

A Criterion for Stability–Instability at Fixation States Involving an Eigenvalue One with Applications in Population Genetics*

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An explicit general criterion for stability–instability at fixation states is provided when the leading eigenvalue of the gradient matrix is one. Several applications in population genetics are presented including cases of familial selection of dominant and recessive genes, models of preferential mating, incompatibility systems, and effects of migration and population structure.

1. INTRODUCTION

The stability analysis of an equilibrium state in population genetic models is usually decided by evaluating the leading eigenvalue of the gradient matrix, i.e., the matrix of the linear approximation that usually dominates the behavior of the transformation equation in the neighborhood of the equilibrium point. The equilibrium is always stable when the leading eigenvalue of the gradient matrix is smaller than one, and generally unstable when this eigenvalue exceeds one. When the leading eigenvalue is one the determination of stability versus instability of the equilibrium generally requires more refined analysis involving the quadratic or higher order approximation terms of the transformation equations. The rate of local convergence or divergence is algebraic for this case.

A leading eigenvalue of one often occurs when recessive and dominant traits are involved. The widespread occurrence of dominance and recessive traits in natural populations is familiar. These include genes responsible for color and shape patterns (e.g., Cain and Sheppard, 1952; Ford, 1975), disease susceptibilities (McKusich, 1978), the +, – functioning of an enzyme (e.g., Erhmann and Parsons, 1976, p. 50), traits relevant to sexual and assort-

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tative mating propensities (O'Donald, 1977, 1980) involving two phenotype classes, one dominant to the other. Moreover, several theoretical studies on the genetics of kin selection (see, e.g., the recent book of Boorman and Levitt, 1980) focus on the case of dominant and recessive genes controlling for altruist behaviour.

There is the impression among some experimental and field population geneticists that if a fixation state is stable with near dominance, then it is also stable with complete dominance. This surmise is usually false. The conditions for stability in terms of the parameters of the model in the case of complete dominance cannot be obtained by continuity arguments. The workings and interpretations are more subtle and require nonlinear analysis. The eigenvalue one complication comes about in an intrinsic way intimately tied to the biology or on account of the features of the mating system and does not result because of a bifurcation, i.e., due to a multiplicity of eigenvalues occurring at special values of the model parameters. The latter circumstance is the usual way in encountering eigenvalue one problems in studies of dynamical systems.

There are other natural population genetic models where the constraints of the mating system (e.g., prohibitive matings associated with sex differentiation, incompatibility mechanisms, sex-ratio determination models) give rise to equilibrium states exhibiting leading eigenvalue one for its associated gradient matrix (Workman, 1964; Karlin, 1968; Karlin and Feldman, 1968). Ad hoc approaches may lead successfully to the stability–instability conditions for eigenvalue one problems of the simplest multidimensional population genetics models (e.g., Karlin, 1968). Converting to Hardy–Weinberg proportions under random mating may aid in reducing the dimensionality of the problem. In fact, with two alleles at one locus under viability selection the genotype frequencies in Hardy–Weinberg form appear in terms of a single real variable (Cockerham *et al.*, 1973; Wright, 1955, 1969; Levitt, 1975; Templeton, 1979; Wade, 1978; Michod, 1980). Justification of these approximations are required in each case (cf. Nagylaki, 1977; Boorman and Levitt, 1980, Chaps. 7 and 8), and these approximations are not easily extended to cases of nonrandom mating processes. Moreover, as a caveat, the use of Hardy–Weinberg approximations does not always provide the correct answers especially in treating differentiated sex effects for familial selection models. A direct nonlinear local analysis is feasible when the gradient matrix is an irreducible stochastic matrix (Karlin, 1977; Nagylaki, 1977; Karlin and Kenett, 1977; Moody, 1981).

The difficulty of finding stability conditions at the fixation states when the leading eigenvalue is one (e.g., Matessi and Scudo, 1975; Matessi and Jayakar, 1976; Charlesworth, 1978; Cavalli–Sforza and Feldman, 1978; Maffi and Jayakar, 1981) motivates the elaboration of an explicit general criterion for their solution. This paper provides an explicit general criterion

for discerning stability versus instability at fixation states for cases where the dominant (leading) eigenvalue of the associated gradient matrix is one. The result is applied to models of brood selection in a sex-differentiated population, a sex-linked trait, for a corresponding haploid-diploid population system, examples associated with imprinting schemes and incompatibility mechanisms, and we consider several nonrandom mating examples of partial assortative mating. Our results are also relevant to kin selection models analyzed by Charlesworth (1978), Cavalli-Sforza and Feldman (1978), Boorman and Levitt (1980, Chaps. 6-8), among others. The wide scope of our criterion is illustrated further in terms of a two-locus model pertaining to meiotic drive modification (e.g., Maffi and Jayakar, 1981). The superposition of migration and multideme effects can also be incorporated in these analyses.

The formal criterion for establishing stability of a fixation state with gradient matrix of leading eigenvalue one is set forth in Section 2 with a detailed proof in the Appendix. The criterion is rigorous without recourse to approximations in terms of Hardy-Weinberg ratio or use of other ad hoc perturbation methods, whose justifications can be formidable. Although the focus of the applications pertains largely to population genetic models, the criterion is undoubtedly useful in studies of ecological dynamics, population demographic changes, and in other contexts as well.

2. A CRITERION FOR STABILITY-INSTABILITY AT FIXATION STATES THAT INVOLVE AN EIGENVALUE ONE

Consider an infinite population with discrete generations. Let the population states be described by frequency vectors $\mathbf{x} = (x_1, \dots, x_n)$ such that $\mathbf{0} = (0, \dots, 0)$ corresponds to a fixation event F . Let $T\mathbf{x} = (U_1(\mathbf{x}), \dots, U_n(\mathbf{x}))$ be the transformation relating the population states over successive generations. Assume $T\mathbf{x} = \mathbf{0}$ if and only if $\mathbf{x} = \mathbf{0}$ and that T is smooth enough in the neighborhood of $\mathbf{0}$. (It is sufficient that the first and second derivatives of all $U_i(\mathbf{x})$ are continuous in a neighborhood of $\mathbf{0}$.) Let L be the gradient matrix of T at $\mathbf{0}$, namely,

$$L = \left\| \left\| \frac{\partial U_i}{\partial x_j}(\mathbf{0}) \right\| \right\|_{i,j=1}^n.$$

Assume that L is nonnegative and denote by $\rho(L)$ its spectral radius.

By definition, the fixation event F is said to be *stable* if the iterates $T^k\mathbf{x} \rightarrow \mathbf{0}$ as $k \rightarrow \infty$ for any initial population state \mathbf{x} near $\mathbf{0}$, and *unstable* if $T^k\mathbf{x} \rightarrow \mathbf{0}$ as $k \rightarrow \infty$ for any initial population state \mathbf{x} different from $\mathbf{0}$. Formally, the first condition corresponds to local asymptotic stability in the

manner that the fixation event F is locally attracting, while the latter property is stronger than a simple negation of the stability condition since it states that the population state F cannot be reached from any nonzero state and thus is strongly repelling. It is well known that the fixation event F will be stable if $\rho(L) < 1$ and usually unstable if $\rho(L) > 1$. Actually the second part requires some mild supplementary conditions. A brief proof of both statements is given at the end of the Appendix in the most common case where there exists $\mathbf{z} = (z_1, \dots, z_n) > \mathbf{0}$ (i.e., $z_i > 0$ for $i = 1, \dots, n$) such that $\mathbf{z}L = \rho(L)\mathbf{z}$. When $\rho(L) < 1$, local convergence to $\mathbf{0}$ occurs at the geometric rate $\rho(L)$, i.e., it decreases to zero after k generations to the order $[\rho(L)]^k$.

Now assume $\rho(L) = 1$ allowing L of the general form

$$L = \begin{pmatrix} A & B \\ 0 & C \end{pmatrix}, \quad (1)$$

where A is an irreducible aperiodic (i.e., primitive, see Appendix) nonnegative matrix of order l and $\rho(C) < 1$. We use the notation $\langle\langle \mathbf{z}, \mathbf{w} \rangle\rangle = \sum_{i=1}^n z_i w_i$ to denote the canonical inner product of the vectors \mathbf{z} and \mathbf{w} . Define the quantity

$$S = \langle\langle \boldsymbol{\xi}, \boldsymbol{\theta}^{(1)} + B(I - C)^{-1}\boldsymbol{\theta}^{(2)} \rangle\rangle \quad (2)$$

(I is the identity matrix), where $\boldsymbol{\xi}(\boldsymbol{\eta})$ is the left (right) principal eigenvector of A corresponding to the eigenvalue 1, that is,

$$\boldsymbol{\xi}A = \boldsymbol{\xi} = (\xi_1, \dots, \xi_l) > \mathbf{0}, \quad A\boldsymbol{\eta} = \boldsymbol{\eta} = (\eta_1, \dots, \eta_l) > \mathbf{0} \quad (3)$$

and

$$\boldsymbol{\theta}^{(1)} = (\theta_1, \dots, \theta_l), \quad \boldsymbol{\theta}^{(2)} = (\theta_{l+1}, \dots, \theta_n)$$

with

$$\theta_i = \sum_{\lambda, \mu=1}^l \frac{\partial^2 U_i(\mathbf{0})}{\partial x_\lambda \partial x_\mu} \eta_\lambda \eta_\mu \quad \text{for } i = 1, \dots, n. \quad (4)$$

We are now prepared to state the following general criterion.

RESULT I. Consider the general nonlinear transformation T with fixation state $\mathbf{0}$ (F) and associated gradient matrix L as in (1) obeying the assumptions as stated above. The fixation event F is stable if $S < 0$ and unstable if $S > 0$. When $S < 0$, local convergence to the fixation state F occurs at an algebraic rate of degree 1, i.e., the deviation of $T^k \mathbf{x}$ from $\mathbf{0}$ after k iterations is of the precise order $1/k$.

This may be viewed as a general multidimensional version of the condition on the second derivative in one dimension. A proof is given in the Appendix in the usual case where the nonnegative matrix $B(I - C)^{-1}$ displays no null columns, which covers most applications.

3. SOME APPLICATIONS IN POPULATION GENETICS

In all the following examples, unless indicated otherwise, we consider two alleles, A and a , segregating at a single locus. In general, it is assumed that allele A is dominant over allele a . In the final example (f) a case without dominance is handled also with the aid of Result I. Result I is applied to determine the exact conditions for stability–instability of A -fixation, i.e., necessary and sufficient conditions for a -protection.

(a) Brood Selection

Consider the arrays of selection parameters given in Tables I–III. These formulations can accommodate diverse selection forces including differential viability, fertility, and segregation distortion effects; we have normalized the parameters relative to Mendelian ratios which facilitates comparisons with standard models and forms of “familial” selection (Haldane, 1924). There is a resurgence of interest in these models as they occur in theoretical studies of kin selection and reciprocal altruism.

With separate sexes the parameter k can be construed as a normalizing factor between the two populations that accounts for differences in the sex ratio. Assuming random mating, Levitt (1975) determined the exact conditions for stability at A -fixation for the models corresponding to Tables I and II, using different methods in each case based on Hardy–Weinberg approximations (cf. Boorman and Levitt, 1980, Chap. 7).

TABLE I
Brood Selection: A Diploid Model

Mating types	Offspring		
	AA	Aa	aa
$AA \times AA$	1	0	0
$AA \times Aa$	1/2	1/2	0
$AA \times aa$	0	a	0
$Aa \times Aa$	$b/4$	$c/2$	$d/4$
$Aa \times aa$	0	$f/2$	$g/2$
$aa \times aa$	0	0	s

TABLE II
Brood Selection: A Haplodiploid Model

♀ × ♂	♀			♂	
	AA	Aa	aa	A	a
AA × A	1	0	0	k	0
AA × a	0	1	0	k	0
Aa × A	1/2	1/2	0	k/2	k/2
Aa × a	0	c ₁ /2	d ₁ /2	kc ₂ /2	kd ₂ /2
aa × A	0	h ₁	0	0	kh ₂
aa × a	0	0	s ₁	0	ks ₂

(i) *Diploid case (Table I)*. Let x, y, z be the frequencies of genotypes $AA, Aa,$ and $aa,$ respectively. Assuming random mating, these are connected over two successive generations by the equations

$$\begin{aligned}
 Wx' &= x^2 + xy + (b/4)y^2, \\
 Wy' &= xy + 2axz + (c/2)y^2 + fyz, \\
 Wz' &= (d/4)y^2 + gyz + sz^2,
 \end{aligned}$$

where W is a normalizing factor to assure that $x' + y' + z' = 1$. Near the A -allele fixation state (i.e., y and z small) we ascertain the expansion

$$\begin{aligned}
 y' &= y + 2az + (c/2 - 1)y^2 + \dots, \text{ etc.}, \\
 z' &= (d/4)y^2 + \dots, \text{ etc.}
 \end{aligned}$$

TABLE III
Brood Selection: A Diploid Model with Differentiated Sexes

♀ × ♂	♀			♂		
	AA	Aa	aa	AA	Aa	aa
AA × AA	1	0	0	k	0	0
AA × Aa	1/2	1/2	0	k/2	k/2	0
AA × aa	0	a ₁	0	0	ka ₂	0
Aa × AA	1/2	1/2	0	k/2	k/2	0
Aa × Aa	b ₁ /4	c ₁ /2	d ₁ /4	kb ₂ /4	kc ₂ /2	kd ₂ /4
Aa × aa	0	f ₁ /2	g ₁ /2	0	kf ₂ /2	kg ₂ /2
aa × AA	0	h ₁	0	0	kh ₂	0
aa × Aa	0	p ₁ /2	q ₁ /2	0	kp ₂ /2	kq ₂ /2
aa × aa	0	0	s ₁	0	0	ks ₂

It follows easily, or by simple application of Result I, that A -fixation is stable (unstable) if

$$c + ad < 2 \quad (>2).$$

(ii) *Haplo-diploid case (Table II)*. Introducing v as the frequency of allele a in the haploid population, we find the following expansion near A -fixation (i.e., for y, z , and v small):

$$\begin{aligned} y' &= y/2 + v + h_1 z + (c_1 - 3) yv/2 + \dots, \text{ etc.}, \\ v' &= y/2 + h_2 z + (d_2 - 1) yv/2 + \dots, \text{ etc.}, \\ z' &= d_1 yv/2 + \dots, \text{ etc.} \end{aligned}$$

Appeal to Result I shows that A -fixation is stable (unstable) if

$$c_1 + (h_1 + h_2) d_1 + d_2 < 4 \quad (>4).$$

(iii) *Diploid case with differentiated sexes (Table III)*. This case is also straightforward. In the neighborhood of A -fixation we obtain the expansion

$$\begin{aligned} y'_1 &= y_1/2 + y_2/2 + h_1 z_1 + a_1 z_2 + (c_1/2 - 1) y_1 y_2 + \dots, \text{ etc.}, \\ y'_2 &= y_1/2 + y_2/2 + h_2 z_1 + a_2 z_2 + (c_2/2 - 1) y_1 y_2 + \dots, \text{ etc.}, \\ z'_1 &= (d_1/4) y_1 y_2 + \dots, \text{ etc.}, \\ z'_2 &= (d_2/4) y_1 y_2 + \dots, \text{ etc.} \end{aligned}$$

(1 and 2 indexing the female and male populations, respectively). Result I in this case yields the condition

$$c_1 + c_2 + \frac{d_1(h_1 + h_2)}{2} + \frac{d_2(a_1 + a_2)}{2} < 4 \quad (>4)$$

for A -fixation stability (instability). These results can be interpreted in the context of kin selection (cf. Cavalli-Sforza and Feldman, 1978; Charlesworth, 1978; Uyenoyama and Feldman, 1981). Moreover, it would be easy to incorporate frequency-dependent parameters on these models.

(b) *Partial Assortative Mating*

Suppose that a proportion α among the females of the dominant phenotype $\bar{A} = \{AA, Aa\}$ have a preference to mate with a male of the same phenotype, and similarly a proportion β of the females of phenotype $\bar{a} = \{aa\}$. The remaining females choose mates at random. Assume all females are fertilized and males are polygynous. Sex ratio is assumed to be 1 : 1. The frequencies of the mating types are displayed in Table IV adhering

TABLE IV
 Partial Assortative Mating: A Polygynous Model

Mating types	Frequencies	
	Assorting	Random mating
$AA \times AA$	$\alpha x^2/(x + y)$	$(1 - \alpha)x^2$
$AA \times Aa$	$2\alpha xy/(x + y)$	$2(1 - \alpha)xy$
$AA \times aa$	0	$(2 - \alpha - \beta)xz$
$Aa \times Aa$	$\alpha y^2/(x + y)$	$(1 - \alpha)y^2$
$Aa \times aa$	0	$(2 - \alpha - \beta)yz$
$aa \times aa$	βz	$(1 - \beta)z^2$

to the notation of Table I and subject to the selection forces as specified in Table I. The local approximation near *A*-fixation reduces to

$$y' = y + a(2 - \alpha - \beta)z + (c/2 - 1)y^2 + \dots, \text{ etc.},$$

$$z' = \beta sz + (d/4)y^2 + \dots, \text{ etc.}$$

Then, provided $\beta s < 1$, the condition for stability (instability) at *A*-fixation is given by

$$c + \frac{ad}{1 - \beta s} \left[1 - \frac{\alpha + \beta}{2} \right] < 2 \quad (>2).$$

When only individual viability is in force (i.e., for $a = b = c = f = 1$ and $d = g = s$), the foregoing condition becomes

$$\beta - \alpha < 2(1 - s)/s \quad (>2(1 - s)/s),$$

in agreement with Scudo and Karlin (1969). Similarly, we can easily obtain the corresponding conditions for a wide spectrum of population genetic models incorporating mating behavioral mechanisms including sexual selection involving forms of encounter processes.

(c) *Superposition of Migration and Population Structure Influences*

Consider a population subdivided into *N* demes and in each deme partial assortative mating and brood selection is in force as described in Tables IV and I with parameters indexed by the deme site *i* ($i = 1, \dots, N$). This may reflect spatial or temporal variation, or general population subdivision effects. Suppose that migration exchange occurs among the demes according to a backward migration matrix $M = \|m_{ij}\|_{i,j=1}^N$, i.e., m_{ij} is the proportion of individuals per generation in deme *i* that originate from parents of deme *j*.

Let M be an irreducible aperiodic stochastic matrix. For definiteness, we assume the following order between the different components of the model:

mating \rightarrow selection \rightarrow migration.

The global transformation equations T near A -fixation over two successive generations is given by the system of equations

$$\begin{aligned} y'_i &= \sum_{j=1}^N m_{ij} y_j + \sum_{j=1}^N m_{ij} a_j (2 - \alpha_j - \beta_j) z_j \\ &+ \sum_{j=1}^N m_{ij} (\tfrac{1}{2} c_j - 1) y_j^2 + \dots, \text{ etc.}, \\ z'_i &= \sum_{j=1}^N m_{ij} \beta_j s_j z_j + \sum_{j=1}^N m_{ij} (\tfrac{1}{3} d_j) y_j^2 + \dots, \text{ etc.}, \quad i = 1, 2, \dots, N, \end{aligned}$$

where y_i and z_i are the genotype frequencies for Aa and aa , respectively, in deme i ($i = 1, \dots, N$). The gradient matrix of the mapping T in the variables (\mathbf{y}, \mathbf{z}) at $\mathbf{0}$ is plainly

$$L = \begin{vmatrix} M & M\Gamma \\ 0 & M\Delta \end{vmatrix},$$

where Γ and Δ are the diagonal matrices

$$\begin{aligned} \Gamma &= \text{diag}\{a_1(2 - \alpha_1 - \beta_1), \dots, \alpha_N(2 - \alpha_N - \beta_N)\}, \\ \Delta &= \text{diag}\{\beta_1 s_1, \dots, \beta_N s_N\}. \end{aligned}$$

Moreover, in this case, the associated vectors of (4) are

$$\boldsymbol{\theta}^{(1)} = M(\mathbf{c} - \mathbf{2}) \quad \text{and} \quad \boldsymbol{\theta}^{(2)} = \tfrac{1}{2} M\mathbf{d},$$

where $\mathbf{c} = (c_1, \dots, c_N)$, $\mathbf{d} = (d_1, \dots, d_N)$, and $\mathbf{2} = (2, \dots, 2)$. If $\rho(M\Delta) < 1$, then A -fixation will be stable (unstable) according to

$$2\langle\langle \boldsymbol{\xi}, \mathbf{c} \rangle\rangle + \langle\langle \boldsymbol{\xi}, \Gamma(I - M\Delta)^{-1} M\mathbf{d} \rangle\rangle < 4 \quad (>4), \quad (6)$$

where $\boldsymbol{\xi} M = \boldsymbol{\xi} = (\xi_1, \dots, \xi_N)$ with $\sum_{i=1}^N \xi_i = 1$. Observe that instability of A -fixation means protection of allele a . Under random mating (all $\alpha_i = \beta_i = 0$) and individual viability only ($a_i = b_i = c_i = f_i = 1$ and $d_i = g_i = s_i$ for $i = 1, \dots, N$), the above condition reduces to

$$\langle\langle \boldsymbol{\xi}, \mathbf{s} \rangle\rangle < 1 \quad (>1),$$

where $\mathbf{s} = (s_1, \dots, s_n)$ in agreement with Karlin (1977) and Nagylaki (1977). An analogous analysis is possible for models with sex differentiated parameters.

(d) *Imprinting Model*

Let us assume that, among the females of a brood from mating type $\bar{A} \times \bar{A}$, a proportion α exhibits a mating preference for the phenotype $\bar{A} = \{AA, Aa\}$, while a proportion β among the females of a brood from mating type $\bar{a} \times \bar{a}$ exercises preference for the phenotype $\bar{a} = \{aa\}$. The remaining females are assumed to mate indifferently (at random). In this model of female choice, males are assumed not to be imprinted in their mating propensities. The sex ratio in progeny numbers is taken to be 1 : 1.

Suppose that males and females mate at random and an encounter is followed by mating if it is compatible with the preference of the female. If not, the female will not be fertilized (mass-action assumption). On the other hand, suppose that brood selection operates according to Table I. The model and transformation equations are summarized in Table V. If v_1, \dots, v_6 denote the frequencies of the mating types with v_1 that of $AA \times AA$, the transformation relating (v_2, \dots, v_6) over two successive generations exhibits the following gradient matrix at $\mathbf{0}$:

$$L = \begin{vmatrix} 1 & 2a & c & f & 0 \\ 0 & 0 & (2-\alpha)d/4 & (2-\alpha)g/2 & (2-\alpha-\beta)s \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{vmatrix}$$

with associated vectors (see Eq. (4))

$$\theta^{(1)} = -1, \quad \theta^{(2)} = (0, \frac{1}{2}, 0, 0).$$

Application of Result I implies that A -fixation is stable (unstable) according to

$$c + ad(1 - \alpha/2) < 2 \quad (>2). \tag{7}$$

It can be shown that the same condition holds if the mass-action assumption is replaced by the polygyny assumption and $\beta s < 1$. Exact analytical solutions are quite rare for such problems. In the special case of no brood selection (i.e., $a = b = c = d = f = g = s = 1$), condition (7) confirms stability at A -fixation as has been predicted from an approximative treatment (Matessi and Scudo, 1975).

Imprinting by only one parent (father's phenotype) coupled with selection as prescribed in Table III yields the corresponding condition

$$c_1 + c_2 + d_1(h_1 + h_2)/2 + (1 - \alpha) d_2(a_1 + a_2 - \beta a_1)/2 < 4 \quad (>4).$$

TABLE V
Imprinting: A Model Combining Brood Selection and Partial Imprinting by Both Parents with Mass-Action Type Mating

Mating types	Frequencies	Brood selection parameters			Imprinting fractions
		<i>AA</i>	<i>Aa</i>	<i>aa</i>	
<i>AA</i> × <i>AA</i>	v_1	1	0	0	α
<i>AA</i> × <i>Aa</i>	v_2	1/2	1/2	0	α
<i>AA</i> × <i>aa</i>	v_3	0	a	0	0
<i>Aa</i> × <i>Aa</i>	v_4	$b/4$	$c/2$	$d/4$	α
<i>Aa</i> × <i>aa</i>	v_5	0	$f/2$	$g/2$	0
<i>aa</i> × <i>aa</i>	v_6	0	0	s	β

Combined genotypic frequencies	Relative frequencies of	
	Randomly mating females	Choosing females
$Wx = v_1 + v_2/2 + v_4 b/4$	$\tilde{x} \approx (1 - \alpha) \left[v_1 + \frac{v_2}{2} + v_4 \frac{b}{4} \right]$	$x_{\bar{A}} \approx av_1 + av_2/2 + av_4 b/4$
$Wy = v_2/2 + v_3 a + v_4 c/2 + v_5 f/2$	$\tilde{y} \approx (1 - \alpha) \left[\frac{v_2}{2} + v_4 \frac{c}{2} \right] + v_3 a + v_5 \frac{f}{2}$	$y_{\bar{A}} \approx av_2/2 + av_4 c/2$
$Wz = v_4 d/4 + v_5 g/2 + v_6 s$	$\tilde{z} \approx (1 - \alpha) v_4 \frac{d}{4} + (1 - \beta) v_6 s + v_5 \frac{g}{2}$	$z_{\bar{A}} \approx av_4 d/4, z_{\bar{a}} \approx \beta v_6 s$

with W such that $x + y + z = 1$. The male genotype frequencies are also (x, y, z) .

Transformation equations

$\tilde{W}v'_1 = x^2$	$\tilde{W}v'_4 = y^2$
$\tilde{W}v'_2 = 2xy$	$\tilde{W}v'_3 = (z - z_{\bar{a}})y + (y - y_{\bar{A}})z$
$\tilde{W}v'_3 = (z - z_{\bar{a}})x + (x - x_{\bar{A}})z$	$\tilde{W}v'_6 = (z - z_{\bar{A}})z$

with \tilde{W} such that $v'_1 + v'_2 + v'_3 + v'_4 + v'_5 + v'_6 = 1$

Actually, many variants on the above model allowing mixed sib-mating systems of partial imprinting determined by brood composition and incorporating behavioral and ecological factors can be handled by similar means.

(e) *A Two-Locus Segregation Distortion Modification Model*

The following model of a sex-linked meiotic drive gene has been proposed by Maffi and Jayakar (1981) to explain sex-ratio deviations in *Aedes aegypti* populations. A first locus with possible alleles M, m is assumed to be respon-

sible for sex determination: males are Mm , and females mm , while a second locus of the male parent with possible alleles A, a governs the sex ratio in the progeny. Assume that a recombination event between those two loci can occur prior to the meiotic drive effects. Let the probability of recombination be r . Thus, for the two loci under consideration, the spectrum of male genotypes $\{MA/ma, MA/ma, Ma/ma, Ma/ma\}$ is composed of haplotypes $MA, Ma, mA,$ and ma , but always heterogametic at the $\{M, m\}$ locus. The female genotype array consists of $\{mA/ma, mA/ma, ma/ma\}$. The sex-ratio expression takes A dominant to a such that a male parent of genotype aa independent of his female mate genotype produces male to female offspring in a ratio of $M_1:1-M_1$, while an $\bar{A} = \{Aa, AA\}$ male parent has offspring in a sex ratio $M_2:1-M_2$.

The recursion relations expressing the changes in male and female genotype frequencies over successive generations can be expressed with only three variables

$$u = \text{freq}(Ma/ma) + \text{freq}(Ma/mA),$$

$$v = \text{freq}(Ma/ma) + \text{freq}(MA/ma),$$

$$w = \text{freq}(ma/ma) + \frac{1}{2}\text{freq}(ma/mA).$$

Under random mating, Maffi and Jayakar (1981) established the recursion relations

$$v' = w,$$

$$u' = \frac{(M_1 - M_2)uv + uM_2(1-r) + vM_2r}{M_2 + (M_1 - M_2)uv},$$

$$2w' = w + \frac{(M_2 - M_1)uv + u(1 - M_2)r + v(1 - M_2)(1 - r)}{(1 - M_2) + (M_2 - M_1)uv}.$$

Maffi and Jayakar asserted that there exist only two possible equilibria, $(0, 0, 0)$ and $(1, 1, 1)$, the former being stable and the latter unstable. Application of Result I, however, establishes that $(0, 0, 0)$ is stable (unstable) if

$$(M_1 - M_2)(1 - 2M_2) < 0 \quad (>0).$$

Moreover, a local linear analysis reveals that $(1, 1, 1)$ is unstable if

$$r(M_1 - M_2)(1 - 2M_2) < (M_1 - M_2)^2$$

or

$$(1 - r)[3M_2/M_1 + (1 - M_2)/(1 - M_1)] > 4.$$

The equilibrium $(1, 1, 1)$ is stable if both inequalities are reversed. Finally, the analysis is completed by noting that under the condition

$$(M_1 - M_2) < r(1 - 2M_2) < 0,$$

there exists an internal equilibrium, namely,

$$u^* = \frac{(1 - 2M_2)}{2(1 - M_2)} + \frac{1}{2(1 - M_2)} \sqrt{1 - \frac{4M_2(1 - M_2)[M_1 - M_2 + r(2M_2 - 1)]}{M_1 - M_2}},$$

$$v^* = w^* = \frac{(1 - M_2)u^* + (2M_2 - 1)}{M_2}.$$

In that case, both fixation states are unstable. It is worth noting that when $M_2 = \frac{1}{2}$, which is the case in the numerical example of Maffi and Jayakar, there is no polymorphic equilibrium, the point $(1, 1, 1)$ is unstable and even a quadratic analysis fails at $(0, 0, 0)$ which may account for the extremely slow rate of convergence reported.

(f) *Incompatibility Model*

This last example illustrates that an eigenvalue one problem is not necessarily associated with dominance. Consider two alleles A and a and assume only that the matings $aa \times aa$ and $Aa \times Aa$ are prohibited. This is a case of pollen elimination. Generally, pollen elimination, especially in plant populations, entails several alleles. The analysis of the present model introduced by Workman (1964) may be suggestive of the general mechanism. Letting u, v , and w be the current frequencies of genotypes AA, Aa , and aa , respectively, the recursion relations are

$$u' = u \left(\frac{v/2}{1-v} \right) + \frac{v}{2} + u,$$

$$v' = \frac{1-u^2}{2} + \frac{uw}{2} \left(\frac{2-w}{1-w} \right),$$

$$w' = \frac{vw(1+u)}{2(u+vw)}.$$

Our criterion (Result I) allows us to conclude that A -fixation, which corresponds to $(1, 0, 0)$, is stable. On the other hand, it can be shown that $(0, \frac{1}{2}, \frac{1}{2})$ is also stable, and then a third equilibrium, which is necessarily unstable, exists between those two (see Karlin and Feldman, 1968).

The extension to an incompatibility model involving multiple alleles (the more usual case) can be treated in the same manner.

4. SUMMARY AND DISCUSSION

Our results provide a far-reaching general criterion for ascertaining local stability (or instability) at an equilibrium state of a nonlinear transformation T , where the gradient matrix L at the fixed point has leading eigenvalue 1. This is usually viewed as a delicate problem since local linear analysis is not

adequate and it is essential to take account of the contributions from quadratic or possibly even higher order terms.

In our analysis we require L to be a nonnegative matrix plus other mild conditions as described in Result I. The prime limiting facet of the result is that the fixed point $\mathbf{0}$ under consideration is a corner point of the domain of T . We elaborated a variety of applications in population genetic models for dominant or recessive alleles in diploid, haplodiploid, and two-sex populations, subject to familial selection forces, partial assortative and sexual selection mating patterns, contingencies of incompatibility processes, and inbreeding systems allowing also for migration and population structure influences.

It appears that a corresponding problem for boundary equilibrium in higher dimensions or internal equilibrium states with leading eigenvalue one for the associated gradient matrix is very difficult, perhaps even prohibitive. Such cases occur in the context of dominance hierarchies with more alleles and/or more loci formulations.

There are also natural models of sex-ratio evolution (e.g., Eshel, 1975; Uyenoyama and Bengtsson, 1981) that lead to eigenvalue one situations at internal or such high-dimensional equilibrium states. Even local quadratic analysis may not be sufficient in these analyses and new techniques have to be developed.

As is familiar, eigenvalue one fixed points enter for parameter values where solutions bifurcate. This can occur both at fixation states and boundary and internal equilibrium; in the former event the general criterion of Result I may be informative for further investigations of biological and/or ecological models.

APPENDIX. PROOF OF RESULT I

For completeness we review some definitions and results in matrix theory for ready reference (see, e.g., Gantmacher, 1959; Seneta, 1973).

Let $A = \|a_{ij}\|_{i,j=1}^l$ be a nonnegative matrix (i.e., $a_{ij} \geq 0$ for $i, j = 1, \dots, l$). Denote by $\rho(A)$ its spectral radius.

THEOREM (Perron–Frobenius). *The number $\rho(A)$ is an eigenvalue of A with the property that there exist nontrivial nonnegative vectors $\xi = (\xi_1, \dots, \xi_l)$ and $\eta = (\eta_1, \dots, \eta_l)$ satisfying*

$$\xi A = \rho(A)\xi, \quad A\eta = \rho(A)\eta.$$

DEFINITION. A is said to be *reducible* if, by simultaneously permuting corresponding rows and columns, A can be put in the form

$$A = \begin{bmatrix} A_{11} & A_{12} \\ 0 & A_{22} \end{bmatrix},$$

where A_{11} , A_{22} are square matrices, and 0 is a matrix with zero entries everywhere. Otherwise, A is said to be *irreducible*.

THEOREM (Perron–Frobenius). *If A is irreducible, then $\rho(A)$ is a positive simple eigenvalue and the associated left and right eigenvectors, ξ and η , display only positive components.*

DEFINITION. A is said to be *primitive* if A is irreducible and $\rho(A)$ is the only eigenvalue with modulus equal to $\rho(A)$. Equivalently, A is irreducible and aperiodic or there exists an integer m such that A^m exhibits all positive elements.

THEOREM (Strong Ergodic Theorem). *Let A be primitive with $\rho(A) = 1$. Then A^k converges to $U = \|\eta_i \xi_j\|_{i,j=1}^l$ as $k \rightarrow \infty$, where $\xi A = \xi > \mathbf{0}$, $A\eta = \eta > \mathbf{0}$, and $\langle\langle \xi, \eta \rangle\rangle = \sum_{i=1}^l \eta_i \xi_i = 1$.*

COROLLARY. *Let $L = \begin{bmatrix} A & B \\ 0 & C \end{bmatrix}$, where A satisfies the conditions of the above theorem and $\rho(C) < 1$. Then*

$$L^k \rightarrow M = \begin{bmatrix} U & UB(I-C)^{-1} \\ 0 & 0 \end{bmatrix} \quad \text{as } k \rightarrow \infty.$$

Proof. By induction, we get

$$L^k = \begin{bmatrix} A^k & \sum_{r=0}^{k-1} A^{k-1-r} B C^r \\ 0 & C^k \end{bmatrix}.$$

We know by the strong ergodic theorem that $A^k \rightarrow U$ as $k \rightarrow \infty$. On the other hand, since $\rho(C) < 1$, we have $C^k \rightarrow 0$ and $\sum_{r=0}^{k-1} C^r \rightarrow (I-C)^{-1}$ as $k \rightarrow \infty$. It follows that

$$\sum_{r=0}^{k-1} (A^{k-1-r} - U) B C^r \rightarrow 0 \quad \text{as } k \rightarrow \infty$$

which completes the proof.

Proof of Result 1. Without loss of generality, we shall assume ξ, η normalized such that $\langle\langle \xi, \eta \rangle\rangle = 1$. Define $\mathbf{z}^* = (z_1^*, \dots, z_l^*, z_{l+1}^*, \dots, z_n^*)$ taking $z_i^* = \xi_i$, $i = 1, 2, \dots, l$, and $(z_{l+1}^*, \dots, z_n^*) = \xi B(I-C)^{-1}$. It is easy to verify that $\mathbf{z}^* L = \mathbf{z}^*$. Under the assumption that $B(I-C)^{-1}$ has no null columns,

we see that the vector $\mathbf{z}^* > 0$ (has all positive components). Throughout the proof, we shall use the absolute value norm $\|\cdot\|$ weighted by the components of \mathbf{z}^* defined explicitly by $\|\mathbf{y}\| = \sum_{i=1}^n z_i^* |y_i|$ for $\mathbf{y} = (y_1, \dots, y_n)$.

Consider the Taylor expansion of T about $\mathbf{0}$ evaluated at a population state $\mathbf{x} = \delta\mathbf{v} > \mathbf{0}$, where $\delta = \|\mathbf{x}\|$ is small enough. Thus,

$$T\mathbf{x} = \delta L\mathbf{v} + \delta^2 \mathbf{Q}(\mathbf{v}) + o(\delta^2),$$

where $\mathbf{Q}(\mathbf{v}) = (Q_1(\mathbf{v}), \dots, Q_n(\mathbf{v}))$ represents the quadratic part with $\mathbf{v} = (v_1, \dots, v_n)$, i.e.,

$$Q_i(\mathbf{v}) = \frac{1}{2} \sum_{\lambda, \mu=1}^n \frac{\partial^2 U_i(\mathbf{0})}{\partial x_\lambda \partial x_\mu} v_\lambda v_\mu \quad \text{for } i = 1, \dots, n.$$

Therefore, the iterates of T are given by

$$T^k \mathbf{x} = \delta L^k \mathbf{v} + \delta^2 \sum_{r=0}^{k-1} L^{k-1-r} \mathbf{Q}(L^r \mathbf{v}) + o(\delta^2).$$

Taking the scalar product with \mathbf{z}^* in both sides yields

$$\|T^k \mathbf{x}\| = \delta + \delta^2 \sum_{r=0}^{k-1} \langle \mathbf{z}^*, \mathbf{Q}(L^r \mathbf{v}) \rangle + o(\delta^2)$$

(note that all the components of $T^k \mathbf{x}$ are necessarily nonnegative). Then

$$\|T^{k+1} \mathbf{x}\| - \|T^k \mathbf{x}\| = \delta^2 \langle \mathbf{z}^*, \mathbf{Q}(L^k \mathbf{v}) \rangle + o(\delta^2). \quad (\text{A.1})$$

It should be noted that the function $o(\delta^2)$ may depend on k . Since $L^k \rightarrow M$ as $k \rightarrow \infty$ and \mathbf{Q} is continuous, we have $\mathbf{Q}(L^k \mathbf{v}) \rightarrow \mathbf{Q}(M\mathbf{v})$ as $k \rightarrow \infty$ uniformly over the compact section $\mathcal{R} = \{\mathbf{v}; \|\mathbf{v}\| = 1\}$. The evaluation of $M\mathbf{v}$ is a multiple of $\boldsymbol{\eta}$ in the first l coordinates and vanishes identically in the remaining $n-l$ coordinates. Explicitly,

$$M\mathbf{v} = \begin{pmatrix} \langle \boldsymbol{\xi}, \mathbf{v}^{(1)} + B(I-C)^{-1} \mathbf{v}^{(2)} \rangle \boldsymbol{\eta} \\ \mathbf{0} \end{pmatrix}, \quad (\text{A.2})$$

where $\mathbf{v}^{(1)} = (v_1, \dots, v_l)$, $\mathbf{v}^{(2)} = (v_{l+1}, \dots, v_n)$.

It follows from (A.2) that

$$\begin{aligned} \langle \mathbf{z}^*, \mathbf{Q}(M\mathbf{v}) \rangle &= \langle \mathbf{z}^*, \mathbf{Q}(\boldsymbol{\eta}) \rangle [\langle \boldsymbol{\xi}, \mathbf{v}^{(1)} + B(I-C)^{-1} \mathbf{v}^{(2)} \rangle]^2 \\ &= \langle \mathbf{z}^*, \mathbf{Q}(\boldsymbol{\eta}) \rangle |\langle \mathbf{z}^*, \mathbf{v} \rangle|^2 \\ &= \langle \mathbf{z}^*, \mathbf{Q}(\boldsymbol{\eta}) \rangle \|\mathbf{v}\|^2 \\ &= \langle \mathbf{z}^*, \mathbf{Q}(\boldsymbol{\eta}) \rangle. \end{aligned}$$

Refer from (3) the notation

$$2\mathbf{Q}(\boldsymbol{\eta}) = (\theta_1, \dots, \theta_l; \theta_{l+1}, \dots, \theta_n) = (\boldsymbol{\theta}^{(1)}, \boldsymbol{\theta}^{(2)})$$

so that by the determination of \mathbf{z}^* we have

$$\begin{aligned} 2\langle\langle \mathbf{z}^*, \mathbf{Q}(\boldsymbol{\eta}) \rangle\rangle &= \langle\langle \boldsymbol{\xi}, \boldsymbol{\theta}^{(1)} \rangle\rangle + \langle\langle \boldsymbol{\xi} B(I - C)^{-1}, \boldsymbol{\theta}^{(2)} \rangle\rangle \\ &= \langle\langle \boldsymbol{\xi}, \boldsymbol{\theta}^{(1)} + B(I - C)^{-1} \boldsymbol{\theta}^{(2)} \rangle\rangle = S, \end{aligned}$$

and the last equation is the definition of S .

The foregoing analysis produces in (A.1) for k large and $\mathbf{x} = \delta \mathbf{v}$ the equation

$$\|T^{k+1}\mathbf{x}\| - \|T^k\mathbf{x}\| = \frac{S}{2} \delta^2 + o(\delta^2), \quad (\text{A.3})$$

the small order term $o(\delta^2)$ generally depending on k .

Case (i), $S < 0$. We can find an integer k_0 and ε positive such that

$$\|T^{k_0+1}\mathbf{x}\| - \|T^{k_0}\mathbf{x}\| < \frac{S}{4} \|\mathbf{x}\|^2 < 0 \quad (\text{A.4})$$

as soon as $\|\mathbf{x}\| < \varepsilon$. By continuity of T at $\mathbf{0}$, there exists $0 < \varepsilon' < \varepsilon$ such that $\|T^r\mathbf{x}\| < \varepsilon$ for $r = 1, \dots, k_0$ if $\|\mathbf{x}\| < \varepsilon'$. For such \mathbf{x} , it follows recursively on the basis of (A.4) that the sequence $\|T^k\mathbf{x}\|$, $k = 0, 1, 2, \dots$, is bounded by ε and decreasing for $k \geq k_0$. But then the inequalities

$$\|T^{k_0+r+1}\mathbf{x}\| - \|T^{k_0+r}\mathbf{x}\| < \frac{S}{4} \|T^r\mathbf{x}\|^2 < 0$$

for all $r \geq 0$ are only compatible with the convergence of $\|T^k\mathbf{x}\|$ to zero, that is, $T^k\mathbf{x} \rightarrow \mathbf{0}$ as $k \rightarrow \infty$.

Case (ii), $S > 0$. One can find an integer k_0 such that

$$\|T^{k_0+1}\mathbf{x}\| - \|T^{k_0}\mathbf{x}\| > 0$$

as soon as $\|\mathbf{x}\|$ is small enough. Assume that $T^k\mathbf{y} \rightarrow \mathbf{0}$ as $k \rightarrow \infty$ for an initial population state $\mathbf{y} \neq \mathbf{0}$. Then we should have

$$\|T^{k_0+r+1}\mathbf{y}\| > \|T^{k_0+r}\mathbf{y}\| > 0$$

for r large enough (the last inequality emanating from the fact that $T\mathbf{x} \neq \mathbf{0}$ if $\mathbf{x} \neq \mathbf{0}$), but this precludes convergence to $\mathbf{0}$.

Remark. Assume $\rho(L) \neq 1$ and $\mathbf{z}^* > \mathbf{0}$ such that $\mathbf{z}^*L = \rho(L)\mathbf{z}^*$. Define the norm $\|\cdot\|$ as in the previous proof with respect to this \mathbf{z}^* . Expanding $T\mathbf{x}$ about $\mathbf{0}$ for a population state \mathbf{x} and taking the scalar product with \mathbf{z}^* yields

$$\|T\mathbf{x}\| = \rho(L)\|\mathbf{x}\| + o(\|\mathbf{x}\|).$$

Thus, T is locally contracting or strongly repelling according to $\rho(L) < 1$ or $\rho(L) > 1$, respectively.

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