  satisfies (3.4). *External stability* of a boundary equilibrium prevails by definition if any new allele introduced in small frequency is ultimately eliminated. External stability is assured if

$$(M\hat{\underline{p}})_k < w(\hat{\underline{p}}) \quad \text{for all } k \text{ where } \hat{p}_k = 0. \quad (3.7)$$

It should be emphasized that when  $M$  is generic in the sense of (3.2), only a finite number of equilibria can exist and the above sufficient conditions for internal and external stability of  $\hat{\underline{p}}$  are actually *necessary* and *sufficient* for local stability of  $\hat{\underline{p}}$ , or equivalently, for strict local maximality of  $w(\underline{p})$  at  $\hat{\underline{p}}$  with respect to  $\Delta$ . Therefore a unique stable equilibrium (interior or on the boundary of  $\Delta$ ) corresponds to a strict global maximum of  $w(\underline{p})$  in  $\Delta$ . Note also that the polymorphic equilibria of (3.1) are exactly the critical points of  $w(\underline{p})$  relative to  $\Delta$ .

Some of the conclusions of the next sections will make appeal to the number of stable equilibria that can coexist in the one-locus multiallele viability model when a new allele is introduced into an equilibrium system. In this respect, we recall the following result (Karlín, 1978, Theorem 3.2): if an equilibrium of (3.1) on the boundary of  $\Delta$  with exactly  $r-1$  positive components (i.e. with exactly one allele not represented) is internally stable, then there exists at most one alternative equilibrium that can be locally stable relative to  $\Delta$ ; if the boundary equilibrium is externally unstable, then there exists one and only one stable equilibrium in  $\Delta$ .

### 3.2. Some preliminary results

The gradient map  $T'(\hat{p})$  at an equilibrium  $\hat{p}$  of (3.1) (i.e. the local linear approximation to  $T$  at  $\hat{p}$ ) is

$$T'(\hat{p})\underline{\xi} = \frac{\underline{\xi} \circ M\hat{p}}{w(\hat{p})} + \frac{\hat{p} \circ M\underline{\xi}}{w(\hat{p})} - \frac{2\langle M\hat{p}, \underline{\xi} \rangle}{[w(\hat{p})]^2} \hat{p} \circ M\hat{p} \quad (3.8)$$

where  $\underline{\xi} = (\xi_1, \dots, \xi_r)$  satisfies  $\sum_{j=1}^r \xi_j = 0$  and is such that  $\hat{p} + \varepsilon \underline{\xi} \in \Delta$  for  $\varepsilon > 0$  small enough. For a polymorphic equilibrium  $p^*$ , we have  $Mp^* = w(p^*)\underline{u}$  where  $\underline{u}$  is the vector displaying all unit components (cf. (3.6)) and the gradient map  $T'(p^*)$  acting on  $\mathcal{L} = \{\underline{\xi}: \langle \underline{\xi}, \underline{u} \rangle = 0\}$  reduces to

$$T'(p^*) = I + \frac{p^* \circ M}{w(p^*)} = \frac{1}{w(p^*)} B(p^*) \quad (3.9)$$

with the definition (2.6) for  $B(p^*)$ . Actually, using the notation

$$\frac{\underline{x}}{\underline{y}} = \frac{(x_1, \dots, x_r)}{(y_1, \dots, y_r)} = \left( \frac{x_1}{y_1}, \dots, \frac{x_r}{y_r} \right) \quad (3.10)$$

and introducing the matrix

$$M(\underline{p}) = \frac{\underline{p}}{Mp} \circ M, \quad (3.11)$$

we have, for every  $p \in \Delta$ ,

$$B(\underline{p}) = D_{Mp} + \underline{p} \circ M = D_{Mp}[I + M(\underline{p})]. \quad (3.12)$$

Recall the following facts from matrix theory (see, e.g. Gantmacher, 1959; Lancaster, 1969). If  $M$  is a symmetric matrix and  $D$  is a diagonal matrix with all positive diagonal elements, then  $DM$ ,  $MD$ , and  $D^{1/2}MD^{1/2}$  share the same eigenvalues which are real since  $D^{1/2}MD^{1/2}$  is a symmetric matrix. Moreover, the matrix  $DM = \underline{d} \circ M$  where  $\underline{d} = (d_1, \dots, d_r)$  is the vector of the diagonal elements of  $D$  acts as a symmetric matrix with respect to the modified inner product

$$\langle\langle \underline{x}, \underline{y} \rangle\rangle = \left\langle \frac{\underline{x}}{\underline{d}}, \underline{y} \right\rangle = \sum_{i=1}^r \frac{x_i y_i}{d_i}. \quad (3.13)$$

Indeed we have

$$\langle\langle DM\underline{x}, \underline{y} \rangle\rangle = \langle M\underline{x}, \underline{y} \rangle = \langle \underline{x}, M\underline{y} \rangle = \langle\langle \underline{x}, DM\underline{y} \rangle\rangle. \quad (3.14)$$

We say that  $DM$  is *symmetrizable*. In such a case, there exists a complete set of eigenvectors orthonormal with respect to the inner product (3.13).

When  $\underline{p}$  is interior to  $\Delta$  (i.e.  $p \in \Delta^0$ ), the matrix  $M(\underline{p})$  of (3.11) is symmetrizable and positive. It is easy to check that

$$M(\underline{p})\underline{p} = \underline{p} \quad \text{and} \quad \underline{u}(\underline{p})M(\underline{p}) = \underline{u}(\underline{p}) \quad (3.15)$$

i.e. one is an eigenvalue of  $M(\underline{p})$  with positive right eigenvector  $\underline{p}$  and left eigenvector  $\underline{u}(\underline{p}) = Mp$ . (In the case where  $p = p^*$  is a polymorphism, then  $\underline{u}(\underline{p}) = w(p^*)\underline{u}$  where  $\underline{u}$  displays all unit components.) Actually one must be a simple eigenvalue equal to the spectral radius of  $M(\underline{p})$  owing to the Perron–Frobenius

theory for positive matrices. Moreover, since  $\underline{u}(\underline{p})$  is a left eigenvector, we have

$$\langle M(\underline{p})\underline{\xi}, \underline{u}(\underline{p}) \rangle = \langle \underline{\xi}, \underline{u}(\underline{p})M(\underline{p}) \rangle = \langle \underline{\xi}, \underline{u}(\underline{p}) \rangle, \quad (3.16)$$

and therefore  $\langle M(\underline{p})\underline{\xi}, \underline{u}(\underline{p}) \rangle = 0$  if  $\langle \underline{\xi}, \underline{u}(\underline{p}) \rangle = 0$ . Finally the other eigenvalues of  $M(\underline{p})$  (apart from one) are real and strictly less than one in magnitude. It immediately follows that, for  $\underline{p} \in \Delta^0$ , the matrix  $I + M(\underline{p})$  is invertible with all positive eigenvalues and so is the matrix  $D_{M\underline{p}}[I + M(\underline{p})] = B(\underline{p})$ . Let us summarize.

**Lemma 3.1.** *For  $\underline{p} \in \Delta^0$ , the symmetrizable (cf. (3.14)) matrix  $M(\underline{p}) = [\underline{p}/M\underline{p}] \circ M$  has a simple eigenvalue one with right eigenvector  $\underline{p}$  which strictly dominates all other eigenvalues in absolute value. Moreover,  $M(\underline{p})$  transforms the linear manifold  $\mathcal{L}(\underline{p}) = \{\underline{\xi}: \langle \underline{\xi}, \underline{u}(\underline{p}) \rangle = 0\}$  into itself.*

**Corollary 3.1.** *The mappings  $I + M(\underline{p})$  and  $I - M(\underline{p})$  for  $\underline{p} \in \Delta^0$  are invertible on  $\mathcal{L}(\underline{p})$  onto itself.*

**Corollary 3.2.** *If  $\underline{p} \in \Delta^0$ , then the symmetrizable matrix  $B(\underline{p}) = D_{M\underline{p}}[I + M(\underline{p})]$  is invertible and all eigenvalues of  $B(\underline{p})$  are positive.*

Finally we record the following lemma.

**Lemma 3.2.** *A frequency vector  $\underline{p}^* \in \Delta^0$  is a polymorphic equilibrium of (3.1) if and only if*

$$B(\underline{p}^*)\underline{p}^* = \lambda^* \underline{p}^*, \quad \text{and then } \lambda^* = 2w(\underline{p}^*) = 2\langle \underline{p}^*, M\underline{p}^* \rangle. \quad (3.17)$$

*Moreover the polymorphic equilibrium  $\underline{p}^*$  is locally stable if and only if the eigenvalues of  $B(\underline{p}^*)$  restricted to  $\mathcal{L} = \{\underline{\xi}: \langle \underline{\xi}, \underline{u} \rangle = 0\}$  are strictly less than  $w(\underline{p}^*)$  (or equivalently by Lemma 3.1 the eigenvalues of  $M(\underline{p}^*)$  restricted to  $\mathcal{L}$  are strictly negative).*

*Proof of Lemma 3.2:* For  $\underline{p}^* \in \Delta^0$ , we have

$$B(\underline{p}^*)\underline{p}^* = D_{M\underline{p}^*}[I + M(\underline{p}^*)]\underline{p}^* = 2\underline{p}^* \circ M\underline{p}^*. \quad (3.18)$$

Therefore  $B(\underline{p}^*)\underline{p}^* = \lambda^* \underline{p}^*$  if and only if  $M\underline{p}^* = (\lambda^*/2)\underline{u}$ , and then  $w(\underline{p}^*) = \langle \underline{p}^*, M\underline{p}^* \rangle = (\lambda^*/2)\langle \underline{p}^*, \underline{u} \rangle = \lambda^*/2$ , i.e.  $\underline{p}^*$  is a polymorphic equilibrium of (3.1) (cf. (3.6)). A necessary and sufficient condition for local stability of  $\underline{p}^*$  is that the gradient matrix at  $\underline{p}^*$  relative to  $\mathcal{L}$  (cf. (3.9)) exhibits all eigenvalues strictly less than one in magnitude as stated in Lemma 3.2.

### 3.3. A characterization of the equilibria based on a spectral radius functional

Recall that  $\rho(\underline{p}) = \rho(B(\underline{p}))$  denotes the spectral radius (the magnitude of the eigenvalue of largest magnitude) of  $B(\underline{p}) = D_{M\underline{p}} + \underline{p} \circ M$  for  $\underline{p}$  in  $\Delta$ . When  $\underline{p} \in \Delta^0$ , then  $B(\underline{p})$  is positive and  $\rho(\underline{p})$  is defined by (2.7). For  $\underline{p}$  on the boundary of  $\Delta$ , let  $I^0(\underline{p})$  be the set of indices corresponding to the positive components of  $\underline{p}$  and  $B^0(\underline{p})$  be the (positive) principal submatrix of  $B(\underline{p})$  restricted to these indices. The rows of  $B(\underline{p})$  corresponding to the zero components of  $\underline{p}$  reduce to the rows of the diagonal matrix  $D_{M\underline{p}}$ . Therefore the eigenvalues of  $B(\underline{p})$  are the eigenvalues of  $B^0(\underline{p})$  and the quantities  $(M\underline{p})_i$  for all  $i$  where  $p_i = 0$ . Denoting the spectral radius of  $B^0(\underline{p})$  by  $\rho^0(\underline{p}) = \rho(B^0(\underline{p}))$ , we have

$$\rho(\underline{p}) = \max \{ \rho^0(\underline{p}), (M\underline{p})_i \text{ for all } i \notin I^0(\underline{p}) \}. \quad (3.19)$$

Observe that if

$$\rho^0(\underline{p}) > (M\underline{p})_i \quad \text{for all } i \notin I^0(\underline{p}), \quad (3.20)$$

then the principal right eigenvector  $\underline{q}$  of  $B(\underline{p})$  in  $\Delta$  is such that  $I^0(\underline{q}) = I^0(\underline{p})$  (i.e.  $\underline{q}$  and  $\underline{p}$  are on the same face of  $\Delta$ ) and the positive components of  $\underline{q}$  form the principal right eigenvector of  $B^0(\underline{p})$  for the corresponding subsystem.

We now state the main results of this section.

**Theorem 3.1.** *Let  $\rho(\underline{p})$  be the spectral radius of  $B(\underline{p}) = D_{M\underline{p}} + \underline{p} \circ M$  for  $\underline{p}$  in  $\Delta$  where  $M$  satisfies the genericity conditions (3.2). Let  $\underline{p}^*$  be a frequency vector interior to  $\Delta$ , i.e. with all positive components.*

(i)  *$\underline{p}^*$  is a polymorphic equilibrium for the viability model  $M$  (i.e. the transformation (3.1)) if and only if  $\underline{p}^*$  is a critical point of the function  $\rho(\underline{p})$ , i.e. the derivative of  $\rho(\underline{p})$  in every direction at  $\underline{p}^*$  relative to  $\Delta$  is zero.*

(ii)  *$\underline{p}^*$  is a locally stable polymorphic equilibrium for  $M$  if and only if  $\rho(\underline{p})$  achieves a strict local maximum with respect to  $\Delta$  at  $\underline{p}^*$ .*

For boundary equilibrium points, the above result is complemented by the following.

**Theorem 3.2.** *Suppose the conditions of Theorem 3.1 are in force.*

(i) *An equilibrium  $\hat{\underline{p}}$  for the viability model  $M$  (interior or on the boundary of  $\Delta$ ) is locally stable if and only if  $\rho(\hat{\underline{p}})$  is a strict local maximum of  $\rho(\underline{p})$  with respect to  $\Delta$ .*

(ii) *Moreover, the local maxima of  $\rho(\underline{p})$  in  $\Delta$  are twice the local maxima of  $\langle \underline{p}, M\underline{p} \rangle$  and are achieved at the same points. A local maximum within  $\Delta$  is actually a global and unique maximum over all  $\Delta$ .*

## 4. Proofs of the theorems of section 3

### 4.1. Proof of Theorem 3.1

We first develop some preliminaries. Let  $\underline{p}^* \in \Delta^0$ . Choose an arbitrary direction  $\underline{\eta} = (\eta_1, \eta_2, \dots, \eta_r)$  in  $\Delta^0$ , that is,  $\underline{\eta}$  satisfying  $\langle \underline{\eta}, \underline{u} \rangle = \sum_{i=1}^r \eta_i = 0$ , and  $s$  small enough to keep  $\underline{p}(s) = \underline{p}^* + s\underline{\eta}$  in  $\Delta^0$ . The Perron–Frobenius theory for positive matrices affirms that the spectral radius  $\rho(s) = \rho(\underline{p}(s))$  of  $B(\underline{p}(s)) = D_{M\underline{p}(s)} + \underline{p}(s) \circ M$  is a simple eigenvalue of  $B(\underline{p}(s))$  analytic in  $s$  and that the components of  $\underline{q}(s)$ , the unique right eigenvector in  $\Delta^0$  of  $B(\underline{p}(s))$  corresponding to  $\rho(s)$ , are also analytic functions of  $s$ . We display these quantities by the relation

$$B(\underline{p}(s))\underline{q}(s) = \rho(s)\underline{q}(s) \quad \text{where } \rho(s) = \rho(\underline{p}(s)). \quad (4.1)$$

We use hereafter the notation

$$\begin{aligned} \dot{\underline{p}}(s) &= \frac{d\underline{p}(s)}{ds} = \left( \frac{dp_1(s)}{ds}, \dots, \frac{dp_r(s)}{ds} \right) \quad \text{and} \quad \dot{\underline{q}}(s) = \left( \frac{dq_1(s)}{ds}, \dots, \frac{dq_r(s)}{ds} \right) \\ \ddot{\underline{p}}(s) &= \frac{d^2\underline{p}(s)}{ds^2} \quad \text{and} \quad \ddot{\underline{q}}(s) = \frac{d^2\underline{q}(s)}{ds^2}, \end{aligned} \quad (4.2)$$

which we abbreviate to  $\dot{\underline{p}}, \dot{\underline{q}}, \ddot{\underline{p}}$  and  $\ddot{\underline{q}}$  at  $s=0$ .



Since  $\langle \underline{p}(s), \underline{u} \rangle = \langle \underline{q}(s), \underline{u} \rangle = 1$  where  $\underline{u}$  is the vector of all unit components, we have

$$\langle \underline{\dot{p}}(s), \underline{u} \rangle = \langle \underline{\ddot{p}}(s), \underline{u} \rangle = \langle \underline{\dot{q}}(s), \underline{u} \rangle = \langle \underline{\ddot{q}}(s), \underline{u} \rangle = 0. \quad (4.3)$$

Observe that, for  $\underline{p} \in \Delta^0$  and every vector  $\underline{\xi}$ , we have

$$\underline{\xi} B(\underline{p}) = \underline{\xi} \circ M\underline{p} + [\underline{\xi} \circ \underline{p}] M = [M\underline{p}] \circ \underline{\xi} + M[\underline{p} \circ \underline{\xi}]. \quad (4.4)$$

Choosing  $\underline{\xi} = \underline{z} = \underline{q}/\underline{p}$  in the notation (3.10) where  $\underline{q}$  is the leading right eigenvector of  $B(\underline{p})$  in  $\Delta^0$ , we get

$$\underline{z} B(\underline{p}) = \rho(\underline{p}) \underline{z}. \quad (4.5)$$

Indeed,  $\underline{z} B(\underline{p}) = [M\underline{p}] \circ [\underline{q}/\underline{p}] + M\underline{q} = [\underline{u}/\underline{p}] \circ [\underline{q} \circ M\underline{p} + \underline{p} \circ M\underline{q}] = [\underline{u}/\underline{p}] \circ B(\underline{p}) \underline{q} = \rho(\underline{p}) \underline{z}$ . Furthermore, we have

$$\begin{bmatrix} \underline{u} \\ \underline{z} \end{bmatrix} B(\underline{q}) = \rho(\underline{p}) \underline{u} \quad (4.6)$$

since

$$\begin{aligned} \begin{bmatrix} \underline{u} \\ \underline{z} \end{bmatrix} B(\underline{q}) &= [M\underline{q}] \circ \frac{\underline{p}}{\underline{q}} + M \left[ \underline{q} \circ \frac{\underline{p}}{\underline{q}} \right] = \frac{\underline{u}}{\underline{q}} \circ [\underline{p} \circ M\underline{q} + \underline{q} \circ M\underline{p}] \\ &= \frac{\underline{u}}{\underline{q}} \circ B(\underline{p}) \underline{q} = \rho(\underline{p}) \underline{u}. \end{aligned}$$

Now differentiating the equation (4.1) with respect to  $s$  produces

$$\dot{B}(\underline{p}(s)) \underline{q}(s) + B(\underline{p}(s)) \dot{\underline{q}}(s) = \dot{\rho}(s) \underline{q}(s) + \rho(s) \dot{\underline{q}}(s)$$

which reduces to

$$B(\underline{q}(s)) \dot{\underline{p}}(s) + B(\underline{p}(s)) \dot{\underline{q}}(s) = \dot{\rho}(s) \underline{q}(s) + \rho(s) \dot{\underline{q}}(s). \quad (4.7)$$

On account of (4.5), the inner product of both sides of (4.7) with the vector  $\underline{z}(s) = \underline{q}(s)/\underline{p}(s)$  yields

$$\langle \underline{z}(s) B(\underline{q}(s)), \dot{\underline{p}}(s) \rangle + \rho(s) \langle \underline{z}(s), \dot{\underline{q}}(s) \rangle = \dot{\rho}(s) \langle \underline{z}(s), \underline{q}(s) \rangle + \rho(s) \langle \underline{z}(s), \dot{\underline{q}}(s) \rangle,$$

i.e.

$$\langle \underline{z}(s) B(\underline{q}(s)), \dot{\underline{p}}(s) \rangle = \dot{\rho}(s) \langle \underline{z}(s), \underline{q}(s) \rangle. \quad (4.8)$$

Note also that on the basis of (4.6), we have

$$\left\langle \begin{bmatrix} \underline{u} \\ \underline{z}(s) \end{bmatrix} B(\underline{q}(s)), \dot{\underline{p}}(s) \right\rangle = \rho(\underline{p}(s)) \langle \underline{u}, \dot{\underline{p}}(s) \rangle = 0, \quad (4.9)$$

the equality to zero resulting from (4.3).

We are now prepared to prove Theorem 3.1.

(i) *Characterization of an internal equilibrium*

*Necessity.* Let  $\underline{p}^* = \underline{p}(0)$  be an equilibrium of (3.1) in  $\Delta^0$ . Lemma 3.2 ensures that  $\underline{q}(0)$ , the leading right eigenvector of  $B(\underline{p}^*)$  in  $\Delta^0$ , is  $\underline{p}^*$ . Therefore

$\underline{z}(0) = \underline{q}(0)/\underline{p}(0) = \underline{u}$  and (4.8) in view of (4.5) gives

$$\dot{\rho}(0) = \langle \underline{u}B(\underline{p}^*), \dot{\underline{p}}(0) \rangle = \rho(\underline{p}^*) \langle \underline{u}, \dot{\underline{p}}(0) \rangle = 0. \quad (4.10)$$

*Sufficiency.* If  $\underline{p}^*$  furnishes a critical point for  $\rho(\underline{p})$  in  $\Delta^0$  and  $\underline{q}^*$  denotes the leading right eigenvector of  $B(\underline{p}^*)$  in  $\Delta^0$ , then the equations (4.8) and (4.9) establish that

$$\left\langle \left[ \begin{array}{c} \underline{q}^* \\ \underline{p}^* \end{array} \right] B(\underline{q}^*), \underline{\eta} \right\rangle = 0 \quad \text{and} \quad \left\langle \left[ \begin{array}{c} \underline{p}^* \\ \underline{q}^* \end{array} \right] B(\underline{q}^*), \underline{\eta} \right\rangle = 0 \quad (4.11)$$

for every  $\underline{\eta} \in \mathcal{L}$ , i.e. for all  $\underline{\eta}$  satisfying  $\langle \underline{\eta}, \underline{u} \rangle = 0$ . Since  $\mathcal{L}$  is  $n-1$  dimensional, the equations (4.11) are compatible only if there exists some scalar  $\alpha$  such that

$$\left[ \begin{array}{c} \underline{q}^* \\ \underline{p}^* \end{array} \right] B(\underline{q}^*) = \alpha \left[ \begin{array}{c} \underline{p}^* \\ \underline{q}^* \end{array} \right] B(\underline{q}^*), \quad \text{and therefore} \quad \frac{\underline{q}^*}{\underline{p}^*} = \alpha \frac{\underline{p}^*}{\underline{q}^*}, \quad (4.12)$$

since  $B(\underline{q}^*)$  is invertible by Corollary 3.2. But this is feasible only if  $\underline{q}^* = \sqrt{\alpha} \underline{p}^* = \underline{p}^*$ . In such a situation, Lemma 3.2 asserts that  $\underline{p}^*$  must be a polymorphic equilibrium of (3.1).

(ii) *Stability criterion for an internal equilibrium*

Let  $\underline{p}^*$  be a polymorphic equilibrium, i.e. a critical point of  $\rho(\underline{p})$  in  $\Delta^0$ . Differentiating in (4.7) and evaluating at  $s=0$  produces in the notation of (4.2) (with  $\underline{q}(0) = \underline{p}(0) = \underline{p}^*$  and  $\rho(\underline{p}^*) = 2\langle \underline{p}^*, M\underline{p}^* \rangle$  referring to Lemma 3.2)

$$B(\underline{p}^*)\ddot{\underline{p}} + B(\underline{p}^*)\ddot{\underline{q}} + 2\underline{\dot{p}} \circ M\dot{\underline{q}} + 2\dot{\underline{q}} \circ M\dot{\underline{p}} = \rho(\underline{p}^*)\ddot{\underline{q}} + \ddot{\rho}(0)\underline{p}^*. \quad (4.13)$$

Observe that  $M\underline{p}^* = w(\underline{p}^*)\underline{u}$  with  $w(\underline{p}^*) = \langle \underline{p}^*, M\underline{p}^* \rangle$  so that  $B(\underline{p}^*) = w(\underline{p}^*)(I + M(\underline{p}^*))$  with the notation

$$M(\underline{p}^*) = \frac{\underline{p}^* \circ M}{w(\underline{p}^*)} \quad (\text{cf. (3.11)}). \quad (4.14)$$

With reference to  $\underline{u}B(\underline{p}^*) = 2w(\underline{p}^*)\underline{u}$  and in view of (4.3), taking the inner product on both sides of (4.13) with  $\underline{u}$  gives

$$\ddot{\rho}(0) = 4\langle \dot{\underline{p}}, M\dot{\underline{q}} \rangle. \quad (4.15)$$

In terms of the modified inner product

$$\langle\langle \underline{x}, \underline{y} \rangle\rangle = w(\underline{p}^*) \left\langle \frac{\underline{x}}{\underline{p}^*}, \underline{y} \right\rangle, \quad (4.16)$$

we have

$$\ddot{\rho}(0) = 4\langle\langle \dot{\underline{p}}, M(\underline{p}^*)\dot{\underline{q}} \rangle\rangle. \quad (4.17)$$

We next rewrite (4.7) at  $s=0$  in the form

$$(I - M(\underline{p}^*))\dot{\underline{q}} = (I + M(\underline{p}^*))\dot{\underline{p}}. \quad (4.18)$$

Both  $I + M(\underline{p}^*)$  and  $I - M(\underline{p}^*)$  are invertible on  $\mathcal{L} = \{\underline{\xi} : \langle \underline{\xi}, \underline{u} \rangle = 0\}$  and leave this linear manifold invariant (cf. Corollary 3.1). Moreover,  $M(\underline{p}^*)$  is symmetric in the inner product (4.16) (cf. (3.14)). Thus, every vector  $\underline{x}$  in  $\mathcal{L}$  can be represented

using an orthonormal basis  $\{\underline{\varphi}_i\}$  of eigenvectors of  $M(\underline{p}^*)$  in  $\mathcal{L}$  such that

$$\underline{x} = \sum_{i=1}^{r-1} \langle \underline{x}, \underline{\varphi}_i \rangle \underline{\varphi}_i. \quad (4.19)$$

In particular,

$$\underline{\dot{q}} = \sum_{i=1}^{r-1} \langle \underline{\dot{q}}, \underline{\varphi}_i \rangle \underline{\varphi}_i, \quad \underline{\dot{p}} = \sum_{i=1}^{r-1} \langle \underline{\dot{p}}, \underline{\varphi}_i \rangle \underline{\varphi}_i. \quad (4.20)$$

Using  $M(\underline{p}^*)\underline{\varphi}_i = \lambda_i \underline{\varphi}_i$ , equation (4.18) implies

$$(1 - \lambda_i) \langle \underline{\dot{q}}, \underline{\varphi}_i \rangle = (1 + \lambda_i) \langle \underline{\dot{p}}, \underline{\varphi}_i \rangle \quad (4.21)$$

where  $\lambda_i$  is real and  $|\lambda_i| < 1$  (cf. Lemma 3.1). Expanding (4.17) via (4.20) and using (4.21), leads to

$$\ddot{\rho}(0) = 4 \sum_{i=1}^{r-1} \lambda_i \langle \underline{\dot{p}}, \underline{\varphi}_i \rangle^2 \left\{ \frac{1 + \lambda_i}{1 - \lambda_i} \right\}. \quad (4.22)$$

Since  $\underline{\dot{p}} = \underline{\eta}$  is an arbitrary vector in  $\mathcal{L}$ , we may conclude that  $\ddot{\rho}(0) < 0$  for all directions within  $\Delta$  if and only if  $\lambda_i < 0$ ,  $i = 1, 2, \dots, r-1$ , that is,  $\underline{p}^*$  is locally stable if and only if  $\rho(\underline{p})$  exhibits a (strict) local maximum at  $\underline{p}^*$ .

This completes the proof of Theorem 3.1.

#### 4.2. Proof of Theorem 3.2: characterization of a locally stable boundary equilibrium

Let  $\underline{\hat{p}}$  be a boundary equilibrium of (3.1) and define  $\underline{p}(s) = \underline{\hat{p}} + s\underline{\eta}$  such that  $\underline{p}(s) \in \Delta$  for  $s \geq 0$  sufficiently small. Assume

$$\rho^0(\underline{\hat{p}}) > (M\underline{\hat{p}})_j \quad \text{for all } j \notin I^0(\underline{\hat{p}}) \quad (4.23)$$

and let  $\underline{q}(s)$  be the principal right eigenvector of  $B(\underline{p}(s))$  in  $\Delta$ . Then according to (3.19) and Lemma 3.2, we have  $\underline{q}(0) = \underline{\hat{p}}$  and  $\rho(\underline{\hat{p}}) = 2\langle \underline{\hat{p}}, M\underline{\hat{p}} \rangle = 2w(\underline{\hat{p}})$ , and therefore the equation (4.7) for  $s = 0$  becomes

$$B(\underline{\hat{p}})\underline{\hat{p}} + B(\underline{\hat{p}})\underline{\dot{q}} = \dot{\rho}(0)\underline{\hat{p}} + 2w(\underline{\hat{p}})\underline{\dot{q}},$$

or equivalently,

$$B(\underline{\hat{p}})[\underline{\hat{p}} + \underline{\dot{q}}] - 2w(\underline{\hat{p}})\underline{\dot{q}} = \dot{\rho}(0)\underline{\hat{p}}. \quad (4.24)$$

Since  $\underline{u}B(\underline{\hat{p}}) = 2M\underline{\hat{p}}$ , taking the inner product with  $\underline{u}$  in (4.24) leads to

$$\begin{aligned} \dot{\rho}(0) &= 2\langle M\underline{\hat{p}}, \underline{\hat{p}} + \underline{\dot{q}} \rangle \\ &= 2w(\underline{\hat{p}}) \sum_{j \in I^0(\underline{\hat{p}})} [\underline{\hat{p}}_j + \underline{\dot{q}}_j] + 2 \sum_{j \notin I^0(\underline{\hat{p}})} (M\underline{\hat{p}})_j [\underline{\hat{p}}_j + \underline{\dot{q}}_j] \\ &= 2 \sum_{j \notin I^0(\underline{\hat{p}})} [(M\underline{\hat{p}})_j - w(\underline{\hat{p}})] [\underline{\hat{p}}_j + \underline{\dot{q}}_j]. \end{aligned} \quad (4.25)$$

But for every  $j \notin I^0(\underline{\hat{p}})$ , we have from (4.24)

$$(M\underline{\hat{p}})_j [\underline{\hat{p}}_j + \underline{\dot{q}}_j] - 2w(\underline{\hat{p}})\underline{\dot{q}}_j = 0$$

i.e.

$$\dot{q}_j = \left[ \frac{(M\hat{p})_j}{2w(\hat{p}) - (M\hat{p})_j} \right] \hat{p}_j. \quad (4.26)$$

Hence (4.25) can be expressed as follows:

$$\dot{\rho}(0) = -4w(\hat{p}) \sum_{j \in I^0(\hat{p})} \left[ \frac{w(\hat{p}) - (M\hat{p})_j}{2w(\hat{p}) - (M\hat{p})_j} \right] \eta_j. \quad (4.27)$$

Therefore  $\dot{\rho}(0) < 0$  in every direction  $\eta = (\eta_1, \dots, \eta_r)$  within  $\Delta$  (i.e.  $\sum_{j=1}^r \eta_j = 0$  and  $\eta_j \geq 0$  for all  $j \in I^0(\hat{p})$  with strict inequality somewhere) if and only if  $(M\hat{p})_j < w(\hat{p})$  for all  $j \in I^0(\hat{p})$  (since equalities are precluded in generic cases), that is,  $\rho(\hat{p})$  is locally decreasing from  $\hat{p}$  toward the interior of  $\Delta$  if and only if  $\hat{p}$  is externally stable (see (3.7)). Moreover it has been established in Theorem 3.1 that  $\rho^0(\hat{p})$  is internally maximized at  $\hat{p}$  (i.e. within the subsystem corresponding to the positive components of  $\hat{p}$ ) if and only if  $\hat{p}$  is internally stable.

It remains to show that a strict local maximum of

$$\rho(\underline{p}) = \max \{ \rho^0(\underline{p}), (M\underline{p})_j \text{ for all } j \in I^0(\underline{p}) \} \quad (4.28)$$

cannot be achieved (only) through the linear terms  $(M\underline{p})_j$ ,  $j \in I^0(\underline{p})$ . Otherwise this must occur at a vertex, say  $A_1$ -fixation, and then (relabeling the alleles if necessary) we must have  $m_{12} > 2m_{11}$  and  $m_{12} > m_{1k}$  for all  $k \geq 3$  (with the genericity conditions (3.2) in force). By continuity, this entails that  $\rho(\underline{p}) = \rho^0(\underline{p})$  within the subsystem  $\{A_1, A_2\}$  near  $A_1$ -fixation. With  $M = \|m_{ij}\|_{i,j=1}^2$  and  $\underline{p} = (p_1, p_2)$ , we have

$$B(\underline{p}) = D_{\underline{p}}M + D_{M\underline{p}} = \begin{bmatrix} 2p_1m_{11} + p_2m_{12} & p_1m_{12} \\ p_2m_{12} & 2p_2m_{22} + p_1m_{12} \end{bmatrix} \quad (4.29)$$

and at  $A_1$ -fixation the relation (4.7) becomes

$$B(\hat{q})\hat{p} + B(\hat{p})\hat{q} = \dot{\rho}(0)\hat{q} + m_{12}\hat{q} \quad (4.30)$$

where  $\hat{p} = (1, 0)$  and  $B(\hat{p})\hat{q} = m_{12}\hat{q}$ , i.e.

$$\hat{q}_2 = \left[ \frac{m_{12} - 2m_{11}}{m_{12}} \right] \hat{q}_1, \quad \hat{q}_1 = 1 - \hat{q}_2 \quad (4.31)$$

Choosing  $\hat{p} = (-1, 1)$ , the equality for the second component in (4.30) is

$$-\hat{q}_2m_{12} + 2\hat{q}_2m_{22} + \hat{q}_1m_{12} = \dot{\rho}(0)\hat{q}_2,$$

i.e.

$$\begin{aligned} \dot{\rho}(0) &= 2m_{22} - m_{12} + \left[ \frac{\hat{q}_1}{\hat{q}_2} \right] m_{12} \\ &= \frac{[2m_{22} - m_{12}][m_{12} - 2m_{11}] + m_{12}^2}{m_{12} - 2m_{11}} \\ &= \frac{2m_{12}[m_{11} + m_{22}] - 4m_{11}m_{22}}{m_{12} - 2m_{11}} > \frac{4m_{11}^2}{m_{12} - 2m_{11}} > 0. \end{aligned}$$

This contradicts the assumption that  $\rho(\underline{p})$  achieves a local maximum at  $A_1$ -fixation and completes the proof of part (i) of Theorem 3.2. Part (ii) is a direct consequence of Lemma 3.2.

## 5. Stability analysis of the sex-determination model

We previously emphasized in Sect. 2 that the model of sex-determination of a random mating population where an offspring of genotype  $A_iA_j$  is male (female) with probability  $m_{ij}$  ( $(1 - m_{ij})$ ) is equivalent to a sex differentiated viability model with viability matrices  $M = \|m_{ij}\|$  and  $U - M = \|1 - m_{ij}\|$  for males and females, respectively. In this section we ascertain the stability conditions for the symmetric and even-sex-ratio equilibrium states introduced in Sect. 2.2.

### 5.1. Stability criteria for the symmetric equilibrium states

A symmetric equilibrium  $\{\underline{\hat{p}}, \underline{\hat{p}}\}$  for the sex determination model (2.2), represented by  $\underline{\hat{p}}$  for brevity, corresponds to an equilibrium for the viability model  $M$  defined by (3.1). To avoid unimportant situations involving special relations among the sex-determination parameters  $\{m_{ij}\}$  it will be judicious unless indicated otherwise to impose the following additional (genericity) postulate.

*Definition 5.1.* A sex-determination matrix  $M$  is said to be *symmetrically generic* if

- (i)  $M$  and  $U - M$  are each generic (in the sense of (3.2));
- (ii)  $\langle \underline{\hat{p}}, M\underline{\hat{p}} \rangle \neq \frac{1}{2}$  for every symmetric equilibrium  $\underline{\hat{p}}$  of (2.2). (In particular  $m_{ii} \neq \frac{1}{2}$  for every  $i$ .)

(5.1)

The requirement (ii) guarantees that a symmetric equilibrium state does not yield an even-sex-ratio.

Let  $\underline{p}^*$  be an interior symmetric equilibrium of the system (2.2) with associated sex ratio  $w^* = \langle \underline{p}^*, M\underline{p}^* \rangle$ . We recall the following result (e.g. Karlin (1978)).

The relevant gradient matrix of the system (2.2) at  $\{\underline{p}^*, \underline{p}^*\}$  is of the form

$$\Gamma = \begin{pmatrix} R & R \\ S & S \end{pmatrix}$$

acting on  $\mathcal{L} \otimes \mathcal{L} = \{ \{ \underline{\xi}, \underline{\eta} \} : \langle \underline{\xi}, \underline{u} \rangle = \langle \underline{\eta}, \underline{u} \rangle = 0 \}$  with

$$R = \frac{1}{2} \left[ I + \frac{\underline{p}^* \circ M}{w^*} \right], \quad S = \frac{1}{2} \left[ I - \frac{\underline{p}^* \circ M}{1 - w^*} \right]. \quad (5.2)$$

The relevant eigenvalues of  $\Gamma$  are those of  $R + S$  relative to the linear manifold  $\mathcal{L}$  plus the eigenvalue 0 which occurs with additional multiplicity  $r$ . Note that the matrix

$$R + S = I + \left[ \frac{1 - 2w^*}{2(1 - w^*)} \right] \frac{\underline{p}^* \circ M}{w^*} \quad (5.3)$$

resembles the gradient matrix at  $\underline{p}^*$  for the viability selection model with associated matrix  $M$  except for the constant multiplier  $(1 - 2w^*)/[2(1 - w^*)]$  (compare

with (3.9)). It follows that if  $\underline{p}^* \in \Delta^0$  is a stable equilibrium of (3.1) (such that  $(\underline{p}^* \circ M)/w^*$  has only negative eigenvalues of magnitude less than 1 with respect to  $\mathcal{L}$ ) and  $w^* < \frac{1}{2}$ , then all eigenvalues of  $R + S$  are also of magnitude less than 1 relative to  $\mathcal{L}$ , and conversely. These facts are worth highlighting.

**Theorem 5.1.** *A symmetric interior equilibrium  $\{\underline{p}^*, \underline{p}^*\}$  with  $w^* = \langle \underline{p}^*, M\underline{p}^* \rangle < \frac{1}{2}$  is stable in the sex-determination model (2.2) if and only if  $\underline{p}^*$  is stable for the one-locus viability model  $M$ , i.e. the transformation (3.1).*

*Analogously, if  $w^* > \frac{1}{2}$ ,  $\{\underline{p}^*, \underline{p}^*\}$  is a symmetric stable equilibrium for the sex-determination model (2.2) if and only if  $\underline{p}^*$  is stable for the viability model  $U - M$ .*

The stability analysis for a symmetric boundary equilibrium  $\{\hat{p}, \hat{p}\}$  entails the internal stability conditions relative to the face of  $\hat{p}$  akin to Theorem 5.1 and the external stability conditions with respect to the alleles not represented in the array of  $\hat{p}$  (cf. (3.7)).

The local linear analysis near  $\{\hat{p}, \hat{p}\}$  with respect to external alleles reveals the first-order approximation

$$(q'_j + p'_j) = (q_j + p_j) \left[ \frac{(M\hat{p})_j}{2\hat{w}} + \frac{((U - M)\hat{p})_j}{2(1 - \hat{w})} \right] \quad \text{for } j \notin I^0(\hat{p}) \quad (5.4)$$

where  $\hat{w} = \langle \hat{p}, M\hat{p} \rangle$ . The following result is then immediate.

**Theorem 5.1'.** *A symmetric equilibrium  $\{\hat{p}, \hat{p}\}$  with  $\hat{w} = \langle \hat{p}, M\hat{p} \rangle < \frac{1}{2}$  is stable for the sex-determination model (2.2) if and only if:*

(i) *The eigenvalues of  $(\hat{p} \circ M)/\hat{w}$  in the face of  $\hat{p}$ , i.e. with respect to  $\mathcal{L}_{\hat{p}} = \{\xi: \sum_{i \in I^0(\hat{p})} \xi_i = 0\}$  are all negative and*

$$(ii) \quad \frac{(M\hat{p})_j}{2\hat{w}} + \frac{((U - M)\hat{p})_j}{2(1 - \hat{w})} < 1 \quad \text{for all } j \notin I^0(\hat{p}),$$

*or equivalently since  $\hat{w} < \frac{1}{2}$ ,*

$$(M\hat{p})_j < \hat{w} \quad \text{for all } j \notin I^0(\hat{p}).$$

*When  $\hat{w} > \frac{1}{2}$ , then the ascertainment of stability for  $\{\hat{p}, \hat{p}\}$  in the sex determination model corresponds to the stability criteria for the one-locus viability model  $U - M$ .*

Thus, a symmetric equilibrium (boundary or interior) of sex ratio  $\hat{w} < \frac{1}{2}$  is stable for the sex-determination model (2.2) if and only if it is stable for the one-locus random mating multiallele system (3.1) with viability matrix  $M$ . The condition for external stability deduced from (5.4) was pointed out by Eshel and Feldman (1982). Theorems 5.1 and 5.1' entail the following consequence.

**Corollary 5.1.** *When  $\hat{p}$  is stable for the viability model  $M$  and  $\hat{w} > \frac{1}{2}$ , then  $\{\hat{p}, \hat{p}\}$  is unstable in the sex-determination model (2.2).*

## 5.2. Nature of the even-sex-ratio equilibria

Let  $\{\tilde{q}, \tilde{p}\}$  be an equilibrium for the sex-determination (2.2) with

$$\langle \tilde{q}, M\tilde{p} \rangle = \frac{1}{2}. \quad (5.5)$$

Recall from (2.5) that an even-sex-ratio equilibrium is completely characterized by the eigenvalue one equation

$$B(\tilde{p})\tilde{q} = \tilde{q} \tag{5.6}$$

where  $B(p) = D_{M_p} + D_p M$  and  $D_p$  is the diagonal matrix with the components of  $p$  down the diagonal. When (5.5) and (5.6) prevail, necessarily  $\tilde{q} \neq \tilde{p}$  owing to the genericity stipulation (ii) of Definition 5.1. In cognizance of the discussion following (2.5), an even-sex-ratio equilibrium exists if and only if  $\rho(\tilde{p}) = \rho(B(\tilde{p})) = 1$  and then  $\tilde{q}$  is the corresponding unique right eigenvector in  $\Delta$  (actually on the same face of  $\Delta$  as  $\tilde{p}$  in view of (3.19) and (3.20)). The basic result of this subsection concerns the existence of even-sex-ratio equilibrium states. Such equilibria comprise a continuum when present. In the following theorem it is understood that an even-sex-ratio equilibrium state is represented by its corresponding allelic frequencies in the female population (i.e. the vector component  $\tilde{p}$  in the pair  $\{\tilde{p}, \tilde{q}\}$  satisfying (5.6)).

**Theorem 5.2.** *Let  $M$  be a symmetrically generic sex-determination matrix according to Definition 5.1.*

(i) *Even-sex-ratio equilibria of the sex-determination model (2.2), when they exist, are part of an equilibrium surface of dimension  $r - 2$  in the simplex of frequency vectors  $\Delta$  of dimension  $r - 1$ . (Only for the case of two alleles are the even-sex-ratio equilibria isolated points.)*

(ii) *An interior stable symmetric equilibrium (or any stable symmetric equilibrium that is the only stable equilibrium for the corresponding viability model according to Theorem 5.1) cannot coexist with an even-sex-ratio equilibrium and any other stable symmetric equilibrium in  $\Delta$ .*

(iii) *Two symmetric equilibria  $\hat{p}_\alpha$  and  $\hat{p}_\beta$  with associated sex ratios  $\hat{w}_\alpha = \langle \hat{p}_\alpha, M\hat{p}_\alpha \rangle < \frac{1}{2}$  and  $\hat{w}_\beta = \langle \hat{p}_\beta, M\hat{p}_\beta \rangle > \frac{1}{2}$ , respectively, are completely separated by at least one even-sex-ratio equilibrium surface.*

*Note.* Coexistence of one or several surfaces of even-sex-ratio equilibria with one or several locally stable boundary symmetric equilibria is not precluded.

*Proof of Theorem 5.2.* (i) Let  $\tilde{p}$  be an even-sex-ratio equilibrium interior to  $\Delta$ , i.e.  $\tilde{p} \in \Delta^0$  satisfies  $\rho(\tilde{p}) = 1$ . Since  $M$  is assumed to be symmetrically generic,  $\tilde{p}$  cannot coincide with a symmetric equilibrium, i.e. a critical point of  $\rho(p)$  owing to Theorem 3.1. Therefore there exists some direction within  $\Delta^0$  along which the derivative of  $\rho(p)$  at  $\tilde{p}$  is nonzero. Hence  $\tilde{p}$  must belong to the common frontier of two components of the open sets  $\{p \in \Delta^0 : \rho(p) > 1\}$  and  $\{p \in \Delta^0 : \rho(p) < 1\}$ , respectively. That frontier is an even-sex-ratio equilibrium surface of dimension  $r - 2$  (and simply connected) in the simplex  $\Delta^0$  of dimension  $r - 1$  by continuity of  $\rho(p)$ .

If  $\tilde{p}$  is on the boundary of  $\Delta$ , then  $\rho(p) = \rho^0(p)$  in some neighborhood of  $\tilde{p}$  by appeal to (3.19) and (3.20). The preceding arguments can be applied mutatis mutandis with respect to the face of  $\tilde{p}$ , and then extended to all  $\Delta$  by continuity.

(ii) An interior stable symmetric equilibrium  $p^*$  with  $w^* = \langle p^*, Mp^* \rangle < \frac{1}{2}$  corresponds to an interior stable equilibrium for the viability model  $M$  (Theorem 5.1) and therefore to a global and unique maximum of  $\rho(p)$  over all  $\Delta$  (Theorem 3.2). This precludes the existence of another stable symmetric equilibrium.

Moreover, since  $\rho(\underline{p}^*) = 2\langle \underline{p}^*, M\underline{p}^* \rangle < 1$  (Lemma 3.2), the function  $\rho(\underline{p})$  cannot achieve the value one in  $\Delta$  and even-sex-ratio equilibria cannot be present. If  $w^* > \frac{1}{2}$ , we replace  $M$  by  $U - M$ .

(iii) If  $\hat{p}_\alpha$  and  $\hat{p}_\beta$  are two symmetric equilibria such that  $\langle \hat{p}_\alpha, M\hat{p}_\alpha \rangle = \hat{w}_\alpha < \frac{1}{2}$  and  $\langle \hat{p}_\beta, M\hat{p}_\beta \rangle = \hat{w}_\beta > \frac{1}{2}$ , then we have  $\rho^0(\hat{p}_\alpha) = 2\hat{w}_\alpha < 1$  and  $\rho^0(\hat{p}_\beta) = 2\hat{w}_\beta > 1$  owing to Lemma 3.2 and therefore

$$\begin{aligned} \rho(\hat{p}_\alpha) &= \max \{ \rho^0(\hat{p}_\alpha), (M\hat{p}_\alpha)_i, i \notin I^0(\hat{p}_\alpha) \} < 1, \\ \rho(\hat{p}_\beta) &= \max \{ \rho^0(\hat{p}_\beta), (M\hat{p}_\beta)_i, i \notin I^0(\hat{p}_\beta) \} > 1. \end{aligned} \quad (5.7)$$

By continuity of  $\rho(\underline{p})$ , all curves connecting  $\hat{p}_\alpha$  and  $\hat{p}_\beta$  in  $\Delta$  must intersect  $\rho(\underline{p}) = 1$  and these points of intersection generate at least one separating even-sex-ratio equilibrium surface.

### 5.3. An optimality property for even-sex-ratio realizations

Eshel and Feldman (1982) considered a symmetric equilibrium  $\{p^*, p^*\}$ ,  $p_i^* > 0$ ,  $i = 1, \dots, r$  for the  $r$ -allele model (2.2) with  $w^* = \langle Mp^*, p^* \rangle < \frac{1}{2}$ . With a new allele  $A_{r+1}$ , let  $m_{i,r+1}$  be the probability for a zygote of genotype  $A_i A_{r+1}$  to be a male and  $(1 - m_{i,r+1})$  to be a female. The marginal fraction of male progeny carrying allele  $A_{r+1}$  at the equilibrium state  $p^*$  is  $w_{r+1}^* = \sum_{i=1}^r p_i^* m_{i,r+1}$ . A symmetric equilibrium  $\{p^*, p^*\}$  stable for the  $r$ -allele sex-determination model becomes unstable with the introduction of  $A_{r+1}$  if and only if

$$w_{r+1}^* > w^* \quad \text{provided } w^* < \frac{1}{2}. \quad (5.8)$$

(The condition for local instability at  $p^*$  is  $w_{r+1}^* < w^*$  if  $w^* > \frac{1}{2}$ .) These conditions do not require that the marginal sex ratio  $w_{r+1}^*$  at  $p^*$  should be closer to  $\frac{1}{2}$  than  $w^*$ . However, in case of departure, it was conjectured that the augmented allele system in the long run would attain a sex-ratio closer to one-to-one than existing at the previous equilibrium.

We can prove the following facts in support of the evolutionary tendency toward an even-sex-ratio.

**Theorem 5.3.** *Let  $p^*$  be a stable polymorphic symmetric equilibrium of (2.2) with sex-ratio  $w^* = \langle p^*, Mp^* \rangle$  that becomes unstable following the introduction of a new allele  $A_{r+1}$ . Then, for the augmented  $(r+1)$ -allele system with the non-degeneracy conditions (5.1) in force either: (i) there exists a unique stable symmetric equilibrium whose sex-ratio is closer to  $\frac{1}{2}$  compared to  $w^*$  and which do not coexist with any even-sex-ratio equilibrium; or (ii)  $p^*$  is enclosed by an even-sex-ratio equilibrium surface containing no stable symmetric equilibria.*

*Remark.* In the conditions of Theorem 5.3, the only possible stable equilibrium points attainable from  $p^*$  entail sex-ratios closer (compared to  $w^*$ ) to  $\frac{1}{2}$  or equal to  $\frac{1}{2}$ . This expresses an optimality property in favor of a one-to-one population sex-ratio. Our numerical iterations have shown *convergence* to either a symmetric equilibrium or an even-sex-ratio equilibrium in agreement with the theme of Theorem 5.3. The paths of the population sex-ratios over successive generations may exhibit small oscillations, but in the long run they always tend (increasingly or decreasingly) in the direction toward  $\frac{1}{2}$ . (See also Sect. 6.2.)



*Proof of Theorem 5.3.* Suppose that  $\underline{p}^*$  is a stable polymorphic symmetric equilibrium for the sex-determination model (2.2) with  $\langle \underline{p}^*, \underline{M}\underline{p}^* \rangle = w^* < \frac{1}{2}$ . (The case  $w^* > \frac{1}{2}$  would be dealt with analogously.) Then Theorem 5.1 tells us that  $\underline{p}^*$  is stable for the viability model (3.1) with matrix  $M = \|m_{ij}\|_{i,j=1}^r$ . But  $\underline{p}^*$  is also externally unstable in both models (compare (5.8) with (3.7)) after the introduction of the allele  $A_{r+1}$ , i.e. with respect to the augmented  $(r+1)$ -dimensional matrix  $\tilde{M} = \|m_{ij}\|_{i,j=1}^{r+1}$ . We make appeal to Theorem 3.2 in Karlin (1978) (see also Sect. 3.1) assuring the existence of a unique stable equilibrium  $\underline{p}^{**}$  (interior or on the boundary of the augmented allelic frequency simplex) for the viability model  $\tilde{M}$ . Moreover, we must have  $\langle \underline{p}^{**}, \tilde{M}\underline{p}^{**} \rangle = w^{**} > w^*$ . In the event  $w^{**} < \frac{1}{2}$ ,  $\underline{p}^{**}$  is a stable symmetric equilibrium for the sex-determination model corresponding to  $\tilde{M}$  and actually the unique stable equilibrium for that model with no even-sex-ratio equilibria present owing to part (ii) of Theorem 5.2. On the other hand, if  $w^{**} > \frac{1}{2}$ , part (iii) of Theorem 5.2 asserts that  $\underline{p}^{**}$  is separated from  $\underline{p}^*$  in the augmented system by an even-sex-ratio equilibrium surface.

In the latter event (i.e.  $w^* < \frac{1}{2} < w^{**}$ ), any stable symmetric equilibrium  $\hat{p}$  for the sex-determination model  $\tilde{M}$  must be associated with a sex ratio  $\langle \hat{p}, \tilde{M}\hat{p} \rangle = \hat{w} > \frac{1}{2}$  (but  $\hat{p} \neq \underline{p}^{**}$  by Corollary 5.1). If such a  $\hat{p}$  exists, it must be separated from  $\underline{p}^*$  by an even-sex-ratio equilibrium surface that cannot intersect the faces of  $\underline{p}^*$  and  $\hat{p}$  because these equilibria are internally stable (see Theorem 5.2). This is possible only if  $\hat{p}$  corresponds to  $A_{r+1}$ -fixation and then

$$m_{i,r+1} > m_{r+1,r+1} > \frac{1}{2}, \quad i = 1, \dots, r. \quad (5.9)$$

#### 5.4. Predominance of the one-to-one sex-ratio equilibria for dichotomous sex-determination systems

Theorem 5.4 below further amplifies the predominant endowment of even-sex-ratio equilibrium realizations under sex genotype determination involving exact allelic variants, i.e. when the sex phenotype is controlled at a single multiallelic locus with exact zero-one genotypic sex ascertainment. In the following the nondegeneracy conditions (5.1) are *not* assumed.

**Theorem 5.4.** *Suppose all genotypes involving  $r$  alleles at a single locus divide into two groups (all genotypes in  $\mathcal{A}_M$  become males unambiguously, while all genotypes in  $\mathcal{A}_F$  become females). Assuming random mating in this dioecious population, the only possibly stable equilibria entail one-to-one sex ratio, i.e. the frequency of a stable equilibrium phenotype representation has  $\text{freq}(\mathcal{A}_M) = \text{freq}(\mathcal{A}_F) = \frac{1}{2}$ .*

*Remark.* It is interesting to contrast Theorems 5.3 and 5.4. When the genotype-phenotype classes of sex-determination is not absolute (that is,  $0 < m_{ij} < 1$ ), then the possibility of a stable non-even-sex ratio can emerge. Theorem 5.4 asserts that with exact genotype sex-determination ( $m_{ij} = 0$  or  $1$  for every  $i, j$ ) creating the sex dimorphism of the two phenotype classes with  $\mathcal{A}_M$  comprising all genotypes with  $m_{ij} = 1$  and  $\mathcal{A}_F$  consisting of all genotypes with  $m_{ij} = 0$ , then only an even-sex-ratio outcome can be stable for such a randomly mating population.

*Proof of Theorem 5.4.* Let  $\underline{p}^*$  be a polymorphic symmetric equilibrium of (2.2) where  $M = \|m_{ij}\|_{i,j=1}^r$  is a dichotomous sex-determination matrix (i.e.,  $m_{ij} = 0$  or  $1$

for every  $i$  and  $j$ ). In this circumstance  $M$  is nonsingular if and only if  $U - M$  is nonsingular since  $M\bar{p}^* = w^*\bar{u}$  has a unique solution in  $\Delta^0$  if and only if  $(U - M)\bar{p}^* = (1 - w^*)\bar{u}$  has a unique solution in  $\Delta^0$ . Consider the case  $\langle \bar{p}^*, M\bar{p}^* \rangle = w^* < \frac{1}{2}$ . We show that  $\bar{p}^*$  cannot be stable. Otherwise  $\bar{p}^*$  would be stable for the viability model  $M$  and  $w(\bar{p}) = \langle \bar{p}, M\bar{p} \rangle$  would achieve a global maximum in  $\Delta$  at  $\bar{p}^*$ . Therefore we would have  $\frac{1}{2} > w^* > m_{ii}$  compelling  $m_{ii} = 0$  for all  $i$ . But then for some  $i \neq j$ ,  $m_{ij} = 1$  and the equilibrium  $\hat{p}$  with  $\hat{p}_i = \hat{p}_j = \frac{1}{2}$  would have mean fitness  $w(\hat{p}) = \frac{1}{2}$  exceeding  $w(\bar{p}^*) = w^*$  which is a contradiction. (The case  $w^* > \frac{1}{2}$  can be dealt with analogously.)

Consider next a symmetric equilibrium  $\bar{p}^*$  with  $w^* \neq \frac{1}{2}$  and corresponding coefficient matrix  $M$  singular. Then  $U - M$  is also singular and there exist nontrivial vectors  $\xi$  and  $\eta$  satisfying  $M\xi = 0$  and  $(U - M)\eta = 0$ . It follows that  $0 = \langle \xi, (U - M)\eta \rangle = \langle \xi, U\eta \rangle - \langle M\xi, \eta \rangle = \langle \xi, U\eta \rangle = \langle \xi, \bar{u} \rangle \langle \eta, \bar{u} \rangle$  and therefore  $\langle \xi, \bar{u} \rangle = 0$  and/or  $\langle \eta, \bar{u} \rangle = 0$ . Assume for definiteness  $\langle \xi, \bar{u} \rangle = 0$ . The line  $\bar{p}^* + t\xi$  in  $\Delta$  for  $t$  real satisfies  $M(\bar{p}^* + t\xi) = M\bar{p}^* = w^*\bar{u}$  and this symmetric equilibrium line must intersect the boundary of  $\Delta$  at some point  $\bar{p}^{**}$ . If the submatrix corresponding to  $\bar{p}^{**}$  is singular, we can reduce again the analysis to a smaller face along an equilibrium line with sex ratio  $w^* \neq \frac{1}{2}$ . Proceeding in this way, we finally arrive at a boundary symmetric equilibrium whose corresponding submatrix is nonsingular and which cannot be internally stable because of the previous arguments. We conclude that  $\bar{p}^*$  must belong to an unstable symmetric equilibrium surface.

### 5.5. Stable equilibrium possibilities with a dominant male (or female) sex-determiner

A dominant male (or female) determining factor (as occurs in standard  $XX - XY$  systems) can be accommodated by (2.2) if we set  $m_{1j} = 1$  for all  $j$  in the sex-determination matrix  $M = \|m_{ij}\|_{i,j=1}$ . Since  $(M\bar{p})_1 = 1$  for all frequency vectors  $\bar{p}$ , the strong sex-determiner represented by allele  $A_1$  cannot be present at any symmetric equilibrium (otherwise the sex ratio would be one which is not biologically feasible). Moreover, a symmetric (non-even-sex-ratio) equilibrium is stable if and only if it is stable with respect to the subsystem  $\bar{M} = \|m_{ij}\|_{i,j=2}$  and associated with a sex ratio exceeding  $\frac{1}{2}$  to ensure external stability against  $A_1$ . In all circumstances, we can draw the following conclusion.

**Theorem 5.5.** *A dominant sex-determiner in (2.2) can be maintained at equilibrium only with an even-sex-ratio.*

## 6. Examples and further results

### 6.1. A sex-determination model based on the state of heterozygosity versus homozygosity

A sex-determination matrix of some biological interest has the form

$$M = (\alpha - \beta)I + \beta U \quad (6.1)$$

where the probability of being a male is either  $\alpha$  or  $\beta$  according as the genotype is either homozygous or heterozygous independently of the allelic composition.

We denote the matrix of type (6.1) with  $r$  alleles by  $M(r)$ . We examine the case  $\alpha < \frac{1}{2} < \beta$ . It is readily verified that the central frequency vector  $\bar{p}^*(r) =$

$(1/r, 1/r, \dots, 1/r)$  is a symmetric equilibrium for  $M(r)$  with associated sex-ratio  $w^*(r) = \beta + (\alpha - \beta)/r$ . Note that  $w^*(r)$  increases with  $r$ . It is simple to check that  $\lambda = (\alpha - \beta) < 0$  is the only eigenvalue (of multiplicity  $r - 1$ ) for  $M(r)$  whose corresponding right eigenvectors  $\underline{\xi}$  satisfy  $\langle \underline{\xi}, \underline{u} \rangle = 0$ . Therefore (see (3.4)),  $\underline{p}^*(r)$  is globally stable (respectively unstable and actually totally repelling) for the viability model with matrix  $M(r)$  (respectively  $U - M(r)$ ). It is easy to check that  $w^*(r) > \frac{1}{2}$  if and only if

$$r \geq \hat{r} = \text{int} \left[ \frac{\beta - \alpha}{\beta - \frac{1}{2}} + 1 \right]. \tag{6.2}$$

( $\text{int}[h]$  stands for the largest integer smaller or equal to  $h$ .) By appeal to Theorem 5.1,  $\underline{p}^*(r)$  is uniquely stable for the sex-determination model corresponding to  $M(r)$  provided  $r < \hat{r}$ , and unstable when  $r \geq \hat{r}$ .

In the case at hand

$$B(\underline{p}) = D_{M\underline{p}} + \underline{p} \circ M = \beta I + 2(\alpha - \beta)D_{\underline{p}} + \beta D_{\underline{p}} U. \tag{6.3}$$

Therefore at an even-sex-ratio equilibrium, the relation

$$\tilde{\underline{q}} = B(\tilde{\underline{p}})\tilde{\underline{q}} = \beta\tilde{\underline{q}} + 2(\alpha - \beta)\tilde{\underline{p}} \circ \tilde{\underline{q}} + \beta\tilde{\underline{p}}$$

holds, or equivalently,

$$\tilde{\underline{q}} = \beta\tilde{\underline{p}} \circ \frac{\underline{u}}{(1 - \beta)\underline{u} + 2(\beta - \alpha)\tilde{\underline{p}}} \tag{6.4}$$

where  $\tilde{\underline{p}}$  and  $\tilde{\underline{q}}$  are frequency vectors. This is possible with  $r$  alleles if and only if the surface

$$h(\underline{p}) = \sum_{i=1}^r \frac{\beta p_i}{(1 - \beta) + 2(\beta - \alpha)p_i} = 1 \tag{6.5}$$

with  $\underline{p} = (p_1, \dots, p_r)$  intersects the frequency simplex  $\Delta$ . Note that  $h(\underline{p})$  spans a concave surface on  $\Delta$  symmetric in the components of  $\underline{p}$  and whose maximum is

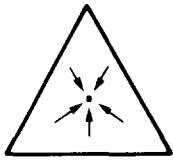
$$h(\underline{p}^*(r)) = \frac{\beta}{1 + \beta - 2w^*(r)}. \tag{6.6}$$

Consistent with Theorem 5.2,  $h(\underline{p}^*(r)) > 1$  if and only if  $w^*(r) > \frac{1}{2}$ , and then even-sex-ratio equilibrium surfaces exist since the value of  $h$  at any corner is  $\beta/(1 + \beta - 2\alpha) < 1$ . A schematic representation of the equilibrium system versus the critical dimension  $\hat{r}$  of (6.2) is given in Fig. 1 (cf. Karlin, 1978, p. 343). The case  $\alpha > \frac{1}{2} > \beta$  is analogous. When  $\frac{1}{2} < \alpha < \beta$  or  $\beta < \alpha < \frac{1}{2}$ , only fixation states can be stable. When  $\frac{1}{2} < \beta < \alpha$  or  $\alpha < \beta < \frac{1}{2}$ , the polymorphic equilibrium  $\underline{p}^*(r)$  is globally stable.

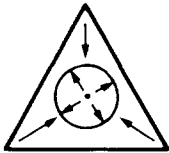
*6.2. Global convergence to a one-to-one sex-ratio for the sex-determination model where all homozygotes determine females while heterozygotes determine males*

Consider an  $r$ -allele system with sex dichotomization

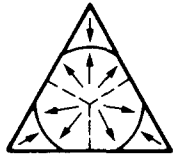
$$\begin{array}{cc} \text{females} & \text{males} \\ \mathcal{A}_F = \{A_i A_i, i = 1, \dots, r\} & \mathcal{A}_M = \{A_i A_j, i \neq j\} \end{array} \tag{6.7}$$



$$\text{for } r \leq \hat{r} - 1 = \text{int} \left[ \frac{\beta - \alpha}{\beta - 1/2} \right]$$



$$\text{for } r = \hat{r}$$



$$\text{for } r \geq \hat{r} + 1.$$

Fig. 1. Equilibrium configurations for the sex-determination model (2.2) with matrix  $M(r) = (\alpha - \beta)I + \beta U$  of dimension  $r$ . The arrows suggest the directions of convergence

Thus the matrix  $M$  of (2.2) corresponding to (6.7) is  $M = U - I$  (cf. (6.1)) and the transformation equations become

$$p'_i = \frac{p_i q_i}{\sum_{k=1}^r p_k q_k} \quad \text{and} \quad q'_i = \frac{p_i + q_i - 2p_i q_i}{2(1 - \sum_{k=1}^r p_k q_k)}, \quad i = 1, 2, \dots, r, \quad (6.8)$$

with sex-ratio  $\sum_{k=1}^r p_k q_k$  in the current generation. Let  $p_i^{(n)}$  and  $q_i^{(n)}$  denote the frequencies of allele  $A_i$  ( $i = 1, \dots, r$ ) in the female and male populations, respectively, at generation  $n$ .

Case (1). Assume in the initial generation

$$p_1^{(0)} > p_2^{(0)} > \dots > p_r^{(0)} \quad \text{and} \quad q_1^{(0)} > q_2^{(0)} > \dots > q_r^{(0)}. \quad (6.9)$$

We prove:

**Lemma 6.1.** For all succeeding generations and  $i < j$ ,  $p_i^{(n)} > p_j^{(n)}$  and  $q_i^{(n)} > q_j^{(n)}$ .

*Proof.* We merely need to prove these inequalities for  $n = 1$ . For  $i < j$ , we have

$$\frac{p'_i}{p'_j} = \frac{p_i q_i}{p_j q_j} > \frac{p_i}{p_j} > 1. \quad (6.10)$$

Consider next

$$\frac{q'_i}{q'_j} = \frac{p_i + q_i - 2p_i q_i}{p_j + q_j - 2p_j q_j}. \quad (6.11)$$

For  $q_i \leq \frac{1}{2}$ , and because  $q_j < q_i$  and necessarily  $2p_j < 1, j \geq 2$ , the right hand fraction is diminished if  $q_j$  is increased to  $q_i$ . The resulting ratio exceeds 1 if and only if  $(p_i - p_j)(1 - 2q_i) \geq 0$  which is correct when  $q_i \leq \frac{1}{2}$ .

Suppose next that  $q_i > \frac{1}{2}$ . Then  $q_j$  varies between 0 and  $1 - q_i$ . The condition that the right-hand side in (6.11) exceeds 1 is

$$p_i - p_j + q_i - q_j > 2p_i q_i - 2p_j q_j. \tag{6.12}$$

This is linear in the variable  $q_j$ . For  $q_j = 0$ , (6.12) becomes  $p_i - p_j + q_i > 2p_i q_i$ , which is linear in  $q_i$ . The last inequality is correct for  $q_i = \frac{1}{2}$  and for  $q_i = 1$  (with equalities permitted) because  $p_i + p_j \leq 1$ . Therefore (6.12) holds for  $q_j = 0$ . When  $q_j = 1 - q_i$ , the inequality reduces to  $p_i + p_j + 2q_i - 1 > 2q_i(p_i + p_j)$  which holds for  $q_i = \frac{1}{2}$  and  $q_i = 1$  as before, and therefore for all  $\frac{1}{2} < q_i < 1$ . We have thus established (6.12) in all cases implying  $q'_i > q'_j$  and the proof of the lemma is complete.

We next prove:

**Lemma 6.2.** (i)  $p_k^{(n)} \rightarrow 0$  as  $n \rightarrow \infty$  for  $k = 3, \dots, r$ . (ii) Either  $p_2^{(n)} \rightarrow 0$  and then  $q_1^{(n)} \rightarrow \frac{1}{2}$  and  $q_2^{(n)} + \dots + q_r^{(n)} \rightarrow \frac{1}{2}$ , or  $\lim_{n \rightarrow \infty} p_2^{(n)} > 0$  and  $\lim_{n \rightarrow \infty} q_1^{(n)} = \lim_{n \rightarrow \infty} q_2^{(n)} = \frac{1}{2}$ . Thus, either  $A_1 A_1$  is exclusively established in  $\mathcal{A}_F$  and  $\mathcal{A}_M = \{A_1 A_k, k = 2, \dots, r\}$  or the limit composition consists of  $\mathcal{A}_F = \{A_1 A_1, A_2 A_2\}$  and  $\mathcal{A}_M = \{A_1 A_2\}$ .

*Proof.* If  $p_1^{(n)}/p_{k+1}^{(n)} \uparrow \infty$ , then  $p_{k+1}^{(n)}, p_{k+2}^{(n)}, \dots, p_r^{(n)} \rightarrow 0$ . Moreover, since  $p_1^{(n)}/p_i^{(n)}$  increases in all cases by (6.10) and  $\sum_{i=1}^r p_i^{(n)} = 1$ , we deduce that  $\lim_{n \rightarrow \infty} p_i^{(n)} = p_i^*$  exists for all  $i$ .

Now suppose  $\lim_{n \rightarrow \infty} p_1^{(n)}/p_k^{(n)}$  is finite. Then  $p_i^{(n)}/p_{i+1}^{(n)}$  increases to a finite limit for each  $i \leq k-1$  and  $q_1^{(n)}/q_k^{(n)} \rightarrow 1$  in view of (6.10). We show that this convergence is impossible for  $k = 3$ . Otherwise,  $p_2^{(n)}/p_3^{(n)}$  increases to a finite limit and necessarily  $q_2^{(n)}/q_3^{(n)} \rightarrow 1$ . But

$$\frac{q_2^{(n+1)}}{q_3^{(n+1)}} = \frac{p_2^{(n)} + q_2^{(n)} - 2p_2^{(n)}q_2^{(n)}}{p_3^{(n)} + q_3^{(n)} - 2p_3^{(n)}q_3^{(n)}} \tag{6.13}$$

which converges for at least a subset of indices  $n$  to some quantity

$$\frac{p_2^* + q_2^* - 2p_2^*q_2^*}{p_3^* + q_3^* - 2p_3^*q_3^*} \tag{6.14}$$

which strictly exceeds 1 because  $q_3^* = q_2^* < \frac{1}{2}$ , while  $p_2^* > p_3^*$ . To avert this contradiction, we must have  $p_1^{(n)}/p_3^{(n)} \uparrow \infty$ .

Consider next the contingency  $p_1^{(n)}/p_2^{(n)} \uparrow \alpha < \infty$ . It follows then that  $p_1^{(n)} \rightarrow p_1^*$ ,  $p_2^{(n)} \rightarrow p_2^*$ , ( $p_1^* + p_2^* = 1$  with  $p_2^* > p_1^*$ ) and  $q_1^{(n)}/q_2^{(n)} \rightarrow 1$ . But

$$\frac{q_1^{(n+1)}}{q_2^{(n+1)}} = \frac{p_1^{(n)} + q_1^{(n)} - 2p_1^{(n)}q_1^{(n)}}{p_2^{(n)} + q_2^{(n)} - 2p_2^{(n)}q_2^{(n)}} \rightarrow 1, \tag{6.15}$$

which is possible only if  $q_1^{(n)}$  and  $q_2^{(n)}$  converge and the limits are  $q_1^* = q_2^* = \frac{1}{2}$ .

In the case  $p_1^{(n)} \rightarrow 1$ , we find that  $q_k^{(n+1)} \approx q_k^{(n)}/[2(1 - q_1^{(n)})], k = 2, \dots, r, q_1^{(n+1)} \approx (1 - q_1^{(n)})/[2(1 - q_1^{(n)})] = \frac{1}{2}$  as  $n \rightarrow \infty$ . So  $q_1^{(n)} \rightarrow \frac{1}{2}$  and  $\sum_{k=2}^r q_k^{(n)} \rightarrow \frac{1}{2}$ .

This completes the analysis for the initial conditions (6.9).

Case (2). Suppose next

$$p_1^{(0)} > p_2^{(0)} > \cdots > p_r^{(0)}$$

(this is no restriction and reflects merely a labeling of the alleles  $A_i$ ) but now

$$q_2^{(0)} > q_1^{(0)} > q_3^{(0)} > \cdots > q_r^{(0)}. \quad (6.16)$$

We deduce, parallel to Case (1), that  $p_i^{(n)}/p_j^{(n)} \uparrow \infty$  and  $q_i^{(n)}/q_j^{(n)} > 1$  for all  $j \geq 3, i < j$ .

Suppose now  $p_1^{(n)} > p_2^{(n)}$  and  $q_2^{(n)} > q_1^{(n)}$  hold for all  $n \geq 1$ . It follows that  $p_1^{(n)}/p_2^{(n)} \downarrow \alpha \geq 1$  and consequently  $q_1^{(n)}/q_2^{(n)} \rightarrow 1$ .

Adapting the arguments of Case (1), we deduce immediately that  $\lim_{n \rightarrow \infty} q_1^{(n)} = \lim_{n \rightarrow \infty} q_2^{(n)} = \frac{1}{2}$  if  $\alpha > 1$ . If  $\alpha = 1$ , then  $[q_1^{(n+1)} + q_2^{(n+1)}] \approx 1/[2 - q_1^{(n)} - q_2^{(n)}]$  as  $n \rightarrow \infty$  and therefore  $q_1^{(n)} + q_2^{(n)} \rightarrow 1$ . In every case, the resulting limiting genotype composition is

$$\begin{array}{cc} \mathcal{A}_F & \mathcal{A}_M \\ \{A_1A_1, A_2A_2\} & \{A_1A_2\} \end{array} \quad (6.17)$$

If  $p_2^{(n)} > p_1^{(n)}$  and  $q_1^{(n)} > q_2^{(n)}$  hold for all  $n \geq 1$ , the same ultimate outcome as (6.17) is realized.

Finally, if for some  $n$ , the relationships

$$p_1^{(n)} > p_2^{(n)} \quad \text{and} \quad q_1^{(n)} > q_2^{(n)} \quad (6.18)$$

or

$$p_2^{(n)} > p_1^{(n)} \quad \text{and} \quad q_2^{(n)} > q_1^{(n)} \quad (6.19)$$

take place then the results of Case (1) apply noting that (6.19) emerges from (6.9) because we are again in Case (1) with alleles  $A_2$  and  $A_1$  interchanged. The relevant global convergence holds, mutatis mutandis.

Case (3). Suppose

$$p_1^{(0)} > p_2^{(0)} > \cdots > p_r^{(0)}$$

but now

$$q_2^{(0)} > q_3^{(0)} > q_1^{(0)} > q_4^{(0)} > \cdots > q_r^{(0)}. \quad (6.20)$$

We deduce as in Case (1),  $p_j^{(n)} \rightarrow 0$  for  $j \geq 4$ ,  $p_2^{(n)}/p_3^{(n)} \uparrow$  and  $q_2^{(n)}/q_3^{(n)} > 1$ . If  $\lim_{n \rightarrow \infty} p_2^{(n)}/p_3^{(n)}$  is finite then  $q_2^{(n)}/q_3^{(n)} \rightarrow 1$ . These results are consistent only if  $\lim_{n \rightarrow \infty} q_2^{(n)} = \lim_{n \rightarrow \infty} q_3^{(n)} = \frac{1}{2}$  and therefore  $q_1^{(n)} \rightarrow 0$  which compels  $p_1^{(n)} \rightarrow 0$ . But then the ordering of (6.20) cannot be maintained for all  $n$ .

Another possibility has  $p_2^{(n)}/p_3^{(n)} \uparrow \infty$  or  $p_3^{(n)} \rightarrow 0$ . If also  $p_1^{(n)} > p_2^{(n)}$  and  $q_2^{(n)} > q_3^{(n)} > q_1^{(n)}$  are maintained for all  $n$ , then  $p_1^{(n)}/p_2^{(n)} \downarrow \alpha \geq 1$  and  $q_1^{(n)}/q_2^{(n)} \rightarrow 1$ , implying as in Case (2) that  $\lim_{n \rightarrow \infty} q_2^{(n)} = \lim_{n \rightarrow \infty} q_1^{(n)} = \frac{1}{2}$  and therefore  $q_3^{(n)} \rightarrow 0$  which is a contradiction.

The foregoing arguments establish that

$$p_1^{(n)} > p_2^{(n)} > p_3^{(n)} \quad \text{and} \quad q_2^{(n)} > q_3^{(n)} > q_1^{(n)} \quad (6.21)$$

cannot prevail for all  $n$ .

The switch to

$$p_2^{(n)} > p_1^{(n)} > p_3^{(n)} \quad \text{and} \quad q_2^{(n)} > q_3^{(n)} > q_1^{(n)} \quad (6.22)$$

or

$$p_2^{(n)} > p_3^{(n)} > p_1^{(n)} \quad \text{and} \quad q_1^{(n)} > q_2^{(n)} > q_3^{(n)},$$

if maintained, would compel  $p_2^{(n)} \rightarrow 1$  and  $q_2^{(n)} \rightarrow \frac{1}{2}$  while the possibilities

$$p_1^{(n)} > p_2^{(n)} > p_3^{(n)} \quad \text{and} \quad \min(q_2^{(n)}, q_1^{(n)}) > q_3^{(n)} \quad (6.23)$$

for some  $n$  reduce directly to Case (1) or (2) by proper relabeling if necessary.

We next examine the possibility

$$p_1^{(n)} > p_2^{(n)} > p_3^{(n)} \quad \text{and} \quad q_3^{(n)} > q_2^{(n)} > q_1^{(n)}. \quad (6.24)$$

If this persists for all  $n$ , we can argue that

$$\lim_{n \rightarrow \infty} p_1^{(n)} = \lim_{n \rightarrow \infty} p_2^{(n)} = \lim_{n \rightarrow \infty} p_3^{(n)} = \frac{1}{3} \quad \text{and} \quad \lim_{n \rightarrow \infty} q_3^{(n)} = \lim_{n \rightarrow \infty} q_2^{(n)} = \lim_{n \rightarrow \infty} q_1^{(n)} = \frac{1}{3}. \quad (6.25)$$

But the central equilibrium representing equally alleles  $A_1$ ,  $A_2$ , and  $A_3$  is totally repelling (see Sect. 6.1) and therefore the convergence (6.25) cannot occur. Therefore the realizations reduce to those of Cases (1) or (2) modulo a relabeling of alleles.

*Case (4). The general case*

$$p_1^{(0)} > p_2^{(0)} > \dots > p_r^{(0)} \quad (6.26)$$

and

$$q_{k_1}^{(0)} > q_{k_2}^{(0)} > \dots > q_{k_r}^{(0)}$$

where  $k_i$  is a permutation of  $\{1, \dots, r\}$  is analyzed by the same methods involving more arduous details.

For example, in the extreme case, if

$$p_1^{(n)} > \dots > p_r^{(n)} \quad (6.27)$$

and

$$q_r^{(n)} > q_{r-1}^{(n)} > \dots > q_1^{(n)}$$

hold for all  $n \geq 0$  we easily deduce that

$$\lim_{n \rightarrow \infty} p_i^{(n)} = \frac{1}{r}, \quad i = 1, 2, \dots, r \quad (6.28)$$

and

$$\lim_{n \rightarrow \infty} q_i^{(n)} = \frac{1}{r}.$$

But the central symmetric equilibrium point is totally repelling so that the outcome (6.28) is precluded. Thus the reverse ordering (6.27) *cannot* be maintained and a switch of order occurs.

We ultimately secure either convergence to

$$\mathcal{A}_F = \{A_k A_k\} \text{ for some } k \text{ while } \mathcal{A}_M = \{A_l A_l, l = 1, 2, \dots, k-1, k+1, \dots, r\}$$

or for some pair  $i \neq j$ ,

$$\mathcal{A}_F = \{A_i A_i, A_j A_j\} \text{ and } \mathcal{A}_M = \{A_l A_l\}.$$

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