

Evolutionary stability in strategic models of single-locus frequency-dependent viability selection

R. Cressman^{1,*}, J. Hofbauer², W.G.S. Hines³

¹ Department of Mathematics, Wilfrid Laurier University, Waterloo, Ontario, Canada N2L 3C5

² Institut für Mathematik, Universität Wien, A-1090 Wien, Austria

³ Department of Mathematics and Statistics, University of Guelph, Guelph, Ontario, Canada N1G 2W1

Received 30 June 1994; received in revised form 7 June 1995

Abstract. The dynamic stability of an evolutionarily stable strategy (ESS) is analyzed for a diploid species under individual viability selection. An individual's viability depends on the genotypic frequencies at a single autosomal locus through a payoff matrix determined by phenotypic behaviours (i.e. strategies). It is shown that an ESS of this payoff matrix is dynamically stable if there are at most three alleles – an intuitive result that strengthens the importance of static game-theoretic methods in genetic models.

Key words: Evolutionary stability – Frequency-dependent selection

1 Introduction

Evolutionary game theory was originally introduced to develop intuitive static stability conditions that explain the evolutionary outcome of a single species undergoing frequency-dependent selection. Thus, a population consisting of two behavior types, each of which does well when rare, can be expected to evolve to a polymorphic state where both types persist. In such a model, evolutionary game theory should predict the eventual balance between the frequencies of the two types. On the other hand, frequency-dependent selection can also be considered as a dynamic population genetic model where an individual's genotype determines its behavior type and thereby its frequency-dependent fitness. An important question is whether the static stability results of evolutionary game theory are consistent with the dynamic stability of the genetic model.

In fact, it is important to know when both approaches give the same result and when they do not. In the former case, genetic considerations can be ignored whereas they cannot in the latter. As an example, Maynard Smith

* Author for correspondence (e-mail: rressma@mach1.wlu.ca)

(1981) showed that, in a randomly mating population where an individual's frequency-dependent viability is determined at a single diallelic locus whose genotypes specify two possible behavior types, the population will evolve in such a way that its mean strategy (i.e. expected behavior of a random individual) is as close as possible given the genetic constraints to an evolutionarily stable strategy (ESS). (That is, the eventual equilibrium allele frequencies at this locus cannot be altered to continuously obtain mean strategies closer to the ESS.) In particular, a population that is currently at an ESS will return to it if the allelic frequencies are slightly perturbed. In this paper, the concept of evolutionary stability in general genetic systems will refer to this latter type of stability under small perturbations. Thus, Maynard Smith (1981) showed the evolutionary stability of an ESS for single-locus, two-allele, frequency-dependent viability selection with two possible behavior types.

The evolutionary stability of an ESS in more complex genetic settings (e.g. multi-allele, multi-locus, multi-behavior models) has been examined by a number of researchers including Hofbauer et al (1982), Eshel (1982, 1991), Lessard (1984, 1988), Hines and Bishop (1984), Cressman and Hines (1984), Thomas (1985a, b), Hofbauer and Sigmund (1988), Cressman (1988, 1992), Gayley and Michod (1990), Hammerstein and Selten (1992), Hines (1994a, b), Brooks (1994). Some of these authors have claimed the evolutionary stability of an ESS in general models and others have claimed evolutionary stability does not always occur at an ESS. This extensive literature has created some confusion as to the accepted game-theoretic model of frequency-dependent selection and the precise meaning of evolutionary stability. Section 2 below summarizes what we call the standard single-species model of frequency-dependent viability selection at a single locus. It also defines the concept of evolutionary stability. The notation adopted follows most closely that of Cressman (1992).

In this standard model, it is generally agreed that the simplest case in which an ESS may fail to correspond to evolutionary stability has three alleles. The main results for this paper (Sects. 4 and 6) combine to prove no such failure occurs. That is, we prove the evolutionary stability of an ESS for single-locus, three-allele, frequency-dependent viability selection.

The method of proof uses techniques (linearizations, Lyapunov functions, centre manifolds) from the theory of dynamical systems that also apply to complex genetic models. The results give strong support to the conjecture that static evolutionary game theory models and dynamic genetic models are consistent for single-locus systems near an ESS. At the same time, a numeric example in Sect. 5 shows evolutionary stability may be a very localized concept in that small perturbations may move the population into a region of instability where genetic considerations are crucial.

2 The single-locus strategic model of frequency-dependent viability selection

The model assumes there is a large population of diploid individuals whose sex-independent viabilities (i.e. survival to adulthood) are determined by their

genotype at the single locus as well as the frequency of all genotypes. Adults mate randomly with all mating pairs having the same fecundity and their offspring are produced through Mendelian segregation in equal sex ratio. Moreover, in the standard strategic model, the individual's genotype specifies its behavior (i.e. strategy or phenotype) and, through a payoff matrix, its frequency-dependent viability.

Suppose there are n possible alleles A_1, \dots, A_n at the single diploid locus and N possible pure strategies exhibited by the population. Let $p_i(t)$ be the frequency of allele A_i in the adult population at time t . By assumption, offspring are produced in Hardy-Weinberg proportions. Let $S_{ij} = S_{ji}$ denote the strategy of $A_i A_j$. Then S_{ij} may be one of the N pure strategies or a mixed strategy in the $N - 1$ dimensional strategy simplex

$$\Delta^N = \left\{ (s_1, \dots, s_N) \mid \sum_{k=1}^N s_k = 1, s_k \geq 0 \right\}.$$

An individual mixed strategy (s_1, \dots, s_N) may be interpreted as saying that this individual has probability s_k of exhibiting the k^{th} pure strategy at any particular instant. In this notation, the k^{th} pure strategy is the unit vector $e_k = (0, \dots, 0, 1, 0, \dots, 0) \in \Delta^N$ that has 1 in the k^{th} component. The population mean strategy before selection is then given in terms of $p \in \Delta^n$ (the allele-frequency simplex) by $S(p)$ (or simply S) where

$$S = \sum_{i,j=1}^n p_i p_j S_{ij} \in \Delta^N. \quad (2.1)$$

In the standard model, the viability of an $A_i A_j$ individual is given by $S_{ij} \cdot AS$ where A is the $N \times N$ payoff matrix with entries a_{kl} and the dot product $u \cdot Av = \sum_{k,l=1}^N u_k a_{kl} v_l$ is the usual inner product of vectors in \mathbf{R}^N . The standard continuous dynamic is

$$\dot{p} = p_i (S^i - S) \cdot AS \quad (2.2)$$

where the derivative on the left is with respect to time and $S^i = \sum_j p_j S_{ij}$ is the effective strategy of allele A_i .

As mentioned in the Introduction, the above model is given in the same notation as Cressman (1992). However, the dynamic (2.2) is equivalent to that analyzed in the references listed there that consider single-locus continuous evolution. It also approximates well the discrete generation single-locus dynamic of the other references when generation time is short or selection is weak. These properties are discussed further in Cressman (1988, 1992) where it is also pointed out that a special case of (2.2) with $N = 2$ gives the classical model (Fisher, 1930) of frequency-independent natural selection.

The map $p \rightarrow S(p)$ given by (2.1) from the allele-frequency simplex Δ^n to the strategy simplex Δ^N is fundamental to the strategic model. Through (2.1), the system of ordinary differential equations (2.2) on Δ^n induces trajectories in Δ^N . It is the limiting properties of these trajectories that evolutionary game theory

should predict. In particular, the theory concerns the evolutionary stability of (2.2) according to the following definition.

Definition 2.1. (a) Suppose $p^* \in \Delta^n$ is an equilibrium of (2.2) with $S^* = S(p^*) \in \Delta^N$. There is evolutionary stability at p^* if, for every neighbourhood U of p^* , there is some neighbourhood V of p^* such that $p(t)$ remains in U and $S(p(t))$ evolves to S^* whenever $p \in \Delta^n$ is initially in V .

(b) Suppose $S^* \in \Delta^N$ and $\{p^* | S(p^*) = S^*\} \neq \emptyset$. There is evolutionary stability at S^* if there is evolutionary stability at p^* whenever $S(p^*) = S^*$.

The reader will recognize part (a) as requiring more than Lyapunov stability at p^* . On the other hand, evolutionary stability at p^* is weaker than the concept of local asymptotic stability (l.a.s.) defined as follows and used extensively in the paper.

Definition 2.2. An equilibrium $p^* \in \Delta^n$ is locally asymptotically stable (l.a.s.) if, for every neighbourhood U of p^* , there is some neighbourhood V of p^* such that $p(t)$ remains in U and evolves to p^* whenever $p \in \Delta^n$ is initially in V .

For the rest of this section, we will analyze a two-allele, two-strategy example based on Maynard Smith (1981). The example is intended to clarify the above dynamic and stability concepts. Let the 2×2 payoff matrix be a typical Hawk-Dove game with

$$A = \begin{bmatrix} -1 & 2 \\ 0 & 1 \end{bmatrix}. \tag{2.3}$$

It is well-known that the only ESS of this game is $S^* = (1/2, 1/2) \in \Delta^N$ where $N = 2$. Take the overdominant genotypic strategies as $S_{11} = (1/9, 8/9)$, $S_{22} = (1, 0)$ and $S_{12} = (0, 1)$. With $p_1 =$ the frequency of allele A_1 , the mean strategy corresponding to $p = (p_1, 1 - p_1) \in \Delta^n$ where $n = 2$ is, from (2.1),

$$\begin{aligned} S &= p_1^2 S_{11} + (1 - p_1)^2 S_{22} + 2p_1(1 - p_1) S_{12} \\ &= (1/9 p_1^2 + (1 - p_1)^2, 8/9 p_1^2 + 2p_1(1 - p_1)). \end{aligned} \tag{2.4}$$

The map (2.1) can be represented as $p_1 \rightarrow 1/9 p_1^2 + (1 - p_1)^2$ which is the parabola of Fig. 1.

The one-dimensional dynamic (2.2) becomes (after a short calculation using $S^1(p) = p_1 S_1 + (1 - p_1) S_{12}$, (2.3) and (2.4)),

$$\begin{aligned} \dot{p}_1 &= p_1(1 - p_1)(10/9 p_1 - 1)(1, -1) \cdot AS \\ &= p_1(1 - p_1)(10/9 p_1 - 1)(10/3 p_1 - 1)(-2/3 p_1 + 1). \end{aligned} \tag{2.5}$$

The equilibria with $0 \leq p_1 \leq 1$ (namely, $p_1 = 0, .3, .9, 1$) are also indicated in Fig. 1 along with their stability properties. There is evolutionary stability at $p_1^* = .3$ and $p_1^* = 1$ since both equilibria are l.a.s. Furthermore, from (2.4), $S(p_1^* = .3) = (1/2, 1/2)$ is the ESS S^* where there is evolutionary stability. On the other hand, there is a no evolutionary stability at $S(p_1^* = 1) = (1/9, 8/9)$ since $S(p_1 = .8) = (1/9, 8/9)$ as well and this is not an equilibrium of (2.5).

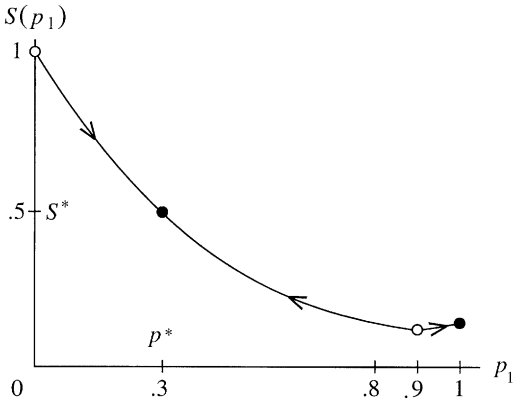


Fig. 1. The map $p_1 \rightarrow 1/9 p_1^2 + (1 - p_1)^2$ given by (2.4). The equilibria of (2.5) are indicated by circles on this parabola (empty circles are unstable and solid circles are stable). The dynamic flow is also indicated on the parabola from which it is clear that non-equilibria mean strategies are evolving towards the ESS, S^*

From this example, it may seem that l.a.s. and evolutionary stability at p^* are the same in general. However, when $n > 2$, examples abound of equilibria of (2.2) that are not isolated (i.e. every neighbourhood of p^* contains other equilibria) and so cannot be l.a.s. These equilibria may well have evolutionary stability, especially if they correspond to an ESS. Finally, it should be noted that the appealing picture of the mean strategy evolving to the ESS in Fig. 1 does not generalize very well to $N > 2$. The intuitive geometric properties of the flow in these higher dimensional strategy simplices (Hines and Bishop, 1984) are potentially misleading.

3 Linearization about a p^* corresponding to an ESS

Sections 3, 4 and 6 analyze exclusively the evolutionary stability of an ESS. Although the same techniques are relevant for non-ESS equilibria, certain mathematical complications arise in their application that would obscure the main point of this paper. For the convenience of the reader, we include the following standard definition of an ESS for matrix games.

Definition 3.1. A strategy $S^* \in \Delta^N$ is an ESS if

- (i) $S \cdot AS^* \leq S^* \cdot AS^*$ for all $S \in \Delta^N$, and
- (ii) $S \cdot AS < S^* \cdot AS$ for all $S \neq S^*$ for which there is equality in (i).

For these three sections assume $p^* \in \Delta^n$ satisfies $S(p^*) = S^*$ where S^* is an ESS in Δ^N and denote the corresponding effective strategy of allele i , $S^i(p^*)$, by $S^{*i} \in \Delta^N$. It turns out that evolutionary stability is closely tied to the relationships among the vectors S^{*1}, \dots, S^{*n} . For instance, if these vectors are linearly independent, there is evolutionary stability at p^* (Theorems 4.1 and 6.2 below). This result is previously known and its most common proof uses the following technique of linearization about p^* .

First, we show p^* is an equilibrium of (2.2). Since S^* is an ESS, $(S^{*i} - S^*) \cdot AS^* \leq 0$ and since $\sum_{i=1}^n \dot{p}_i = \sum p_i (S^i(p) - S(p)) \cdot AS(p) = (S - S^*) \cdot AS = 0$, $(S^{*i} - S^*) \cdot AS^* = 0$ whenever $p_i^* \neq 0$. Thus, from (2.2), $\dot{p}_i = 0$ for all i when $p = p^*$.

To linearize about p^* , let $p_i = p_i^* + x_i$ where $x = (x_1, \dots, x_n) \in X^n$ and $X^n = \{x \in \mathbf{R}^n \mid \sum x_i = 0\}$. Then

$$\begin{aligned} \dot{x}_i &= p_i(S^i - S) \cdot AS \\ &= (p_i^* + x_i) \left(\sum_j (p_j^* + x_j) S_{ij} - \sum_{k,l} (p_k^* + x_k)(p_l^* + x_l) S_{kl} \right) \\ &\quad \cdot A \sum_{k,l} (p_k^* + x_k)(p_l^* + x_l) S_{kl} \\ &= (p_i^* + x_i) \left(\sum_j p_j^* S_{ij} - \sum_{k,l} p_k^* p_l^* S_{kl} \right) \cdot A \sum_{k,l} p_k^* p_l^* S_{kl} \\ &\quad + p_i^* \left[\left(\sum_j x_j S_{ij} - 2 \sum p_k^* x_l S_{kl} \right) \cdot A \sum_{k,l} p_k^* p_l^* S_{kl} \right. \\ &\quad \left. + \left(\sum_j p_j^* S_{ij} - \sum p_k^* p_l^* S_{kl} \right) \cdot A 2 \sum p_k^* x_l^* S_{kl} \right] \\ &\quad + \text{higher order (nonlinear) terms} \\ &= x_i (S^{*i} - S^*) \cdot AS^* + p_i^* \left[\left(\sum_j x_j S_{ij} - 2 \sum_l x_l S^{*l} \right) \right. \\ &\quad \left. \cdot AS^* + 2(S^{*i} - S^*) \cdot A \sum_l x_l S^{*l} \right] + \dots \\ &= \sum_j L_{ij} x_j + \dots \end{aligned}$$

where L is the $n \times n$ matrix with entries

$$L_{ij} = \begin{cases} \delta_{ij} (S^{*i} - S^*) \cdot AS^* & \text{if } p_i^* = 0 \\ p_i^* [(S_{ij} - 2S^{*j}) \cdot AS^* + 2(S^{*i} - S^*) \cdot AS^{*j}] & \text{if } p_i^* \neq 0 \end{cases} \quad (3.1)$$

Here δ_{ij} is the Kronecker delta function that is 1 if $i = j$ and 0 otherwise.

The equilibrium, p^* , will be l.a.s. if all eigenvalues of L restricted to its invariant $n - 1$ dimensional subspace X^n have negative real part. The form of L in (3.1) suggests stability be analyzed in two steps; the first when $p_i^* > 0$ for all i so that p^* is in the interior of Δ^n (this will be thought of as the (completely) polymorphic case) is carried out in Sect. 4; the second when at least one allele is absent at p^* so that p^* is on the boundary of Δ^n as in Sect. 6.

4 Evolutionary stability at an interior p^* corresponding to an ESS

For this section, we assume $p_i^* > 0$ for all i and $S(p^*) = S^*$ is an ESS. The method to prove evolutionary stability depends on how the vectors S^{*1}, \dots, S^{*n} are related.

Theorem 4.1. *If $\{S^{*1}, \dots, S^{*n}\}$ is a linearly independent set of (mixed) strategy vectors in Δ^N , then p^* is l.a.s.*

Proof. Introduce the Shahshahani inner product (Akin, 1979) on X^n given by

$$\langle x, y \rangle = \sum_i x_i y_i / p_i^* .$$

From (3.1),

$$\begin{aligned} \langle x, Lx \rangle &= \sum_{ij} x_i L_{ij} x_j / p_i^* = \sum_{ij} x_i \left[\left(S_{ij} x_j - 2 \sum_k x_k S^{*k} \right) \right. \\ &\quad \left. \cdot AS^* + 2(S^{*i} - S^*) \cdot A \sum_k x_k S^{*k} \right] . \end{aligned}$$

Since S^* is a strict convex combination of $\{S^{*i}\}$ and of $\{S_{ij}\}$, $\text{supp}(S^{*i}) \subset \text{supp}(S^*)$ and $\text{supp}(S_{ij}) \subset \text{supp}(S^*)$ for all i and j where the support of $S = (s_1, \dots, s_N) \in \Delta^N$ is $\text{supp}(S) = \{k | s_k > 0\}$. From Definition 3.1, $S^{*i} \cdot AS^* = S^* \cdot AS^* = S_{ij} \cdot AS^*$ and so

$$\langle x, Lx \rangle = 2 \sum_i x_i S^{*i} \cdot A \sum_j x_j S^{*j} .$$

For all $x \in X^n$, $\xi = \sum_i x_i S^{*i}$ is in the span of $\{S - S^* | S \in \Delta^N, \text{supp} S \subset \text{supp} S^*\}$ on which A is negative definite by Definition 3.1. Thus $\langle x, Lx \rangle \leq 0$ for all $x \in X^n$ with equality if and only if $\xi = 0$. The linear independence of $\{S^{*i}\}$ implies $\langle x, Lx \rangle < 0$ unless $x = 0$. Thus all eigenvalues of L restricted to X^n have negative real part and so p^* is l.a.s. \square

The linear independence of $\{S^{*1}, \dots, S^{*n}\}$ can be regarded as an extreme case. Another possibility is that all these vectors may be equal (i.e. $S^{*i} = S^*$ for all i). In this latter extreme, p^* is called a genetic equilibrium (Hofbauer and Sigmund, 1988) after a similar definition in Lessard (1984) when $N = 2$. The following proof of evolutionary stability at a genetic equilibrium follows the method of Lyapunov functions suggested by Hofbauer and Sigmund (1988, Exercise 28.4.2).

Theorem 4.2. *If p^* is a genetic equilibrium, then there is evolutionary stability at p^* .*

Proof. A local Lyapunov function $V : \Delta^n \rightarrow \mathbf{R}$ for the equilibrium p^* is one that has p^* as an isolated local minimum and $\dot{V}(p) \leq 0$ for all p in some neighbourhood of p^* . As an example, $V(p) = \frac{1}{2} \sum_i x_i^2 / p_i^*$ is a local Lyapunov

function for the proof of Theorem 4.1 since V has a unique global minimum at $p = p^*$ and

$$\dot{V}(p) = \sum_i x_i \dot{x}_i / p_i^* = \langle x, Lx \rangle + \text{higher order terms} < 0 \tag{4.1}$$

for all p sufficiently close (but not equal) to p^* . In fact, $V(p)$ is a strict local Lyapunov function (since $\dot{V}(p) < 0$ here) and this implies p^* is l.a.s. Unfortunately, this $V(p)$ fails at a genetic equilibrium where $\langle x, Lx \rangle = 0$ for all $x \in X^n$ and the higher order terms in (4.1) may be positive.

It turns out that a suitable Lyapunov function at p^* is

$$V(p) = - \sum_i p_i^* \ln p_i . \tag{4.2}$$

In fact, the Taylor expansion of $V(p)$ about p^* , given by

$$\begin{aligned} V(p^* + x) &= - \sum_i p_i^* \left(\ln p_i^* + \frac{1}{p_i^*} x_i - \frac{1}{2(p_i^*)^2} x_i^2 + \dots \right) \\ &= - \sum_i p_i^* \ln p_i^* + \frac{1}{2} \sum_i x_i^2 / p_i^* - \dots \end{aligned}$$

shows that the Lyapunov function for (4.1) is the quadratic approximation of (4.2) up to a constant which implies (4.2) also proves Theorem 4.1. From (2.2) and (4.2),

$$\begin{aligned} \dot{V}(p) &= - \sum_i p_i^* \dot{p}_i / p_i \\ &= - \sum_i p_i^* (S^i(p) - S(p)) \cdot AS(p) \\ &= - \sum_i p_i^* \left(S^{*i} + \sum_j x_j S_{ij} - \left(S^* + 2 \sum_j x_j S^{*j} + \sum_{kl} x_k x_l S_{kl} \right) \right) \\ &\quad \cdot A \left(S^* + 2 \sum_j x_j S^{*j} + \sum_{kl} x_k x_l S_{kl} \right) \\ &= (\sum x_j S^{*j} + \sum x_k x_l S_{kl}) \cdot A(2 \sum x_j S^{*j} + \sum x_k x_l S_{kl}) \\ &= (\xi + \eta) \cdot A(2\xi + \eta) \end{aligned}$$

where $\xi = \sum_i x_i S^{*i}$ and $\eta = \sum_{i,j} x_i x_j S_{ij}$.

In the presence of a genetic equilibrium, p^* , $\xi = 0$ since $S^{*i} = S^*$ for all i and $x \in X^n$. Thus, $\dot{V}(p) = \eta \cdot A\eta \leq 0$ with equality if and only if $\eta = 0$. Furthermore, given any initial p in the interior of Δ^n , $V(p)$ is a decreasing nonnegative function of time and so $\lim_{t \rightarrow \infty} V(p(t))$ exists. Since the trajectory of (2.2) is contained in the compact set Δ^n , the limit set of this trajectory is nonempty and any point $p(\infty)$ in the limit set satisfies $\eta = 0$. Then $S(p(\infty)) = S^* + 2\xi + \eta = S^*$ and so the trajectory induced in Δ^N evolves to S^* . Moreover, by redoing the proof with p^* replaced by $p(\infty)$, it is clear the

trajectory evolves to the unique limit point $p(\infty)$ and that $p(t)$ remains close to p^* since $V(p)$ has a unique global minimum with respect to the interior of Δ^n . \square

It should be noted here that the above proof also shows that S^* is globally stable in the sense that, if there is a genetic equilibrium in the interior of Δ^n , any initial polymorphic population evolves to mean strategy S^* . It should also be emphasized here that Theorems 4.1 and 4.2 apply to frequency-dependent viability selection models with any number of alleles and not only to the case $n = 3$ that is the main focus of this paper. In particular, Theorems 4.1 and 4.2 combine with the corresponding results in Sect. 6 for boundary p^* to prove the evolutionary stability of an ESS in the diallelic model (i.e. when $n = 2$). Other, more straightforward, proofs for $n = 2$ (for example, Hofbauer and Sigmund (1988, Section 28.2) use Shahshahani gradients) are possible but the one presented here seems to be best for generalization to multi-alleles.

For $n > 2$, Theorems 4.1 and 4.2 are the two extreme cases for the effective strategies S^{*1}, \dots, S^{*n} . Intermediate are situations where these strategies are linearly dependent but not all equal. As in the proof of Theorem 4.1, the linearization (3.1) of (2.2) satisfies

$$\begin{aligned} \langle x, Ly \rangle &= 2 \sum_{ij} x_i (S^{*i} - S^*) \cdot AS^{*j} y_j \\ &= 2 \xi_x \cdot A \xi_y \end{aligned}$$

where $x, y \in X^n$ and $\xi_x \equiv \sum x_i S^{*i}$. Let $C = \{x \in X^n \mid \xi_x = 0\}$. Then $\langle x, Ly \rangle = 0$ whenever x or y are in C . Thus, C and its orthogonal complement in X^n with respect to the Shahshahani inner product are both invariant subspaces of L . Since L is negative definite on the orthogonal complement, C is the zero eigenspace for the linearized dynamic that is tangent to an invariant centre manifold (Wiggins, 1990) for the dynamic (2.2). The stability of p^* depends on the analysis of higher order terms for this manifold. The analysis is quite difficult in general as can be seen by that carried out in the remainder of this section for $n = 3$.

Theorems 4.1 and 4.2 combine to prove the evolutionary stability of an interior p^* for the 3-allele model except in the situation where $\{S^{*1}, S^{*2}, S^{*3}\}$ is linearly dependent but not all equal to S^* . That is, by permuting indices if necessary, we may assume for the remainder of this section that $S^{*1} \neq S^*$ and $S^{*1} + a_2 S^{*2} + a_3 S^{*3} = 0$ where $a = (1, a_2, a_3)$ is automatically on X^3 .

Let us first determine the eigenvalues of (3.1). From the above discussion, a is an eigenvector of L with eigenvalue 0. For the other eigenvector, note that S^{*1}, S^{*2}, S^{*3} and S^* all lie on one line in Δ^N . Define $b \in X^3$ by

$$b_i (S^{*1} - S^*) = p_i^* (S^{*i} - S^*) \tag{4.3}$$

Then b is an eigenvector of L with negative eigenvalue $2 \langle b, b \rangle (S^{*1} - S^*) \cdot A(S^{*1} - S^*)$ that is orthogonal to a with respect to the Shahshahani

inner product since

$$\begin{aligned}
 e_i \cdot Lb &= 2b_i(S^{*1} - S^*) \cdot A(b_1(S^{*1} - S^*) + b_2(S^{*2} - S^*) + b_3(S^{*3} - S^*)) \\
 &= 2b_i(b_1^2/p_1^* + b_2^2/p_2^* + b_3^2/p_3^*)(S^{*1} - S^*) \cdot A(S^{*1} - S^*) \\
 &= b_i 2 \langle b, b \rangle (S^{*1} - S^*) \cdot A(S^{*1} - S^*) \\
 \langle a, b \rangle (S^{*1} - S^*) \cdot A(S^{*1} - S^*) &= \left(\sum_i a_i b_i / p_i^* \right) (S^{*1} - S^*) \cdot A(S^{*1} - S^*) \\
 &= \left(\sum_i a_i (S^{*i} - S^*) \right) \cdot A(S^{*1} - S^*) \\
 &= 0.
 \end{aligned}$$

These eigenvectors when $n = 3$ imply the dynamic (2.2) on Δ^3 has a one-dimensional invariant centre manifold (c.m.) that determines the stability of p^* . In particular, if p^* is l.a.s. with respect to this c.m., then p^* is l.a.s. for (2.2). From Wiggins (1990) (see also Cressman, 1992), the c.m. can be parameterized as

$$p(x) = p^* + x(1, a_2, a_3) + h(x)(b_1, b_2, b_3)$$

where $h(x)$ is a continuously differentiable function of x that satisfies $h(0) = 0$ and $h'(0) = 0$. In fact, given any positive integer k , we can assume our c.m. has an associated h with continuous derivatives up to order k . The power series expansion of $h(x)$ into $y = h(x) = \alpha x^2 + \beta x^3 + \dots$ can be found to any order by equating the corresponding coefficients of powers of x in the differential equation

$$\dot{y} = h'(x)\dot{x} \tag{4.4}$$

that $h(x)$ must satisfy (Wiggins, 1990) where $h'(x) = 2\alpha x + 3\beta x^2 + \dots$. The substitution of this power series for y into \dot{x} produces an autonomous differential equation in x whose stability at p^* is determined by its first nonzero coefficient. The method is illustrated in the proof of the following theorem where earlier notation is generalized to

$$\xi_a = \sum a_i S^{*i}, \quad \eta_a = \sum a_i a_j S_{ij}, \quad \eta_{ab} = \sum a_i b_j S_{ij} \tag{4.5}$$

for any vectors $a, b \in X^3$.

Theorem 4.3. *Suppose $\{a, b\}$ is an orthogonal basis of X^3 with respect to the Shahshahani inner product with $\xi_a = 0$ and $\xi_b \neq 0$.*

- (a) *If $\{\xi_b, \eta_a\}$ is linearly independent in X^N , then p^* is l.a.s.*
- (b) *If $\eta_a = 0$, then there is evolutionary stability at p^* .*

Proof. (a) With respect to the orthogonal basis $\{a, b\}$ of X^3 , the dynamic (2.2) about p^* takes the form

$$\begin{aligned}
 \frac{d}{dt}(x(1, a_2, a_3) + y(b_1, b_2, b_3)) &= \dot{x}(1, a_2, a_3) + \dot{y}(b_1, b_2, b_3) \\
 &= (c_1, c_2, c_3)
 \end{aligned} \tag{4.6}$$

where the i^{th} component of $c = (c_1, c_2, c_3) \in X^3$ is given by

$$(p_i^* + a_i x + b_i y)[S^{*i} + x(S_{i1} + a_2 S_{i2} + a_3 S_{i3}) + y(b_1 S_{i1} + b_2 S_{i2} + b_3 S_{i3}) - S] \cdot A(S - S^*). \quad (4.7)$$

Also, in terms of this basis,

$$S = S^* + 2y\zeta_b + x^2\eta_a + y^2\eta_b + 2xy\eta_{ab}. \quad (4.8)$$

The orthogonality of a and b implies $\dot{x} = \langle c, a \rangle / \langle a, a \rangle$ and $\dot{y} = \langle c, b \rangle / \langle b, b \rangle$. It turns out that the proof only requires the quadratic terms of \dot{y} and the cubic terms of \dot{x} (both as functions of x). That is, from $y = \alpha x^2 + \beta x^3 + \dots$, we consider the x, y, x^2, xy, x^3 terms of $\langle c, a \rangle$ and the x, y, x^2 terms of $\langle c, b \rangle$ exclusively. These are

$$\begin{aligned} \langle c, a \rangle &= \sum_{i=1}^3 a_i (S^{*i} - S^*) \cdot A(2y\zeta_b + x^2\eta_a + 2xy\eta_{ab}) \\ &\quad + \sum_i \left(\frac{a_i^2 x}{p_i^{*2}} (S^{*i} - S^*) + a_i x (S_{i1} + a_2 S_{i2} + a_3 S_{i3}) \right) \cdot A(2y\zeta_b + x^2\eta_a) \\ &= x \left(\sum_i \frac{a_i^2 b_i}{p_i^{*2}} (S^{*1} - S^*) + \eta_a \right) \cdot A(2y\zeta_b + x^2\eta_a) \end{aligned} \quad (4.9)$$

$$\begin{aligned} \langle c, b \rangle &= \sum b_i (S^{*i} - S^*) \cdot A(2y\zeta_b + x^2\eta_a) \\ &= \zeta_b \cdot A(2y\zeta_b + x^2\eta_a). \end{aligned} \quad (4.10)$$

Substitution of $y = \alpha x^2 + \beta x^3 + \dots$ into $\dot{y} = y' \dot{x}$ produces

$$\begin{aligned} &\frac{\zeta_b \cdot A(2(\alpha x^2 + \beta x^3 + \dots)\zeta_b + x^2\eta_a)}{\langle b, b \rangle} \\ &= \frac{(2\alpha x + \beta x^2 + \dots)}{\langle a, a \rangle} \left(x \sum_i \frac{a_i^2 b_i}{p_i^{*2}} (S^{*1} - S^*) + \eta_a \right) \cdot A(2\alpha x^2 \zeta_b + x^2\eta_a). \end{aligned}$$

From the quadratic terms, $2\alpha \zeta_b \cdot A\zeta_b + \zeta_b \cdot A\eta_a = 0$. That is,

$$\alpha = -\frac{\zeta_b \cdot A\eta_a}{2\zeta_b \cdot A\zeta_b}. \quad (4.11)$$

Then, up to cubic terms,

$$\begin{aligned} \langle a, a \rangle \dot{x} &= x \left(\sum_i \frac{a_i^2 b_i}{p_i^{*2}} (S^{*1} - S^*) + \eta_a \right) \cdot A \left(-2 \frac{\zeta_b \cdot A\eta_a}{2\zeta_b \cdot A\zeta_b} \zeta_b + \eta_a \right) x^2 \\ &= x^3 \left(\sum_i \frac{a_i^2 b_i}{p_i^{*2}} (S^{*1} - S^*) + \eta_a \right) \cdot A \left(\frac{(\zeta_b \cdot A\zeta_b)\eta_a - (\zeta_b \cdot A\eta_a)\zeta_b}{\zeta_b \cdot A\zeta_b} \right) \\ &= x^3 \frac{\zeta_b \cdot A\zeta_b \eta_a \cdot A\eta_a - \zeta_b \cdot A\eta_a \eta_a \cdot A\zeta_b}{\zeta_b \cdot A\zeta_b} \end{aligned} \quad (4.12)$$

since $S^{*1} - S^*$ is a scalar multiple of ζ_b .

Since ξ_b and η_a are in the span of $\{S - S^* | S \in \Delta^N, \text{supp } S \subset \text{supp } S^*\}$ on which A is negative definite, the linear independence of $\{\xi_b, \eta_a\}$ implies $\xi_b \cdot A \xi_b < 0$ and

$$\xi_b \cdot A \xi_b \eta_a \cdot A \eta_a - \xi_b \cdot A \eta_a \eta_a \cdot A \xi_b > 0 . \tag{4.13}$$

Inequality (4.13) is the Schwartz inequality for the inner product given by the symmetrization of A in the case $\xi_b \cdot A \eta_a$ and $\eta_a \cdot A \xi_b$ have the same sign. Thus, from (4.12), the first nonzero coefficient of \dot{x} along the c.m. is the negative cubic term from which it follows that p^* is l.a.s.

(b) If $\eta_a = 0$, then $S(p^* + x(1, a_2, a_3)) = S^*$ from (4.8). That is, for x sufficiently close to zero, the line $x \rightarrow p^* + x(1, a_2, a_3)$ in Δ^3 consists of equilibrium points of (2.2) all of which must be in the c.m. (Cressman, 1992). Furthermore, by centre manifold theory (Wiggins, 1990), given a neighbourhood of p^* , any initial point sufficiently close to p^* evolves asymptotically to one of these equilibria in the neighbourhood. That is, $S(p)$ evolves to S^* and $p(t)$ remains close to p^* . □

The c.m. calculations in Theorem 4.3 simplify considerably in the case that $p^* = (1/3, 1/3, 1/3)$ and $S^{*1} = S^{*2} \neq S^*$; a case considered numerically by Hines (1994b) and Brooks (1994) for certain 3×3 payoff matrices with interior ESS at $(1/3, 1/3, 1/3)$. By Theorem 4.3, p^* is l.a.s. if $\eta_a = S_{11} + S_{22} - 2S_{12}$ and $S^{*1} - S^*$ are linearly independent (here $a = (1, -1, 0)$); a condition satisfied by Brooks' (1994) explicit example and by the numerical examples referred to by Hines (1994b) (see also Hines (1995)). Thus, these examples do not provide counterexamples to the evolutionary stability of an ESS.

On the other hand, Theorems 4.1 to 4.3 do not complete the proof of evolutionary stability of an ESS at an interior p^* when $n = 3$. In general, if ξ_b and η_a are linearly dependent in Theorem 4.3, higher order terms in the expansion of \dot{x} on the c.m. must be analyzed. It turns out in certain circumstances, terms up to order seven may be needed (see the proof of Theorem 4.5 in the Appendix). The c.m. analysis of the Appendix proves the following two theorems which then combine with Theorems 4.1 to 4.3 to give the main result, Theorem 4.6.

Theorem 4.4. *Suppose $\{a, b\}$ is an orthogonal basis of X^3 with $\xi_a = 0$ and $\xi_b \neq 0$ and that η_a is a nonzero scalar multiple of ξ_b . If $\{\xi_b, \eta_{ab}\}$ is linearly independent, then p^* is l.a.s.*

Theorem 4.5. *Take the same hypothesis as Theorem 4.4 except assume $\{\xi_b, \eta_{ab}\}$ is linearly dependent. Then*

- (a) *If $\{\xi_b, \eta_b\}$ is linearly independent, p^* is l.a.s.*
- (b) *If $\{\xi_b, \eta_b\}$ is linearly dependent, there is evolutionary stability at p^* .*

Theorem 4.6. *For the three-allele single-locus strategic model of frequency-dependent viability selection, if p^* is an interior equilibrium of (2.2) corresponding to an ESS, then there is evolutionary stability at p^* .*

5 A three-allele three-strategy example

The previous section has proved the evolutionary stability of an interior equilibrium corresponding to an ESS. In particular, by Definition 2.1, if p^* corresponds to the ESS S^* , then $S(p)$ evolves to S^* whenever p is initially sufficiently close to p^* . The purpose of this section is to demonstrate numerically that this basin of attraction may be exceedingly small and that this, in turn, may lead to the mistaken impression of evolutionary instability at p^* . The example is based on the well-known rock-scissors-paper game with three pure strategies and payoff matrix

$$\begin{pmatrix} 0 & -1 & 1 \\ 1 & 0 & -1 \\ -1 & 1 & 0 \end{pmatrix}.$$

In this form, the game has no ESS but $S^* = (1/3, 1/3, 1/3)$ is an equilibrium for the asexual model of evolutionary game theory (Hofbauer and Sigmund, 1988) around which the frequency dynamic cycles. For our purposes, the payoff matrix is modified as in Hofbauer et al. (1982) to

$$\begin{pmatrix} 1.5 & 1.5 & 1.5 \\ 1.5 & 1.5 & 1.5 \\ 1.5 & 1.5 & 1.5 \end{pmatrix} + \begin{pmatrix} 0 & -1 & 1 \\ 1 & 0 & -1 \\ -1 & 1 & 0 \end{pmatrix} + \varepsilon \begin{pmatrix} 0 & 0 & 1 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{pmatrix}$$

where $\varepsilon > 0$ and the constant matrix with entries 1.5 is included to ensure all payoffs are positive. Now S^* is an ESS and so is a global attractor for the asexual dynamic.

For the standard sexual model at a diploid locus, we need to specify the genotypic strategies S_{ij} . The symmetric choice of homozygote and heterozygote strategies in the 3-allele system of Hofbauer et al. (1982) leads to a phase portrait with evolutionary stability at $p^* = (1/3, 1/3, 1/3)$ whose basin of attraction is surrounded by three other i.a.s. interior equilibria. For our 3-allele model, let all heterozygote strategies be $(1/4, 1/4, 1/2)$ and the three homozygote strategies be $S_{11} = (1, 0, 0)$, $S_{22} = (0, 1, 0)$ and $S_{33} = (1/2, 1/2, 0)$. It is not difficult to verify that $S(p^*) = S^*$ and that $S^{*3} = S^*$ (i.e. $S^{*1} + S^{*2} - 2S^{*3} = 0$). Thus $\xi_a = 0$ and $\xi_b = S^{*1} - S^{*2} = (1/3, -1/3, 0) \neq 0$ where $a = (1, 1, -2)$ and $b = (1, -1, 0)$ form a basis of X^3 . By Theorem 4.3, there is evolutionary stability at p^* (actually p^* is i.a.s.) since $\eta_a = 3/2(1, 1, -2)$ is not a scalar multiple of ξ_b .

Figure 2 simulates the dynamic for two choices of ε . The c.m. at p^* has vertical tangent while the other (negative) eigenvalue corresponds to the horizontal direction at p^* . In this latter direction, there is a saddle equilibrium q^* that approaches p^* as ε approaches 0. For large ε , Fig. 2(a), it is clear that p^* is i.a.s. with a large basin attraction. In fact, every initial point in the interior of Δ^3 evolves to p^* except for those points lying on the trajectory joining q^* to the boundary equilibrium $(1, 0, 0)$ that is degenerate on each of its

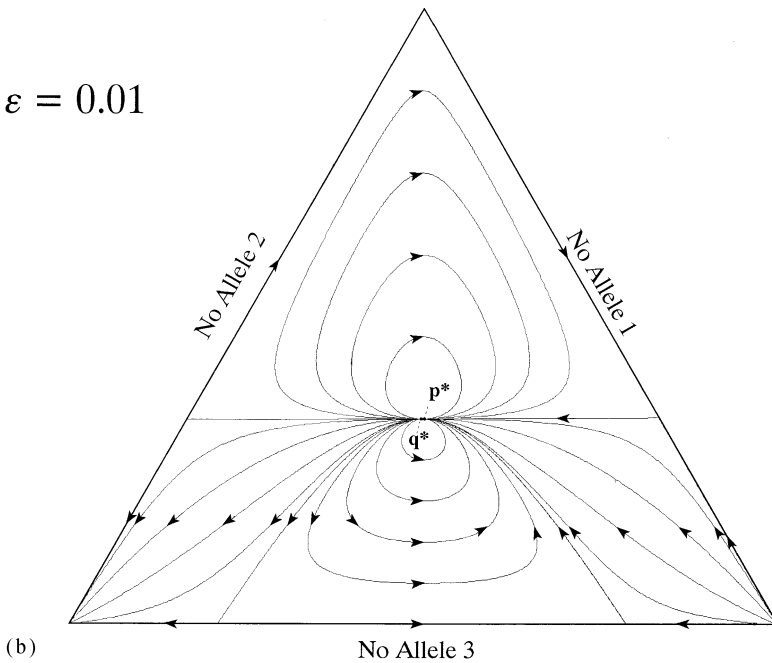
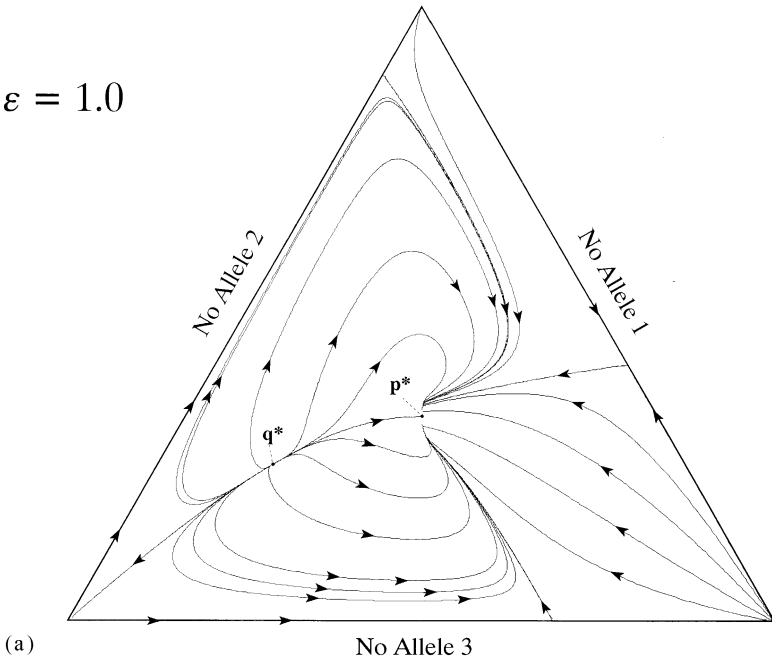


Fig. 2. The dynamic trajectories for the example of Sect. 5 when **a** $\varepsilon = 1$ and **b** $\varepsilon = 0.01$. Boundary equilibria are indicated by interior trajectories that intersect the boundary and divide the interior into basins of attraction of the different equilibria

adjacent edges. However, for small ε , Fig. 2(b), the proximity of q^* to p^* obscures this basin. Initial p on the other side of q^* from p^* evolve to the monomorphic population with only the first allele present. Without this detail Fig. 2(b) is misleading in suggesting the evolutionary instability of p^* .

Our choice of genotypic strategies also leads to an interesting result in the case when $\varepsilon = 0$. Then S^* is a neutrally stable strategy (also called a weak ESS) in that it satisfies the static conditions of Definition 3.1 with the second inequality replaced by $S \cdot AS \leq S^* \cdot AS$. For the asexual model of evolutionary game theory, Bomze and Weibull (1995) have shown S^* is automatically Lyapunov stable for matrix games. In particular, in the asexual dynamic, if $S(t)$ is initially sufficiently close to S^* it will remain close to S^* for all t . This is no longer true for the diploid dynamic (2.2). With $\varepsilon = 0$, $p^* = q^*$ in Fig. 2(b) from which it is clear that S^* is not Lyapunov stable (in fact, S^* is unstable).

6 Evolutionary stability at a boundary p^* corresponding to an ESS

The mathematical techniques to prove evolutionary stability at a boundary p^* are essentially those used in Sect. 4. However, there are two types of complications that arise regularly in their application. The first is that S^* need not be a strict linear combination of the genotypic strategies (i.e. S^* does not have to be in the interior of the convex hull spanned by the S_{ij}) and so A may not be negative definite on all of Δ^N . Secondly, the c.m. may have dimension greater than 1 at nongenetic equilibria in which case (for $n = 3$) c.m. methods seem initially irrelevant. Both complications are already apparent from the linearization (3.1) (where both possibilities $p_i^* = 0$ and $p_i^* \neq 0$ need analysis) and its elementary use in the proof of Theorem 4.1.

The proofs presented below for the following theorems emphasize the refinements needed to generalize the theorems of Sect. 4 and leave many straightforward (though difficult) calculations based on the proofs of Sect. 4 to the readers. For this section, we assume p^* is on the boundary of Δ^n and that $S(p^*) = S^*$ is an ESS. From Sect. 3, $S^{*i} \cdot AS^* = S^* \cdot AS^*$ whenever $p_i^* \neq 0$. By Theorem 6.1, we may assume this equality holds for all i .

Theorem 6.1. *Suppose $S^{*i} \cdot AS^* < S^* \cdot AS^*$ for some i with $p_i^* = 0$.*

- (a) *There is evolutionary stability at p^* if and only if there is evolutionary stability at p^* with respect to the $n - 2$ dimensional face $\{p \in \Delta^n | p_i = 0\}$ of Δ^n .*
- (b) *If $n = 3$, there is evolutionary stability at p^* .*

Proof. (a) It is clear evolutionary stability at p^* implies evolutionary stability on the invariant face. Conversely, assume evolutionary stability at p^* with respect to the face. Then, from (3.1),

$$\dot{x}_i = x_i [(S^{*i} - S^*) \cdot AS^* + \dots] < 0 \tag{6.1}$$

if p is sufficiently close to p^* and $x_i > 0$. Since all eigenvalues of (3.1) have nonpositive real part, evolutionary stability of p^* reduces to the analysis on

the c.m. which is contained in the given face by (6.1). Evolutionary stability of p^* follows.

(b) If $n = 3$ the invariant face is one dimensional. Assume $p_3^* = 0$. Then, on this face,

$$\begin{aligned} \dot{p}_1 &= p_1(S^1 - S) \cdot AS \\ &= p_1(1 - p_1)(S^1 - S^2) \cdot AS \\ &= p_1(1 - p_1)[(S^{*1} - S^{*2}) \cdot A(S^* + x_1(S^{*1} - S^{*2})) + \dots] \end{aligned}$$

If $(S^{*1} - S^{*2}) \cdot AS^* \neq 0$, then either p_1^* or p_2^* is zero. By part (a), evolutionary stability follows from that on the 0 dimensional face (i.e. by the fact p^* is an equilibrium point). On the other hand if p_1^* and p_2^* are nonzero, then $(S^{*1} - S^{*2}) \cdot AS^* = 0$ and so $(S^{*1} - S^{*2}) \cdot A(S^{*1} - S^{*2}) < 0$ since both have support contained in that of S^* . Thus, $x_1 = 0$ is l.a.s. and so p^* has evolutionary stability. \square

Theorem 6.2. Assume $S^{*i} \cdot AS^* = S^* \cdot AS^*$ for all i .

(a) If $\xi_a \neq 0$ for all nonzero $a \in X^n$ such that $a_i \geq 0$ whenever $p_i^* = 0$, then p^* is l.a.s.

(b) If $\xi_a = 0$ for all $a \in X^n$ with $a_i \geq 0$ whenever $p_i^* = 0$, there is evolutionary stability at p^* .

Proof. As in (4.2), let $V(p) = -\sum p_i^* \ln p_i$ where the sum is taken over those i for which $p_i^* \neq 0$. Following the proof of Theorem 4.2, we find

$$\begin{aligned} \dot{V}(p) &= (\xi_x + \eta_x) \cdot A(S^* + 2\xi_x + \eta_x) \\ &= 2\xi_x \cdot A\xi_x + \eta_x \cdot AS^* + \text{higher order terms in } x. \end{aligned} \tag{6.2}$$

For all $p \in \Delta^n$ sufficiently close to p^* , $S^* + \eta_x \in \Delta^N$ and so $(S^* + \eta_x - S^*) \cdot AS^* \leq 0$. By the initial assumption and Definition 3.1, $\xi_x \cdot A\xi_x < 0$ whenever $\xi_x \neq 0$. Thus, consideration of the quadratic terms of $\dot{V}(p)$ proves part (a). Part (b) follows similarly. \square

Theorem 6.2 is the generalization of Theorems 4.1 and 4.2 to boundary p^* . The linear independence and genetic equilibrium conditions on the set $\{S^{*1}, \dots, S^{*n}\}$ now correspond to parts (a) and (b) respectively. Mathematically, a somewhat disturbing trend has emerged. Linearization is no longer sufficient to prove evolutionary stability for linearly independent S^{*i} – rather quadratic terms were required. We will see this trend to higher order expansions of the dynamic continues as we analyze the c.m. in the following theorems that generalize Theorems 4.3 to 4.5.

To complete the proof of evolutionary stability at p^* when $n = 3$ it can be assumed for the remainder of this section that $S^{*1} \neq S^{*2}$ and that $\xi_a = 0$ for some nonzero $a \in X^3$ with $a_i \geq 0$ whenever $p_i^* = 0$. Furthermore, by Theorem 6.1(b), we assume $S^{*i} \cdot AS^* = S^* \cdot AS^*$ for all i . At this point, it seems necessary for the proofs to consider the monomorphic case $p^* = (0, 0, 1)$ separate from the situation where $p^* = (p_1^*, p_2^*, 0)$ with $p_1^* \neq 0 \neq p_2^*$. When $p^* = (0, 0, 1)$, $S^* = S_{33} = S^{*3}$ and $S^{*i} = S_{i3}$. Then both eigenvalues of (3.1)

are zero so that the c.m. does not initially simplify the dynamic (2.2). The following proof emphasizes the additional mathematical complexities in the dynamical analysis of this case.

Theorem 6.3. *Suppose $p^* = (0, 0, 1)$ and $\{a = (a_1, a_2, -(a_1 + a_2)), b = (b_1, b_2, -(b_1 + b_2))\}$ is a basis of X^3 with $a_i \geq 0$, $b_i \geq 0$, $\xi_a = 0$ and $\xi_b \neq 0$.*

(a) *If $\{\xi_b, \eta_a\}$ is linearly independent, then p^* is l.a.s.*

(b) *If $\eta_a = 0$, there is evolutionary stability at p^* .*

Proof. (a) Since $S^{*1} \neq S^{*3}$, $a_2 > 0$. In terms of $x_1 = p_1$ and $x_2 = p_2$, the dynamic (2.2) has the form

$$\begin{aligned}\dot{x}_1 &= x_1 G_1(x_1, x_2) \\ \dot{x}_2 &= x_2 G_2(x_1, x_2)\end{aligned}\tag{6.3}$$

$$\begin{aligned}G_i(x_1, x_2) &= \left(S^{*i} - S^* + \sum_{j=1}^2 x_j (S_{ij} - S^{*j}) - 2\xi_x - \eta_x \right) \cdot A(S^* + 2\xi_x + \eta_x) \\ \xi_x &= x_1(S^{*1} - S^*) + x_2(S^{*2} - S^*) \\ \eta_x &= x_1^2(S_{11} - 2S^{*1} + S^*) + x_2^2(S_{22} - 2S^{*2} + S^*) \\ &\quad + 2x_1 x_2(S_{12} - S^{*1} - S^{*2} + S^*).\end{aligned}$$

Since $(S^{*i} - S^*) \cdot AS^* = 0$, $G_1(0, 0) = G_2(0, 0) = 0$ and this implies the c.m. is two dimensional.

If $a_1 = 0$, then $S^{*2} = S^*$ and from (6.2) p^* is l.a.s. if $\eta_a \cdot AS^* \neq 0$. That is, we may assume that $\eta_a \cdot AS^* = (S_{22} - S^*) \cdot AS^* = 0$. Take $b = (1, 0, -1)$. In this case, it turns out that $2x_1 + x_2$ is a local Lyapunov function for (6.3) since it has a unique minimum at $(0, 0)$ and the dominating terms of its derivative are given by

$$\begin{aligned}2\dot{x}_1 + \dot{x}_2 &= 2(2x_1^2 \xi_b \cdot A\xi_b + x_1 x_2 (S_{12} - S^*) \cdot AS^* + x_1 x_2^2 \xi_b \cdot A\eta_a) \\ &\quad + (x_1 x_2 (S_{12} - S^*) \cdot AS^* + 2x_1 x_2^2 \eta_a \cdot A\xi_b \\ &\quad - 2x_1 x_2^2 (S_{12} - S^*) \cdot AS^* + x_2^4 \eta_a \cdot A\eta_a) \\ &= (2x_1 \xi_b + x_2^2 \eta_a) \cdot A(2x_1 \xi_b + x_2^2 \eta_a) \\ &\quad + x_1 x_2 (3 - 2x_2) (S_{12} - S^*) \cdot AS^*.\end{aligned}$$

That is, $2\dot{x}_1 + \dot{x}_2 < 0$ if (x_1, x_2) is sufficiently close (but not equal) to $(0, 0)$ whenever $\{\xi_b, \eta_a\}$ is linearly independent.

For the remainder of the proof, assume $a_1 \neq 0$. Take $a = (1, k, -(1 + k))$ and $b = (0, 1, -1)$. Then $\eta_a \cdot AS^* = (S_{11} - S^*) \cdot AS^* + k^2(S_{22} - S^*) \cdot AS^* + 2k(S_{12} - S^*) \cdot AS^*$. From (6.2), we may assume $S_{ij} \cdot AS^* = S^* \cdot AS^*$ for all i, j . The quadratic terms of the dynamic (6.3) has a line of fixed points $x_2 = kx_1$ through the origin. Although the higher order terms will destroy these fixed points, the following blowing up technique (Arrowsmith and Place, 1990) shows there will be an attractive invariant curve through the origin that

is tangent to this line. It is then shown, using the Taylor series expansion of this curve, that the origin is l.a.s.

The origin is blown up in the x_1 direction by letting $x = x_1$, and $z = x_2/x_1$. The dynamic (6.3) becomes

$$\begin{aligned} \dot{x} &= x G_1(x, xz) \\ \dot{z} &= z(G_2(x, xz) - G_1(x, xz)) \end{aligned} \tag{6.4}$$

Since x is a common factor of \dot{x} and \dot{z} , each point on the z -axis is a fixed point of (6.4) corresponding to the original origin. Furthermore, dividing through by x , the orbits of (6.4) are unchanged for $x > 0$. On the positive z -axis, $(x, z) = (0, 0)$ is a repelling fixed point and $(0, k)$ is another equilibrium (the only one) in this new dynamic since $\zeta_{(x,z)}/x = (S^{*1} - S^*) + z(S^{*2} - S^*) = (z - k)\zeta_b$ and $\eta_{(x,z)}/x = 0$ along the z -axis. To complete the proof, we must show $(0, k)$ is l.a.s. and this is begun by linearization.

Let $y = z - k$. Then $\zeta_{(x,y)}/x = y(S^{*2} - S^*)$ and $\eta_{(x,y)}/x = x\eta_a + 2kxy\eta_{ab} + xy^2\eta_b$. Dividing (6.4) by x yields

$$\begin{aligned} \dot{x} &= -kx\zeta_b \cdot A(x\eta_a + 2y\zeta_b) + \dots \\ \dot{y} &= k(1 + k)\zeta_b \cdot A(x\eta_a + 2y\zeta_b) + \dots \end{aligned} \tag{6.5}$$

The eigenvalues of (6.5) are 0 and $2k(1 + k)\zeta_b \cdot A\zeta_b < 0$. Thus the l.a.s. of (6.5) is determined by a one dimensional invariant c.m. through $(x, y) = (0, 0)$. In terms of the original (x_1, x_2) coordinates, this c.m. is of the form

$$x_2 = kx_1 + \alpha x_1^2 + \beta x_1^3 + \dots \tag{6.6}$$

since its tangent vector is a . It seems technically better to show l.a.s. using (6.6) in place of (6.5). From (4.4), (6.3) and (6.6),

$$(k + 2\alpha x_1 + 3\beta x_1^2 + \dots)x_1 G(x_1, x_2) = (kx_1 + \alpha x_1^2 + \beta x_1^3 + \dots)G_2(x_1, x_2). \tag{6.7}$$

There are no linear or quadratic terms on either side of (6.7). From the cubic terms, we determine that α is given by (4.11) and the fourth order terms produce an expression for $\zeta_b \cdot A(\beta\zeta_b + \alpha\eta_{ab})$ that has $2\alpha\zeta_b + \eta_a$ on the right side of the payoff matrix. From these, the dynamic (6.3) on the c.m. becomes

$$\dot{x}_1 = \frac{x_1^4}{k + 1} \frac{\zeta_b \cdot A\zeta_b \eta_a \cdot A\zeta_a - \zeta_b \cdot A\eta_a \eta_a \cdot A\zeta_b}{\zeta_b \cdot A\zeta_b} + \dots \tag{6.8}$$

which is essentially (4.12). Since $x_1 \geq 0$, (4.13) implies p^* is l.a.s.

(b) If $\eta_a = 0$ the one dimensional c.m. of (6.5) is the line $x_2 = kx_1$ of equilibrium points from which the evolutionary stability of p^* follows as in Theorem 4.3(b). □

If ζ_b and η_a are nonzero scalar multiples, then higher order terms in the expansion of (6.3) must be analyzed. If $S^{*2} = S^*$, evolutionary stability is

shown by considering the dominating terms of (6.3) in analogy to the proof of Theorem 6.5 below. If $S^{*2} \neq S^*$, (6.8) is expanded up to order eight in some cases to obtain the first nonzero term of the dynamic on the c.m. of (6.5) as,

$$\dot{x}_1 = \frac{6\alpha^2}{k+1} \left(\frac{\zeta_b \cdot A\zeta_b \eta_{ab} \cdot A\eta_{ab} - \zeta_b \cdot A\eta_{ab} \eta_{ab} \cdot A\zeta_b}{\zeta_b \cdot A\zeta_b} \right) x_1^6 + \dots$$

when $\{\zeta_b, \eta_{ab}\}$ are linearly independent and, if not, then

$$\dot{x}_1 = \frac{\alpha^4}{k+1} \left(\frac{\eta_b \cdot A\eta_b \zeta_b \cdot A\zeta_b - \eta_b \cdot A\zeta_b \zeta_b \cdot A\eta_b}{\zeta_b \cdot A\zeta_b} \right) x_1^8 + \dots$$

The interested reader should verify these expansions and compare them to the similar expressions of one less order in the proofs given in the Appendix of Theorems 4.4 and 4.5 for interior p^* . The following theorem summarizes these results.

Theorem 6.4. *Suppose $p^* = (0, 0, 1)$ and $\{a, b\}$ is a basis of X^3 as in the statement of Theorem 6.3 with $\zeta_a = 0$ and $\zeta_b \neq 0$. Furthermore, assume η_a is a nonzero scalar multiple of ζ_b . If $\{\zeta_b, \eta_{ab}\}$ is linearly independent, then p^* is l.a.s. If $\{\zeta_b, \eta_{ab}\}$ is linearly dependent, then*

- (a) *If $\{\zeta_b, \eta_b\}$ is linearly independent, p^* is l.a.s.*
- (b) *If $\{\zeta_b, \eta_b\}$ is linearly dependent, there is evolutionary stability at p^* .*

The remainder of this section outlines the proof of evolutionary stability at $p^* = (p_1^*, p_2^*, 0)$. From (3.1), $(1, -1, 0)$ is an eigenvector of (2.2) with eigenvalue $2p_1^* p_2^* (S^{*1} - S^{*2}) \cdot A(S^{*1} - S^{*2})$. The other eigenvalue is zero. Thus, if $S^{*1} \neq S^{*2}$, there is a one-dimensional c.m. through p^* for (2.2) of the form $y = \alpha x^2 + \beta x^3 + \dots$ with respect to the basis $\{(a_1, a_2, 1), (1, -1, 0)\}$ of X^3 where $a_1 S^{*1} + a_2 S^{*2} + S^{*3} = 0$. Then α is again given by (4.11) and \dot{x} has no terms less than order four. The analogue of (4.12) is

$$\dot{x} = \left(\frac{\zeta_b \cdot A\zeta_b \eta_a \cdot A\eta_a - \zeta_b \cdot A\eta_a \eta_a \cdot A\zeta_b}{\zeta_b \cdot A\zeta_b} \right) x^4 + \dots$$

which implies l.a.s. of p^* if $\{\zeta_b, \eta_a\}$ are linearly independent since $x \geq 0$. Higher order expansions yield Theorem 6.4 with $p^* = (p_1^*, p_2^*, 0)$ in place of $(0, 0, 1)$.

If $S^{*1} = S^{*2}$, the c.m. is again two dimensional, indicating a more careful analysis is needed. The following theorem is the first step in the analysis.

Theorem 6.5. *Suppose $p^* = (p_1^*, p_2^*, 0)$ and $S^{*1} = S^{*2}$. Take $a = (1, -1, 0)$ and $b = (-p_1^*, -p_2^*, 1)$ as a basis of X^3 .*

- (a) *If $\{\zeta_b, \eta_a\}$ is linearly independent, then p^* is l.a.s.*
- (b) *If $\eta_a = 0$, there is evolutionary stability at p^* .*

Proof. (a) Note that $\zeta_a = 0$, $\zeta_b = S^{*3} - S^* \neq 0$ and $y \geq 0$. From (4.6), (4.7) and (4.8),

$$\dot{y} = 2y^2 \zeta_b \cdot A\zeta_b + x^2 y \zeta_b \cdot A\eta_a + \dots \tag{6.9}$$

where the remaining terms are dominated by those given. Also, $\dot{x} = c_1 + p_1^* c_3$ where c_i is given by (4.7). That is,

$$\dot{x} = p_1^* p_2^* (2xy\eta_a \cdot A\zeta_b + x^3\eta_a \cdot A\eta_a + 2y^2\eta_{ab} \cdot A\zeta_b) + \dots \tag{6.10}$$

Suppose $\zeta_b \cdot A\eta_a > 0$. Then $\dot{y} = 0$ when $y = \alpha x^2 + \beta x^3 + \dots$ where, from (6.9),

$$\alpha = -\frac{\zeta_b \cdot A\eta_a}{2\zeta_b \cdot A\zeta_b} > 0. \tag{6.11}$$

On the other hand, if $y \leq \alpha x^2 + \beta x^3 + \dots$, then $\dot{y} \geq 0$ and, from (6.10),

$$\dot{x} \leq p_1^* p_2^* \left(-\frac{\zeta_b \cdot A\eta_a}{\zeta_b \cdot A\zeta_b} \eta_a \cdot A\zeta_b + \eta_a \cdot A\eta_a \right) x^4 + \dots$$

which is negative by (4.13) if x is sufficiently close to zero. This is illustrated in Fig. 3 and shows that the rectangles indicated there with base on the x -axis and vertices sufficiently close to the origin are forward invariant for the dynamic. Since $(0, 0)$ is the only equilibrium in these rectangles, it is l.a.s.

Now, suppose $\zeta_b \cdot A\eta_a \leq 0$. From (6.9), for any $\alpha > 0$, if $y \geq \alpha x^2$ then $\dot{y} < 0$ whenever x is sufficiently close to zero. Furthermore, by (6.10), there is a choice $\alpha > 0$ such that $\dot{x} < 0$ if $y \leq \alpha x^2$. The rectangles of Fig. 3 are again forward invariant and the conclusion is that $(0, 0)$ is l.a.s.

(b) If $\eta_a = 0$, then all terms of (6.9) are dominated by $2y^2\zeta_b \cdot A\zeta_b$ since $S - S^* = y(2\zeta_b + y\eta_b + 2x\eta_{ab})$ from (4.8). Thus $\dot{y} < 0$ for $y > 0$ and the trajectories approach a point on the x -axis in Fig. 3 that corresponds to S^* . That is, there is evolutionary stability at p^* . \square

If ζ_b and η_a are nonzero scalar multiples, the above proof shows p^* is l.a.s. when $\zeta_b \cdot A\eta_a \leq 0$. On the other hand, if $\eta_a = -2\alpha\zeta_b$ where $\alpha > 0$ as in (6.11),

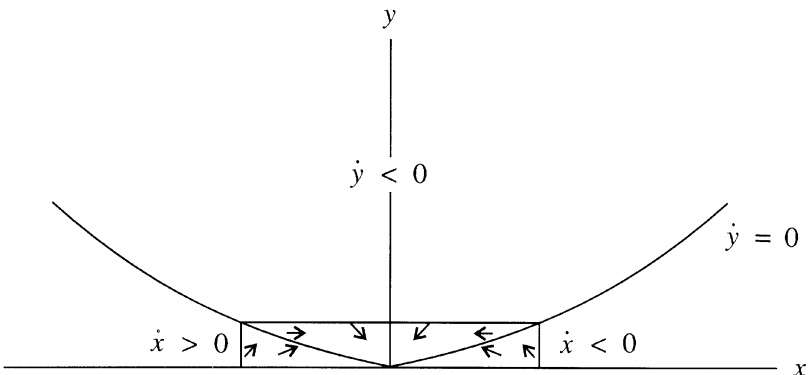


Fig. 3. Flow diagram for the dynamics (6.9) and (6.10) when $\zeta_b \cdot A\eta_a > 0$

then expansion of (6.9) shows $\dot{y} = 0$ when $y = \alpha x^2 + \beta x^3 + \dots$ where (cf. (A.5))

$$\beta = -\alpha \frac{\xi_b \cdot A \eta_{ab}}{\xi_b \cdot A \xi_b}.$$

Expansion of (6.10) up to fifth order and the local convexity of $\dot{y} = 0$ produces the same flow diagram as in Fig. 3 when $\{\xi_b, \eta_{ab}\}$ are linearly independent. Finally, if $\{\xi_b, \eta_{ab}\}$ are linearly dependent, seventh order terms yield the evolutionary stability of p^* . This is, if η_a is a negative multiple of ξ_b , we have the analogue of Theorem 6.4 in the case $p^* = (p_1^*, p_2^*, 0)$ and $S^{*1} = S^*$.

This completes the proof of evolutionary stability at boundary p^* .

7 Conclusion

Sections 4 and 6 combine to prove the main result of this paper; namely,

Theorem 7.1. *Suppose $S^* \in \Delta^N$ is an ESS and there is some p^* in the three-allele single-locus strategic model of frequency-dependent viability selection with $S(p^*) = S^*$. Then there is evolutionary stability at S^* .*

This extends the well-known result of Maynard Smith (1981) for the diallelic locus. The proof for three alleles is quite complex in that it relies heavily on the centre manifold (c.m.) analysis in cases where the extensive previous literature was unable to push a proof through. The fact that the c.m. is one dimensional (or can be reduced to one dimensional) makes the analysis possible and suggests evolutionary stability of an ESS will hold for any number of alleles when the c.m. is of dimension at most one. For example, Theorem 4.3 readily generalizes to a basis of X^n with a single degenerate direction with $\xi_a = 0$.

On the other hand, if the c.m. has dimension greater than one and p^* is not a genetic equilibrium, the dynamical analysis appears formidable. In fact, a number of the more complex higher-order expansions in this paper were verified symbolically using MAPLE since they approached the limit of our manual reliability. We are hesitant to conjecture publicly whether a multi-allele (i.e. $n \geq 4$) ESS always exhibits evolutionary stability since we cannot agree among ourselves. However, we do agree that the resolution of this question is important for the foundations of evolutionary game theory and will undoubtedly be based on some novel mathematical analysis or a counter-example with a two-dimensional c.m.

Appendix

For the proofs of Theorems 4.4 and 4.5, we may assume that $S^{*1} \neq S^{*2}$ as in Theorem 4.3.

Proof of Theorem 4.4. From (4.11), since ξ_b and η_a are linearly dependent and nonzero,

$$\eta_a = -2\alpha\xi_b \tag{A.1}$$

where $\alpha \neq 0$. With $y = \alpha x^2 + \beta x^3 + \gamma x^4 + \delta x^5 + \epsilon x^6 + \dots$ on the c.m., from (4.8),

$$\begin{aligned} S - S^* &= 2\alpha x^2 \xi_b + x^2 \eta_a + 2(\beta x^3 + \gamma x^4 + \dots) \xi_b + 2x(\alpha x^2 + \beta x^3 + \dots) \eta_{ab} \\ &\quad + (\alpha^2 x^4 + 2\alpha\beta x^5 + \dots) \eta_b \\ &= (2\beta \xi_b + 2\alpha \eta_{ab}) x^3 + (2\gamma \xi_b + 2\beta \eta_{ab} + \alpha^2 \eta_b) x^4 + \dots \end{aligned} \tag{A.2}$$

Consider the expansion of \dot{x} and \dot{y} on the c.m. in terms of x . From (4.9), \dot{x} has no terms up to third order and so, by (4.4), $\dot{y} = 0$ up to fourth order. The higher order extension of (4.10) is

$$\begin{aligned} \langle b, b \rangle \dot{y} &= \sum c_i b_i / p_i^* \\ &= \left[\begin{aligned} &\sum b_i (S^{*i} - S^*) + x \left(\sum b_i (a_1 S_{i1} + a_2 S_{i2} + a_3 S_{i3}) + \sum \frac{a_i b_i}{p_i^*} (S^{*i} - S^*) \right) + \\ &x^2 \left(\sum \frac{a_i b_i}{p_i^*} (a_1 S_{i1} + a_2 S_{i2} + a_3 S_{i3}) + \alpha \sum b_i (b_1 S_{i1} + b_2 S_{i2} + b_3 S_{i3}) \right. \\ &\quad \left. + \alpha \sum \frac{b_i^2}{p_i^*} (S^{*i} - S^*) \right) \\ &+ \dots \end{aligned} \right] \cdot A(S - S^*) \\ &= \xi_b \cdot A(2\beta \xi_b + 2\alpha \eta_{ab}) x^3 + \xi_b \cdot A(2\gamma \xi_b + 2\beta \eta_{ab} + \alpha^2 \eta_b) x^4 \\ &\quad + \left(\eta_{ab} + \sum \frac{a_i b_i}{p_i^*} (S^{*i} - S^*) \right) \cdot A(2\beta \xi_b + 2\alpha \eta_{ab}) x^4 + \dots \end{aligned}$$

Equating coefficients to zero, we have

$$\xi_b \cdot (\beta \xi_b + \alpha \eta_{ab}) = 0 \tag{A.3}$$

$$\xi_b \cdot A(2\gamma \xi_b + 2\beta \eta_{ab} + \alpha^2 \eta_b) + \eta_{ab} \cdot A(2\beta \xi_b + 2\alpha \eta_{ab}) = 0 . \tag{A.4}$$

In particular, the first condition implies

$$\beta = -\alpha \frac{\xi_b \cdot A \eta_{ab}}{\xi_b \cdot A \xi_b} . \tag{A.5}$$

Similarly the higher order extension of $\langle a, a \rangle \dot{x}$ in (4.9) is, from (A.2) and (A.3),

$$\begin{aligned} & \left[\begin{aligned} & x \left(\sum a_i (a_1 S_{i1} + a_2 S_{i2} + a_3 S_{i3}) + \sum \frac{a_i^2}{p_i^*} (S^{*i} - S^*) \right) + \\ & x^2 \left(\sum \frac{a_i^2}{p_i^*} (a_1 S_{i1} + a_2 S_{i2} + a_3 S_{i3}) + \alpha \sum a_i (b_1 S_{i1} + b_2 S_{i2} + b_3 S_{i3}) \right. \\ & \quad \left. + \alpha \sum \frac{a_i b_i}{p_i^*} (S^{*i} - S^*) \right) \\ & + \dots \end{aligned} \right] \cdot A(S - S^*) \\ & = \eta_a \cdot A(2\beta \zeta_b + 2\alpha \eta_{ab}) x^4 + \left(\eta_a + \sum \frac{a_i^2}{p_i^*} (S^{*i} - S^*) \right) \cdot A(2\gamma \zeta_b + 2\beta \eta_{ab} + \alpha^2 \eta_b) x^5 \\ & \quad + \left(\sum \frac{a_i^2}{p_i^*} (a_1 S_{i1} + a_2 S_{i2} + a_3 S_{i3}) + \alpha \eta_{ab} \right) \cdot A(2\beta \zeta_b + 2\alpha \eta_{ab}) x^5 \dots \end{aligned}$$

From (A.1) and (A.3), the fourth order term of \dot{x} is zero on the c.m. From (4.3), (A.1) and (A.4), the coefficient of x^5 is

$$\begin{aligned} & \left(\left(2\alpha - \sum \frac{a_i^2 b_i}{\langle b, b \rangle p_i^{*2}} \right) \eta_{ab} + \sum \frac{a_i^2}{p_i^*} (a_1 S_{i1} + a_2 S_{i2} + a_3 S_{i3}) + \alpha \eta_{ab} \right) \\ & \quad \cdot A(2\beta \zeta_b + 2\alpha \eta_{ab}) \end{aligned}$$

To simplify this coefficient, write the vector $\left(\frac{a_1^2}{p_1^*}, \frac{a_2^2}{p_2^*}, \frac{a_3^2}{p_3^*} \right)$ in terms of the orthogonal basis $\{a, b, p^*\}$ of \mathbf{R}^3 as $\sum \frac{a_j^3}{\langle a, a \rangle p_j^{*2}} a + \frac{a_j^2 b_j}{\langle b, b \rangle p_j^{*2}} b + \sum \frac{a_j^2}{p_j^*} p^*$.

Then

$$\sum \frac{a_i^2}{p_i} (a_1 S_{i1} + a_2 S_{i2} + a_3 S_{i3}) = \sum \frac{a_j^3}{\langle a, a \rangle p_j^{*2}} \eta_a + \sum \frac{a_j^2 b_j}{\langle b, b \rangle p_j^{*2}} \eta_{ab} \quad (A.6)$$

That is, on the c.m., from (A.5)

$$\begin{aligned} \langle a, a \rangle \dot{x} & = 3\alpha \eta_{ab} \cdot A \left(-2\alpha \frac{\zeta_b \cdot A \eta_{ab}}{\zeta_b \cdot A \zeta_b} \zeta_b + 2\alpha \eta_{ab} \right) x^5 + \dots \\ & = 6\alpha^2 \left(\frac{\zeta_b \cdot A \zeta_b \eta_{ab} \cdot A \eta_{ab} - \zeta_b \cdot A \eta_{ab} \eta_{ab} \cdot A \zeta_b}{\zeta_b \cdot A \zeta_b} \right) x^5 + \dots \end{aligned}$$

For the same reasons that led to (4.13), the linear independence of ζ_b and η_{ab} implies the l.a.s. of p^* . □

Proof of Theorem 4.5. (a) It turns out we need \dot{x} and \dot{y} to seventh order in x on the c.m. From (A.5),

$$\eta_{ab} = -\beta / \alpha \zeta_b \quad (A.7)$$

where α is nonzero. On the c.m.,

$$\begin{aligned}
 S - S^* &= (2\gamma\zeta_b - 2\beta^2/\alpha\zeta_b + \alpha^2\eta_b)x^4 + \\
 &\quad (2\delta\zeta_b - 2\gamma\beta/\alpha\zeta_b + 2\alpha\beta\eta_b)x^5 + \\
 &\quad (2\varepsilon\zeta_b - 2\delta\beta/\alpha\zeta_b + (2\alpha\gamma + \beta^2)\eta_b)x^6 + \dots
 \end{aligned}$$

Since $\dot{x} = 0$ up to order 5 on the c.m., from (4.4), $\dot{y} = 0$ up to order 6.

Now the extension of (4.10) implies for the terms of order 4, 5, and 6 that

$$\zeta_b \cdot A(2\gamma\zeta_b - 2\beta^2/\alpha\zeta_b + \alpha^2\eta_b) = 0 \tag{A.8}$$

$$\zeta_b \cdot A(2\delta\zeta_b - 2\gamma\beta/\alpha\zeta_b + 2\alpha\beta\eta_b) = 0 \tag{A.9}$$

$$\begin{aligned}
 &\left(\sum \frac{a_i b_i}{p_i^*} (a_1 S_{i1} + a_2 S_{i2} + a_3 S_{i3}) + \alpha\eta_b \right) \cdot A(2\gamma\zeta_b - 2\beta^2/\alpha\zeta_b + \alpha^2\eta_b) + \zeta_b \\
 &\quad \cdot A(2\varepsilon\zeta_b - 2\delta\beta/\alpha\zeta_b + (2\alpha\gamma + \beta^2)\eta_b) = 0 .
 \end{aligned}$$

By a calculation similar to that leading to (A.6), $\sum a_i b_i/p_i^* (a_1 S_{i1} + a_2 S_{i2} + a_3 S_{i3})$ is a linear combination of η_a and η_{ab} . Thus the last condition simplifies to

$$\alpha\eta_b \cdot A(2\gamma\zeta_b - 2\beta^2/\alpha\zeta_b + \alpha^2\eta_b) + \zeta_b \cdot A(2\varepsilon\zeta_b - 2\delta\beta/\alpha\zeta_b + (2\alpha\gamma + \beta^2)\eta_b) = 0 . \tag{A.10}$$

From the extension of (4.9), the coefficients of \dot{x} of order 5, 6 and 7 are

$$\left(\eta_a + \sum \frac{a_i^2}{p_i^*} (S^{*i} - S^*) \right) \cdot A(2\gamma\zeta_b - 2\beta^2/\alpha\zeta_b + \alpha^2\eta_b) \tag{A.11}$$

$$\begin{aligned}
 &\left(\eta_a + \sum \frac{a_i^2}{p_i^*} (S^{*i} - S^*) \right) \cdot A(2\delta\zeta_b - 2\gamma\beta/\alpha\zeta_b + 2\alpha\beta\eta_b) \\
 &\quad + \left(\sum \frac{a_i^2}{p_i^*} (a_1 S_{i1} + a_2 S_{i2} + a_3 S_{i3}) + \alpha\eta_{ab} + \alpha \sum \frac{a_i b_i}{p_i^*} (S^{*i} - S^*) \right) \\
 &\quad \cdot A(2\gamma\zeta_b - 2\beta^2/\alpha\zeta_b + \alpha^2\eta_b) .
 \end{aligned} \tag{A.12}$$

$$\begin{aligned}
 &\left(\eta_b + \sum \frac{a_i^2}{p_i^*} (S^{*i} - S^*) \right) \cdot A(2\varepsilon\zeta_b - 2\delta\beta/\alpha\zeta_b + (2\alpha\gamma + \beta^2)\eta_b) \\
 &\quad + \left(\sum \frac{a_i^2}{p_i^*} (a_1 S_{i1} + a_2 S_{i2} + a_3 S_{i3}) + \alpha\eta_{ab} + \alpha \sum \frac{a_i b_i}{p_i^*} (S^{*i} - S^*) \right) \\
 &\quad \cdot A(2\delta\zeta_b - 2\gamma\beta/\alpha\zeta_b + 2\alpha\beta\eta_b) \\
 &\quad + \left(\beta\eta_{ab} + \beta \sum \frac{a_i b_i}{p_i^*} (S^{*i} - S^*) + \alpha \sum \frac{a_i b_i}{p_i^*} (a_1 S_{i1} + a_2 S_{i2} + a_3 S_{i3}) \right) \\
 &\quad \cdot A(2\gamma\zeta_b - 2\beta^2/\alpha\zeta_b + \alpha^2\eta_b) \\
 &\quad + \alpha \sum \frac{a_i^2}{p_i^*} (b_1 S_{i1} + b_2 S_{i2} + b_3 S_{i3}) \cdot A(2\gamma\zeta_b - 2\beta^2/\alpha\zeta_b + \alpha^2\eta_b)
 \end{aligned}$$

respectively. Since

$$\sum \frac{a_i^2}{p_i^*} (S^{*i} - S^*), \sum \frac{a_i^2}{p_i^*} (a_1 S_{i1} + a_2 S_{i2} + a_3 S_{i3}), \sum \frac{a_i b_i}{p_i^*} (S^{*i} - S^*),$$

and $\sum a_i b_i / p_i^* (a_1 S_{i1} + a_2 S_{i2} + a_3 S_{i3})$ are all multiples of ξ_b due to (A.1) and (A.7), (A.8) and (A.9) combine to show (A.11) and (A.12) are zero and that the coefficient of x^7 simplifies to

$$\begin{aligned} & \left(\eta_a + \sum \frac{a_i^2}{p_i^*} (S^{*i} - S^*) \right) \cdot A(2\varepsilon \xi_b - 2\delta \beta / \alpha \xi_b + (2\alpha \gamma + \beta^2) \eta_b) \\ & + \alpha \sum \frac{a_i^2}{p_i^*} (b_1 S_{i1} + b_2 S_{i2} + b_3 S_{i3}) \cdot A(2\gamma \xi_b - 2\beta^2 / \alpha \xi_b + \alpha^2 \eta_b). \end{aligned} \quad (\text{A.13})$$

By a calculation similar to that leading to (A.6),

$$\sum \frac{a_i^2}{p_i^*} (b_1 S_{i1} + b_2 S_{i2} + b_3 S_{i3}) = \sum \frac{a_j^3}{\langle a, a \rangle p_j^{*2}} \eta_{ab} + \sum \frac{a_j^2 b_j}{\langle b, b \rangle p_j^{*2}} \eta_b + \sum \frac{a_j^2}{p_j^*} \xi_b$$

Also, from (A.10) and (4.3), (A.13) becomes

$$\begin{aligned} & \left(\left(-2\alpha + \sum \frac{a_i^2 b_i}{\langle b, b \rangle p_i^{*2}} \right) (-\alpha \eta_b) + \alpha \sum \frac{a_j^2 b_j}{\langle b, b \rangle p_j^{*2}} \eta_b \right) \\ & \cdot A(2\gamma \xi_b - 2\beta^2 / \alpha \xi_b + \alpha^2 \eta_b) \\ & = 2\alpha^2 \eta_b \cdot A(2\gamma \xi_b - 2\beta^2 / \alpha \xi_b + \alpha^2 \eta_b). \end{aligned}$$

From (A.8), $2\gamma - 2\beta^2 / \alpha = -\alpha^2 \xi_b \cdot A \eta_b / \xi_b \cdot A \xi_b$. Thus, on the c.m.,

$$\langle a, a \rangle \dot{x} = 2\alpha^4 \left(\frac{\eta_b \cdot A \eta_b \xi_b \cdot A \xi_b - \eta_b \cdot A \xi_b \xi_b \cdot A \eta_b}{\xi_b \cdot A \xi_b} \right) x^7 + \dots$$

Since η_b and ξ_b are linearly independent, p^* is l.a.s. by the analogue of (4.13).

(b) From (4.8) and the preceding proof,

$$S = S^* + 2\gamma \xi_b - 2\alpha x^2 \xi_b - 2\beta / \alpha x y \xi_b + y^2 \eta_b.$$

If $\eta_b = 0$, then $S = S^*$ when $y - \alpha x^2 - 2\beta / \alpha x y = 0$. For x close to 0, let $y = \alpha^2 x^2 / (\alpha + \beta x)$. Since $\alpha \neq 0$, this defines a curve through p^* such that $S(p) = S^*$ for all points on this curve. The one-dimensional c.m. consists of equilibrium points of (2.2) and, by the centre manifold theorem (Wiggins, 1990), any initial point p sufficiently close to p^* will stay close to p^* and evolve to one of these equilibrium points. Similarly, if $\eta_b \neq 0$, say $\eta_b = k \xi_b$ with $k \neq 0$,

$$y = \frac{-(1 - \beta / \alpha x) + \sqrt{(1 + \beta / \alpha x)^2 - 2\alpha k x^2}}{k}$$

is a curve of equilibria corresponding to S^* through p^* .

Alternatively, $S(p)$ all lie in a one dimensional linear subspace of Δ^N as do all the S_{ij} . Thus the strategic model of viability selection can be reduced to a two-phenotype model where the evolutionary stability of an ESS is well-known. In fact, the dynamic (2.2) induces a monotone evolution of the mean strategy that is locally towards the ESS (Lessard, 1984; Cressman, 1992). \square

Acknowledgements. Comments and suggestions by Ethan Akin on the original version of this paper were greatly appreciated. This research was partially supported by the Natural Sciences and Engineering Research Council of Canada Research Grants GP7822 (R.C.) and A6187 (W.G.S.H.)

References

- Akin, E., *The Geometry of Population Genetics*, Volume 31, Lecture Notes in Biomathematics, Springer-Verlag; New York, Heidelberg, Berlin (1979)
- Arrowsmith, D. K. and Place, C. M., *An Introduction to Dynamical Systems*, Cambridge University Press (1990)
- Bomze, I. M. and Weibull, J., Does neutral stability imply Lyapunov stability? *Games Econ. Behav.* (1995) to appear
- Brooks, B. P., Some aspects of evolutionary game theory applied to diploid organisms with frequency dependent fitness, Thesis, University of Guelph (1994)
- Cressman, R., Frequency-dependent viability selection (a single-locus, multi-phenotype model), *J. Theor. Biol.* **130** (1988) 147–165
- Cressman, R., *The Stability Concept of Evolutionary Game Theory (A Dynamic Approach)*, Volume 94, Lecture Notes in Biomathematics, Springer-Verlag; Berlin, Heidelberg, New York (1992)
- Cressman, R. and Hines, W. G. S., Evolutionarily stable strategies of diploid populations with semi-dominant inheritance patterns, *J. Appl. Prob.* **23** (1984) 1–9
- Eshel, I., Evolutionarily stable strategies and viability selection in Mendelian populations, *Theor. Pop. Biol.* **22** (1982) 204–217
- Eshel, I., Game theory and population dynamics in complex genetical systems: The role of sex in short term and in long term evolution, in: *Game Equilibrium Models I (Evolution and Game Dynamics)*, R. Selten (Ed.), Springer-Verlag; Berlin, Heidelberg, New York, Tokyo (1991) 6–28
- Fisher, R. A., *The Genetical Theory of Natural Selection*, Clarendon Press; Oxford (1930)
- Gayley, T. W. and Michod, R. E., The modification of genetic constraints on frequency-dependent selection, *Am. Nat.* **136** (1990) 406–427
- Hammerstein, P. and Selten, R., Evolutionary game theory, manuscript (1992)
- Hines, W. G. S., Searching for degenerate dynamics in animal conflict game models involving sexual reproduction (1995) preprint
- Hines, W. G. S., ESS modelling of diploid populations. I: Anatomy of one-locus allelic frequency simplices, *J. Appl. Prob.* **26** (1994a) 341–360
- Hines, W. G. S., ESS modelling of diploid populations. II: Stability analysis of possible equilibria, *J. Appl. Prob.* **26** (1994b) 361–376
- Hines, W. G. S. and Bishop, D. T., Can and will a sexual diploid population attain an evolutionarily stable strategy? *J. Theor. Biol.* **111** (1984) 667–686
- Hofbauer, J., Schuster, P. and Sigmund, K., Game dynamics in Mendelian populations, *Biol. Cybern.* **43** (1982) 51–57
- Hofbauer, J. and Sigmund K., *The Theory of Evolution and Dynamical Systems*, Cambridge University Press (1988)
- Lessard, S., Evolutionary dynamics in frequency-dependent two-phenotype models, *Theor. Pop. Biol.* **25** (1984) 210–234

- Lessard, S., Resource allocation in Mendelian populations: Further in ESS theory, in: *Mathematical Evolutionary Theory*, M. W. Feldman (Ed.), Princeton University Press, Princeton (1988), 207–246
- Maynard Smith J., Will a sexual population evolve to an ESS? *Am. Nat.* **117** (1981) 1015–1018
- Thomas, B., Genetical ESS-models. I. Concepts and basic model, *Theor. Pop. Biol.* **28** (1985a) 18–32
- Thomas, B., Genetical ESS-models. II. Multi-strategy models and multiple alleles, *Theor. Pop. Biol.* **28** (1985b) 33–49
- Wiggins, S., *Introduction to Applied Nonlinear Dynamical Systems and Chaos*, Springer-Verlag: New York, Heidelberg, Berlin (1990)