



Evolutionarily Stable Strategy in a Sex- and Frequency-Dependent Selection Model*

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In this paper, a sex-dependent matrix game haploid model is investigated. For this model, since the phenotypes of female and male individuals are determined by alleles located at a single locus and are sex dependent, any given genotype corresponds to a strategy pair. Thus, a strategy pair is an ESS if and only if the allele corresponding to this strategy pair cannot be invaded by any mutant allele. We show that an ESS equilibrium must be locally asymptotically stable if it exists.

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1. Introduction

Maynard Smith (1974, 1982) (see also Maynard Smith & Price, 1973) introduced the fundamental notion of an evolutionarily stable strategy (ESS) in order to explain the evolution of behaviours. Over the past two decades, the concept of ESS has not only proved to be of practical use in the study of animal conflicts but has also generated enormous theoretical research in this area. The matrix game model is one of the most important theoretical models in evolutionary game theory. As pointed out by Lessard (1984), theoretical population biology models based on random pairwise interactions are an important source of ideas and principles that provide insight into intraspecific selection. The original matrix game model developed by Maynard Smith (1982) includes symmetric or asymmetric interactions

between two individuals (see also Hofbauer & Sigmund, 1988), for example, the Hawk–Dove model and the Battle-of-the-Sexes model. In order to model inter-specific frequency-dependent selection, Cressman (1996) extended the classical matrix game model to two-species interactions, both symmetric and asymmetric. A similar model was also discussed by Schuster *et al.* (1981). For the two-species matrix game model, Cressman (1996) defined the concept of a two-species ESS as a pair of strategies (one for each species) for which, in any given system near the ESS, at least one of the species is fitter if it adopts its ESS component.

The standard matrix game model always operates on the phenotypic level. This implies an assumption of parthenogenetic inheritance (Maynard Smith, 1982). However, most populations of interest have sexual inheritance. In the context of diploid populations, Maynard Smith (1982) pointed out that if the phenotype (pure or mixed strategy) produced by a genetic homozygote is an ESS, then a sexual population with this genotype will be stable against invasion by

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any mutant allele. If the ESS cannot be produced by a genetic homozygote, Maynard Smith also analysed the stability of a genetically polymorphic population with two alleles that can generate the ESS proportions.

The matrix game diploid model has been investigated by many authors (Maynard Smith, 1981, 1982; Eshel, 1982; Hofbauer *et al.*, 1982; Bomze *et al.*, 1983; Hines & Bishop, 1984a, b; Lessard, 1984; Cressman & Hines, 1984; Maynard Smith & Hofbauer, 1986; Koth & Sigmund, 1987; Hofbauer & Sigmund, 1988; Cressman, 1988a, b; Gayley & Michod, 1990; Hines, 1994a, b; Cressman *et al.*, 1996; Tao *et al.*, 1999). A simple two-species matrix game diploid model was also discussed by Tao (1998). All these models assume that the phenotype is sex independent. This assumption implies that the pure strategy sets for female and male individuals are the same and the phenotypes for female and male individuals are determined by the same loci, i.e. the female and male individuals with the same genotype will have the same phenotype (see also Lessard, 1984; Cressman *et al.*, 1996). If the pure strategy sets for female and male individuals are different, the phenotypes for female and male individuals can be determined by different loci (see also Koth & Sigmund, 1987; Tao, 1998). For sex-dependent but frequency-independent viability selection, Karlin & Lessard (1986) provided a thorough analysis of the one-locus model.

In this paper, a sex- and frequency-dependent matrix game model is investigated. The model is a haploid genetic model. In this model, the phenotypes for female and male individuals are determined by alleles located at a single locus and are sex dependent. This model is similar in some aspects to Cressman's (1996) two-species matrix game model, but the concept of a two-species ESS cannot be applied directly. Our main purpose is to develop ESS theory for sex- and frequency-dependent viability selection. In Section 3, the definition of an ESS for sex- and frequency-dependent viability selection and necessary and sufficient conditions for an equilibrium strategy pair to be an ESS are given. In Section 4, we show that an ESS equilibrium must be locally asymptotically stable if it exists.

2. Basic Assumptions and Model

In this paper, the following assumptions are made:

(I) Consider an infinite two-sex haploid population undergoing discrete non-overlapping generations in which there are two possible phenotypes (pure strategies), denoted by S_1 and S_2 , in the female population and two phenotypes, denoted by R_1 and R_2 , in the male population. Suppose that two alleles A_1 and A_2 located at a single locus are responsible for the phenotypic determination such that a female (male) individual with genotype A_i expresses phenotype S_1 (R_1) with probability γ_i (δ_i) and phenotype S_2 (R_2) with complementary probability $1 - \gamma_i$ ($1 - \delta_i$) for $i = 1, 2$. Therefore, a particular genotype corresponds to a strategy pair (γ, δ) where γ represents the female strategy $(\gamma, 1 - \gamma)$ and δ represents the male strategy $(\delta, 1 - \delta)$.

(II) Following Maynard Smith (1982) (see also Lessard, 1984, 1990; Hofbauer & Sigmund, 1988; Cressman, 1992, 1996), we assume that, before the time of reproduction in each generation, the individuals in the population compete randomly in pairwise contests, and that the outcomes of the contests affect the viability of the individuals (i.e. the probability of survival from the time of conception to the time of reproduction). From Maynard Smith's (1982) definition of symmetric and asymmetric contests, the payoff matrices of symmetric contests between two females and between two males are defined by $[a_{kl}]_{k,l=1,2}$ and $[d_{kl}]_{k,l=1,2}$, respectively, where a_{kl} (d_{kl}) is the viability of a female (male) exhibiting phenotype S_k (R_k) in a contest against a female (male) exhibiting phenotype S_l (R_l), and $a_{kl} \geq 0$ and $d_{kl} \geq 0$ for $k, l = 1, 2$. The payoff matrices of asymmetric contests between a female and a male are defined by $[b_{kl}]_{k,l=1,2}$ and $[c_{kl}]_{k,l=1,2}$, respectively, where b_{kl} (c_{kl}) is the viability of a female (male) exhibiting phenotype S_k (R_k) in a contest against a male (female) exhibiting phenotype R_l (S_l), and $b_{kl} \geq 0$ and $c_{kl} \geq 0$ for $k, l = 1, 2$ (Cressman, 1996; Tao, 1998).

(III) Mating between mature females and males is random in each generation at the time of reproduction. A further assumption is that there is no fertility selection in the population.

Moreover, from a mating between a female with genotype A_i and a male with genotype A_j , half of the female (male) offspring will have genotype A_i and the other half will have genotype A_j for $i, j = 1, 2$. Finally, for every mating type, let

$$\varphi = \varphi_f + \varphi_m \quad (1)$$

be the expected total number of offspring where φ_f and φ_m are the expected numbers of female and male offspring, respectively. This means that the sex ratio in the population is a fixed constant at the time of conception in each generation (actually, the proportions of female and male individuals in the population are φ_f/φ and φ_m/φ , respectively, at the time of conception).

Let p and q be the frequencies of allele A_1 in the female and male populations, respectively, at the time of conception. Then, from assumption (I), the frequency of phenotype S_1 in the female population, denoted by x , and the frequency of phenotype R_1 in the male population, denoted by y , are given by

$$\begin{aligned} x &= p\gamma_1 + (1-p)\gamma_2, \\ y &= q\delta_1 + (1-q)\delta_2, \end{aligned} \quad (2)$$

respectively. Taking into account the sex ratio at the time of conception, the viability fitnesses of phenotypes S_1 and S_2 in the female population, denoted by f_1 and f_2 , and the viability fitnesses of phenotypes R_1 and R_2 in the male population, denoted by m_1 and m_2 , are given by the following functions of x and y :

$$\begin{aligned} f_1 &= \frac{\varphi_f}{\varphi} [xa_{11} + (1-x)a_{12}] \\ &+ \frac{\varphi_m}{\varphi} [yb_{11} + (1-y)b_{12}], \\ f_2 &= \frac{\varphi_f}{\varphi} [xa_{21} + (1-x)a_{22}] \\ &+ \frac{\varphi_m}{\varphi} [yb_{21} + (1-y)b_{22}], \end{aligned} \quad (3)$$

and

$$\begin{aligned} m_1 &= \frac{\varphi_f}{\varphi} [xc_{11} + (1-x)c_{12}] \\ &+ \frac{\varphi_m}{\varphi} [yd_{11} + (1-y)d_{12}], \\ m_2 &= \frac{\varphi_f}{\varphi} [xc_{21} + (1-x)c_{22}] \\ &+ \frac{\varphi_m}{\varphi} [yd_{21} + (1-y)d_{22}], \end{aligned} \quad (4)$$

respectively. Therefore, from assumption (II), the viability fitnesses of females and males whose genotype is A_i , denoted by F_i and M_i , are given by

$$\begin{aligned} F_i &= \gamma_i f_1 + (1-\gamma_i) f_2, \\ M_i &= \delta_i m_1 + (1-\delta_i) m_2, \end{aligned} \quad (5)$$

respectively, for $i = 1, 2$, and the mean viability fitnesses of the female and male populations can be written in the forms

$$\begin{aligned} \bar{F} &= pF_1 + (1-p)F_2 \\ &= xf_1 + (1-x)f_2, \\ \bar{M} &= qM_1 + (1-q)M_2 \\ &= ym_1 + (1-y)m_2, \end{aligned} \quad (6)$$

respectively.

From eqns (5) and (6), the frequencies of allele A_1 in the female and male populations at the time of reproduction, denoted by \tilde{p} and \tilde{q} , are given by

$$\tilde{p} = \frac{pF_1}{\bar{F}}, \quad \tilde{q} = \frac{qM_1}{\bar{M}}, \quad (7)$$

respectively. Then, from assumption (III), the frequencies of allele A_1 in the female and male populations at the beginning of the next

generation will be

$$p' = \frac{\tilde{p}\tilde{q}\varphi_f + \frac{1}{2}\tilde{p}(1-\tilde{q})\varphi_f + \frac{1}{2}(1-\tilde{p})\tilde{q}\varphi_f}{\tilde{p}\tilde{q}\varphi_f + \tilde{p}(1-\tilde{q})\varphi_f + (1-\tilde{p})\tilde{q}\varphi_f + (1-\tilde{p})(1-\tilde{q})\varphi_f} = \frac{1}{2}(\tilde{p} + \tilde{q}),$$

$$q' = \frac{\tilde{p}\tilde{q}\varphi_m + \frac{1}{2}\tilde{p}(1-\tilde{q})\varphi_m + \frac{1}{2}(1-\tilde{p})\tilde{q}\varphi_m}{\tilde{p}\tilde{q}\varphi_m + \tilde{p}(1-\tilde{q})\varphi_m + (1-\tilde{p})\tilde{q}\varphi_m + (1-\tilde{p})(1-\tilde{q})\varphi_m} = \frac{1}{2}(\tilde{p} + \tilde{q}), \quad (8)$$

respectively. Equation (8) shows that, for any initial frequencies of allele A_1 in the female and male populations, we always have $p' = q'$ at the beginning of the next generation. Thus, the line

$$p - q = 0 \quad (9)$$

is invariant after the initial generation. This implies that the female and male populations have the same gene frequency distribution at the time of conception at least after the initial generation. From this property and using eqn (7), eqn (8) can be rewritten as

$$p' = q' = p \frac{F_1\bar{M} + M_1\bar{F}}{2\bar{F}\bar{M}}, \quad (10)$$

where

$$F_1\bar{M} + M_1\bar{F}$$

is the marginal fitness of allele A_1 (see e.g. Ewens, 1979). Similarly,

$$F_2\bar{M} + M_2\bar{F}$$

will be the marginal fitness of allele A_2 .

3. Evolutionarily Stable Strategy

The concept of an equilibrium strategy is one of the most important theoretical concepts in classical evolutionary game theory (Maynard Smith, 1982; Hofbauer & Sigmund, 1988; Lessard, 1990; Cressman, 1992; Weibull, 1995). Following Cressman's (1996) approach for two-species models, we define a strategy pair (x^*, y^*) (where $0 \leq x^*, y^* \leq 1$) as an equilibrium strategy if and only if

$$f_1(x^*, y^*) = f_2(x^*, y^*) = f^*,$$

$$m_1(x^*, y^*) = m_2(x^*, y^*) = m^*, \quad (11)$$

i.e. both female phenotypes S_1 and S_2 and both male phenotypes R_1 and R_2 have the same fitnesses. It is assumed throughout that $f^*, m^* > 0$. Notice that condition (11) involves only the phenotypic parameters of the model. Solving eqn (11) yields

$$x^* = \frac{\beta_1\alpha_{22} - \beta_2\alpha_{12}}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}},$$

$$y^* = \frac{\beta_2\alpha_{11} - \beta_1\alpha_{21}}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}}, \quad (12)$$

where

$$\alpha_{11} = \frac{\varphi_f}{\varphi} (a_{11} - a_{12} - a_{21} + a_{22}),$$

$$\alpha_{12} = \frac{\varphi_m}{\varphi} (b_{11} - b_{12} - b_{21} + b_{22}),$$

$$\alpha_{21} = \frac{\varphi_f}{\varphi} (c_{11} - c_{12} - c_{21} + c_{22}),$$

$$\alpha_{22} = \frac{\varphi_m}{\varphi} (d_{11} - d_{12} - d_{21} + d_{22}),$$

$$\beta_1 = \frac{\varphi_f}{\varphi} (a_{22} - a_{12}) + \frac{\varphi_m}{\varphi} (b_{22} - b_{21}),$$

$$\beta_2 = \frac{\varphi_f}{\varphi} (c_{22} - c_{12}) + \frac{\varphi_m}{\varphi} (d_{22} - d_{12}) \quad (13)$$

and

$$\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} \neq 0. \quad (14)$$

This inequality implies that both α_{i1} and α_{i2} cannot be zero for $i = 1, 2$. Equation (12) shows that

if an equilibrium strategy (x^*, y^*) exists, then it must be unique.

From the classical evolutionary game model, an ESS is a strategy with the property that, if all members of the population adopt it, then no mutant can invade under the influence of natural selection. For the two-species model developed by Cressman (1996), which concerns the coevolution of two populations, an ESS (which is also called a two-species ESS by Cressman) is defined to be a strategy pair that cannot be successfully invaded by any mutant pair.

For our model, since both the female and male strategies are determined by alleles located at a single locus, i.e. the strategy is sex dependent, we have the following definition:

Definition 1. An equilibrium strategy pair (x^*, y^*) corresponding to the genotype A^* is an ESS if and only if the allele A^* cannot be invaded by any mutant allele under the influence of natural selection when all members of the population have genotype A^* .

In order to illustrate this definition, suppose that the population consists of individuals with genotype A^* or \hat{A} where the genotype \hat{A} corresponds to the strategy pair (\hat{x}, \hat{y}) . Since the female and male populations have the same gene frequency distribution at the time of conception, let $1 - \varepsilon$ and ε be the frequencies of alleles A^* and \hat{A} in the population, respectively, at the time of conception. Then the frequency of phenotype S_1 in the female population and the frequency of phenotype R_1 in the male population are given by

$$\begin{aligned} x &= (1 - \varepsilon)x^* + \varepsilon\hat{x}, \\ y &= (1 - \varepsilon)y^* + \varepsilon\hat{y}, \end{aligned} \quad (15)$$

respectively. From eqn (5), the viability fitnesses of the females and males whose genotype is A^* are

$$\begin{aligned} F_{(A^*)} &= x^*f_1 + (1 - x^*)f_2, \\ M_{(A^*)} &= y^*m_1 + (1 - y^*)m_2, \end{aligned} \quad (16)$$

respectively. Similarly, the viability fitnesses of the females and males whose genotype is \hat{A} are

$$\begin{aligned} F_{(\hat{A})} &= \hat{x}f_1 + (1 - \hat{x})f_2, \\ M_{(\hat{A})} &= \hat{y}m_1 + (1 - \hat{y})m_2, \end{aligned} \quad (17)$$

respectively. From eqn (10), the dynamics for ε is given by the recurrence equation

$$\varepsilon' = \varepsilon \frac{F_{(\hat{A})}\bar{M} + M_{(\hat{A})}\bar{F}}{2\bar{F}\bar{M}}, \quad (18)$$

where

$$\begin{aligned} \bar{F} &= (1 - \varepsilon)F_{(A^*)} + \varepsilon F_{(\hat{A})} \\ &= xf_1 + (1 - x)f_2, \\ \bar{M} &= (1 - \varepsilon)M_{(A^*)} + \varepsilon M_{(\hat{A})} \\ &= ym_1 + (1 - y)m_2. \end{aligned} \quad (19)$$

Our definition means that if the strategy pair (x^*, y^*) is an ESS, then, when $\varepsilon > 0$ is sufficiently small, we must have $\varepsilon' < \varepsilon$, that is,

$$\begin{aligned} &[F_{(\hat{A})} - \bar{F}]\bar{M} + [M_{(\hat{A})} - \bar{M}]\bar{F} \\ &= \varepsilon[(\hat{x} - x^*)(f_1 - f_2)\bar{M} \\ &\quad + (\hat{y} - y^*)(m_1 - m_2)\bar{F}] < 0 \end{aligned} \quad (20)$$

for all possible (\hat{x}, \hat{y}) but $(\hat{x}, \hat{y}) \neq (x^*, y^*)$. Notice that, when ε is sufficiently small, \bar{F} and \bar{M} can be approximated as

$$\begin{aligned} \bar{F} &\approx \bar{F}(x^*, y^*) = x^*f_1(x^*, y^*) \\ &\quad + (1 - x^*)f_2(x^*, y^*) = f^*, \\ \bar{M} &\approx \bar{M}(x^*, y^*) = y^*m_1(x^*, y^*) \\ &\quad + (1 - y^*)m_2(x^*, y^*) = m^*. \end{aligned} \quad (21)$$

Since the strategy pair (x^*, y^*) is an equilibrium strategy defined by eqn (11), then, from the

equalities

$$\begin{aligned} f_1 - f_2 &= \alpha_{11}(x - x^*) + \alpha_{12}(y - y^*) \\ &= \varepsilon[\alpha_{11}(\hat{x} - x^*) + \alpha_{12}(\hat{y} - y^*)], \end{aligned}$$

$$\begin{aligned} m_1 - m_2 &= \alpha_{21}(x - x^*) + \alpha_{22}(y - y^*) \\ &= \varepsilon[\alpha_{21}(\hat{x} - x^*) + \alpha_{22}(\hat{y} - y^*)], \end{aligned}$$

inequality (20) holds if and only if

$$\begin{aligned} (x^* - \hat{x})[\alpha_{11}(\hat{x} - x^*) + \alpha_{12}(\hat{y} - y^*)]m^* \\ + (y^* - \hat{y})[\alpha_{21}(\hat{x} - x^*) \\ + \alpha_{22}(\hat{y} - y^*)]f^* > 0 \end{aligned} \tag{22}$$

for all possible (\hat{x}, \hat{y}) but $(\hat{x}, \hat{y}) \neq (x^*, y^*)$.

Let

$$s = \hat{x} - x^*, \quad t = \hat{y} - y^*, \tag{23}$$

so that inequality (22) can be rewritten as

$$\alpha_{11}m^*s^2 + (\alpha_{12}m^* + \alpha_{21}f^*)st + \alpha_{22}f^*t^2 < 0 \tag{24}$$

for all possible (s, t) but $(s, t) \neq (0, 0)$.

For convenience, let

$$Z(s, t) = as^2 + bst + ct^2, \tag{25}$$

where

$$\begin{aligned} a &= \alpha_{11}m^*, \quad b = \alpha_{12}m^* + \alpha_{21}f^*, \\ c &= \alpha_{22}f^*. \end{aligned} \tag{26}$$

Since $Z(s, 0) < 0$ holds for all possible $s \neq 0$ if and only if $a < 0$, i.e. $\alpha_{11} < 0$, and $Z(0, t) < 0$ holds all possible $t \neq 0$ if and only if $c < 0$, i.e. $\alpha_{22} < 0$, the necessary condition for inequality (24) to hold is

$$\alpha_{ii} < 0 \quad \text{for } i = 1, 2. \tag{27}$$

In order to determine a sufficient condition for inequality (24) to hold, we first consider the

situation for $s \neq 0$. For $s \neq 0$, $Z(s, t)$ can be expressed as

$$Z(s, t) = s^2\tilde{Z}(v), \tag{28}$$

where

$$v = \frac{t}{s} \tag{29}$$

and

$$\tilde{Z}(v) = a + bv + cv^2. \tag{30}$$

Notice that $\tilde{Z}(0) = a < 0$ owing to eqn (27) and the solution of the equation $d\tilde{Z}/dv = 0$ is

$$v^* = -\frac{b}{2c}. \tag{31}$$

Moreover, we know that

$$\tilde{Z}(v^*) = \frac{1}{4c}(4ac - b^2) \tag{32}$$

is the maximum of $\tilde{Z}(v)$, where

$$\begin{aligned} 4ac - b^2 &= 4\alpha_{11}\alpha_{22}f^*m^* \\ &\quad - (\alpha_{12}m^* + \alpha_{21}f^*)^2. \end{aligned} \tag{33}$$

Clearly, if $4ac - b^2 > 0$, then $\tilde{Z}(v) < 0$ holds for all possible v . If $4ac - b^2 \leq 0$, then we have $\tilde{Z}(v^*) \geq 0$. It is necessary to point out that when the variable v is defined in the interval $(-\infty, \infty)$, i.e. the equilibrium strategy (x^*, y^*) is not a pure strategy pair, $\tilde{Z}(v^*) \geq 0$ implies that there must exist some v such that $\tilde{Z}(v) < 0$ cannot be satisfied. Thus, if the equilibrium strategy (x^*, y^*) is not a pure strategy pair, then $\tilde{Z}(v) < 0$ holds for all possible v if and only if $4ac - b^2 > 0$.

On the other hand, when the variable v is defined in the interval $[0, \infty)$, i.e. pure strategy pair $(0, 0)$, or $(1, 1)$, is an equilibrium strategy (this means that $(x^*, y^*) = (0, 0)$, or $(1, 1)$), or when the variable v is defined in the interval $(-\infty, 0]$, i.e. pure strategy pair $(0, 1)$, or $(1, 0)$, is an equilibrium strategy (this means that $(x^*, y^*) = (0, 1)$, or $(1, 0)$), the nature of $\tilde{Z}(v)$ is determined by the sign of b under the condition $4ac - b^2 \leq 0$. Since

$v^* < 0$ if $b < 0$ and $v^* > 0$ if $b > 0$, then we have that $\tilde{Z}(v) < 0$ holds for $v \geq 0$ if $b < 0$, or for $v \leq 0$ if $b > 0$. Otherwise, for $v \geq 0$, or $v \leq 0$, if $b > 0$, or $b < 0$, there must exist some v such that $\tilde{Z}(v) < 0$ cannot be satisfied. Thus, under the condition $4ac - b^2 \leq 0$, when the pure strategy pair $(0, 0)$, or $(1, 1)$, is an equilibrium strategy, $\tilde{Z}(v) < 0$ holds for all possible v in the interval $[0, \infty)$ if and only if $b < 0$, and when the pure strategy pair $(0, 1)$, or $(1, 0)$, is an equilibrium strategy, $\tilde{Z}(v) < 0$ holds for all possible v in the interval $(-\infty, 0]$ if and only if $b > 0$.

For $t \neq 0$, we can get similar results.

Summarizing the above analysis, we have:

Result 1. (i) *If an equilibrium strategy (x^*, y^*) is not a pure strategy pair, then it is an ESS if and only if $\alpha_{ii} < 0$ for $i = 1, 2$ and $4\alpha_{11}\alpha_{22}f^*m^* - (\alpha_{12}m^* + \alpha_{21}f^*)^2 > 0$;*

(ii) *When the pure strategy pair $(0, 0)$, or $(1, 1)$, is an equilibrium strategy, $\alpha_{ii} < 0$ for $i = 1, 2$, and $4\alpha_{11}\alpha_{22}f^*m^* - (\alpha_{12}m^* + \alpha_{21}f^*)^2 > 0$, then it is an ESS. On the other hand, if $4\alpha_{11}\alpha_{22}f^*m^* - (\alpha_{12}m^* + \alpha_{21}f^*)^2 \leq 0$, then the pure strategy pair $(0, 0)$, or $(1, 1)$, is an ESS if and only if $\alpha_{ii} < 0$ for $i = 1, 2$ and $\alpha_{12}m^* + \alpha_{21}f^* < 0$;*

(iii) *When the pure strategy pair $(0, 1)$, or $(1, 0)$, is an equilibrium strategy, $\alpha_{ii} < 0$ for $i = 1, 2$ and $4\alpha_{11}\alpha_{12}f^*m^* - (\alpha_{12}m^* + \alpha_{21}f^*)^2 > 0$, then it is an ESS. On the other hand, if $4\alpha_{11}\alpha_{22}f^*m^* - (\alpha_{12}m^* + \alpha_{21}f^*)^2 \leq 0$, then the pure strategy pair $(0, 1)$, or $(1, 0)$, is an ESS if and only if $\alpha_{ii} < 0$ for $i = 1, 2$ and $\alpha_{12}m^* + \alpha_{12}f^* > 0$.*

It is useful to point out the following facts:

(1) If there are no asymmetric contests in the population, i.e. $\alpha_{12} = 0$ and $\alpha_{21} = 0$, then an equilibrium strategy is an ESS if and only if $\alpha_{11} < 0$ and $\alpha_{22} < 0$. This result corresponds to Maynard Smith's (1982) classical Hawk-Dove model (see also Lessard, 1984; Hofbauer & Sigmund, 1988; Cressman, 1992; Weibull, 1995).

(2) If there are no symmetric contests in the population, i.e. $\alpha_{11} = 0$ and $\alpha_{22} = 0$, then no equilibrium strategy can be an ESS. This result corresponds to Maynard Smith's (1982) classical Battle-of-the-Sexes model (see also Hofbauer & Sigmund, 1988; Cressman, 1992; Weibull, 1995).

(3) If both symmetric and asymmetric contests coexist in the population, our result is similar in some aspects to Cressman's (1996) result for the two-species model, but our condition for an equilibrium strategy to be an ESS is more restrictive. This means that if an equilibrium strategy is an ESS under our definition, then it must be a two-species ESS under Cressman's (1996) definition (see also Tao, 1998).

4. Stability Analysis

4.1. EQUILIBRIUM POINTS

Obviously, an interior fixed point of eqn (10), that is a frequency p in $(0, 1)$ satisfying $p' = p$, is characterized by the equation

$$(F_1 - F_2)\bar{M} + (M_1 - M_2)\bar{F} = 0. \quad (34)$$

Notice that at most three interior fixed points can exist since eqn (34) is a cubic equation in p .

Similar to Lessard's (1984) definition of phenotypic and genotypic equilibria (see also Hofbauer & Sigmund, 1988; Cressman, 1992), we introduce the following terminology.

Definition 2. (i) If there exists some p^* in $(0, 1)$ such that $x(p^*) = x^*$ and $y(p^*) = y^*$ (where $0 \leq x^*, y^* \leq 1$) satisfy (11), then p^* is called a phenotypic equilibrium corresponding to an attainable equilibrium strategy pair (x^*, y^*) , i.e.

$$p^* = \frac{x^* - \gamma_2}{\gamma_1 - \gamma_2} = \frac{y^* - \delta_2}{\delta_1 - \delta_2}. \quad (35)$$

For convenience, p^* is called an ESS equilibrium if and only if (x^*, y^*) is an ESS. Otherwise, p^* is called a non-ESS equilibrium.

(ii) All possible non-phenotypic interior fixed points of eqn (10), where the marginal fitnesses of alleles A_1 and A_2 are equal, i.e.

$$F_1\bar{M} + M_1\bar{F} = F_2\bar{M} + M_2\bar{F}$$

but

$$F_1 \neq F_2, \quad M_1 \neq M_2,$$

are called genotypic equilibria.

(iii) If (γ_1, δ_1) , or (γ_2, δ_2) , is an equilibrium strategy, then $p = 1$, or $p = 0$, is called a boundary-phenotypic equilibrium. Furthermore, $p = 1$, or $p = 0$, is called an ESS boundary-phenotypic equilibrium if and only if the strategy pair (γ_1, δ_1) or (γ_2, δ_2) , is an ESS. Conversely, if (γ_1, δ_1) , or (γ_2, δ_2) , is not an equilibrium strategy, then $p = 1$, or $p = 0$, is called a boundary-genotypic equilibrium.

4.2. DYNAMICAL PROPERTIES

In this subsection, we study the dynamical properties of eqn (10). From the theory of difference equations, a possible equilibrium of eqn (10) (interior or on the boundary) is stable if $|dp'/dp| < 1$ at this point. Moreover, the transformation is monotone if $dp'/dp > 0$.

From eqn (10), we get

$$\begin{aligned} \frac{dp'}{dp} = \frac{1}{2} & \left[\frac{F_1 F_2 + p(1-p) \left(\frac{dF_1}{dp} F_2 - F_1 \frac{dF_2}{dp} \right)}{\bar{F}^2} \right. \\ & \left. + \frac{M_1 M_2 + p(1-p) \left(\frac{dM_1}{dp} M_2 - M_1 \frac{dM_2}{dp} \right)}{\bar{M}^2} \right]. \end{aligned} \quad (36)$$

Notice that F_i and M_i are linear function of p , and

$$\begin{aligned} F_i(0) &= \gamma_i f_1(\gamma_2, \delta_2) + (1 - \gamma_i) f_2(\gamma_2, \delta_2) > 0, \\ F_i(1) &= \gamma_i f_1(\gamma_1, \delta_1) + (1 - \gamma_i) f_2(\gamma_1, \delta_1) > 0, \\ M_i(0) &= \delta_i m_1(\gamma_2, \delta_2) + (1 - \delta_i) m_2(\gamma_2, \delta_2) > 0, \\ M_i(1) &= \delta_i m_1(\gamma_1, \delta_1) + (1 - \delta_i) m_2(\gamma_1, \delta_1) > 0 \end{aligned} \quad (37)$$

for $i = 1, 2$. Then F_i and M_i can be expressed as

$$\begin{aligned} F_i &= pF_i(1) + (1 - p)F_i(0), \\ M_i &= pM_i(1) + (1 - p)M_i(0) \end{aligned} \quad (38)$$

for $i = 1, 2$. Using this, we have

$$\begin{aligned} F_1 F_2 + p(1-p) \left(\frac{dF_1}{dp} F_2 - F_1 \frac{dF_2}{dp} \right) \\ = p^2 F_1(1) F_2(1) + 2p(1-p) F_1(1) F_2(0) \\ + (1-p)^2 F_1(0) F_2(0) > 0 \end{aligned} \quad (39)$$

and

$$\begin{aligned} M_1 M_2 + p(1-p) \left(\frac{dM_1}{dp} M_2 - M_1 \frac{dM_2}{dp} \right) \\ = p^2 M_1(1) M_2(1) + 2p(1-p) M_1(1) M_2(0) \\ + (1-p)^2 M_1(0) M_2(0) > 0. \end{aligned} \quad (40)$$

Therefore, for all p in $(0, 1)$, we have always $dp'/dp > 0$. This property implies the following dynamical result.

Result 2. *For eqn (10), periodic and chaotic behaviours cannot exist, and the iterates always monotonically converge to a stable equilibrium for any initial point.*

Obviously, the above result should be considered to be an extension of Lessard's (1984) result for the classical two-phenotype diploid model (see also Hofbauer & Sigmund, 1988; Cressman, 1992).

Notice that the fixation states $p = 1$ and $p = 0$ correspond to the strategy pairs (γ_1, δ_1) and (γ_2, δ_2) , respectively. According to the definition of an ESS in Section 3, if (γ_1, δ_1) , or (γ_2, δ_2) , is an ESS, then, when all members of the population have genotype A_1 , or A_2 , the allele A_1 , or A_2 , cannot be invaded by any mutant allele under the influence of natural selection. Thus, the fixation state $p = 1$, or $p = 0$, is stable if and only if strategy pair (γ_1, δ_1) , or (γ_2, δ_2) , is an ESS.

Since at most three interior fixed points can exist, the relationship between the existence and stability of interior fixed points and the stability of the fixation states can easily be deduced.

Result 3. (i) *If both fixation states $p = 0$ and $p = 1$ are stable, then one or three interior fixed points*

can exist. If only one interior fixed point exists, then it must be unstable. If there are three interior fixed points, denoted by \hat{p}_1 , \hat{p}_2 and \hat{p}_3 and $\hat{p}_1 < \hat{p}_2 < \hat{p}_3$, then \hat{p}_2 is stable and \hat{p}_1 and \hat{p}_3 are unstable.

(ii) If both fixation states $p = 0$ and $p = 1$ are unstable, then one or three interior fixed points can exist. If only one interior fixed point exists, then it must be stable. If there are three interior fixed points, denoted by \hat{p}_1 , \hat{p}_2 and \hat{p}_3 and $\hat{p}_1 < \hat{p}_2 < \hat{p}_3$, then \hat{p}_2 is unstable and \hat{p}_1 and \hat{p}_3 are stable.

(iii) If $p = 0$ is stable and $p = 1$ is unstable, or $p = 0$ is unstable and $p = 1$ is stable, then no or two interior fixed points can exist. If there exist two interior fixed points, denoted by \hat{p}_1 and \hat{p}_2 and $\hat{p}_1 < \hat{p}_2$, then \hat{p}_1 is unstable and \hat{p}_2 is stable if and only if $p = 0$ is stable and $p = 1$ is unstable, and \hat{p}_1 is stable and \hat{p}_2 is unstable if and only if $p = 0$ is unstable and $p = 1$ is stable.

4.3. LOCAL STABILITY OF THE ESS EQUILIBRIUM

If a phenotypic equilibrium p^* corresponding to the strategy pair (x^*, y^*) exists and p^* is an ESS equilibrium, then p^* is locally asymptotically stable if

$$\left. \frac{dp'}{dp} \right|_{p^*} < 1. \quad (41)$$

From the definition of an ESS equilibrium and eqns (36)–(38), we get

$$\begin{aligned} \left. \frac{dp'}{dp} \right|_{p^*} &= 1 + \frac{p^*(1-p^*)}{2f^*m^*} \{(\gamma_1 - \gamma_2)[(\gamma_1 - \gamma_2)\alpha_{11} \\ &+ (\delta_1 - \delta_2)\alpha_{12}]m^* \\ &+ (\delta_1 - \delta_2)[(\gamma_1 - \gamma_2)\alpha_{21} \\ &+ (\delta_1 - \delta_2)\alpha_{22}]f^*\}. \end{aligned} \quad (42)$$

Since p^* is an ESS equilibrium, we have inequality (22) and

$$\begin{aligned} &(x^* - \gamma_1)[\alpha_{11}(\gamma_1 - x^*) + \alpha_{12}(\delta_1 - y^*)]m^* \\ &+ (y^* - \delta_1)[\alpha_{21}(\gamma_1 - x^*) + \alpha_{22}(\delta_1 - y^*)]f^* \end{aligned}$$

$$\begin{aligned} &= -(1-p^*)^2 \{(\gamma_1 - \gamma_2)[(\gamma_1 - \gamma_2)\alpha_{11} \\ &+ (\delta_1 - \delta_2)\alpha_{12}]m^* + (\delta_1 - \delta_2)[(\gamma_1 - \gamma_2)\alpha_{21} \\ &+ (\delta_1 - \delta_2)\alpha_{22}]f^*\} > 0, \end{aligned}$$

which implies that

$$\begin{aligned} &(\gamma_1 - \gamma_2)[(\gamma_1 - \gamma_2)\alpha_{11} + (\delta_1 - \delta_2)\alpha_{12}]m^* \\ &+ (\delta_1 - \delta_2)[(\gamma_1 - \gamma_2)\alpha_{21} \\ &+ (\delta_1 - \delta_2)\alpha_{22}]f^* < 0. \end{aligned} \quad (43)$$

Therefore, if p^* is an ESS equilibrium, then, we must have $dp'/dp|_{p^*} < 1$. This result can be summarized as follows.

Result 4. For eqn (10), an ESS equilibrium is locally asymptotically stable if it exists.

5. Conclusion

The main purpose of this paper is to develop ESS theory for sex- and frequency-dependent viability selection model. In our model, since the strategies of female and male individuals are determined by alleles located at a single locus and are sex dependent, any given genotype corresponds to a strategy pair. Thus, a strategy pair is an ESS if and only the allele corresponding to this strategy pair cannot be invaded by any mutant allele. Obviously, this definition is identical to Maynard Smith's (1982) definition for the sex-independent matrix game diploid model (see Section 1). On the other hand, although the two-species ESS defined by Cressman (1996) also concerns a strategy pair, the concept of a two-species ESS cannot be applied directly to our model. In fact, the ESS condition for the sex- and frequency-dependent viability selection model turns out to be more restrictive than the condition for a two-species ESS.

In Section 4, we have shown that an ESS equilibrium must be locally asymptotically stable if it exists. This means that for the sex- and frequency-dependent viability selection model, the population may evolve to an ESS. But this may not necessarily be the case for the two-species discrete-time model.

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