



Frequency-dependent Selection in Sexual Family-structured Populations†

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In this paper, a two-phenotype, single-locus, n -allele matrix game diploid model incorporating interactions between full sibs influencing personal fitness is investigated. Necessary and sufficient conditions for an ESS are given. We show that if a strategy is an ESS for this model with the payoff matrix \mathbf{A} , then it must be an ESS for the standard game formulation with payoff matrix $\mathbf{A} + (r/2)\mathbf{A}^T$ where r is the probability to interact with a sib, but it is also possible that no ESS exists. Moreover, under the assumption of weak selection, the partial change in phenotype frequencies brings the population closer to an ESS when it exists.

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1. Introduction

It is well known that the classical explanation in theoretical biology of altruistic behaviour is due to Hamilton (1964a,b), who first recognized that genes could succeed without necessarily enhancing the reproductive fitness of their particular bearers but by improving the reproductive success of their kin, who bear copies of the same genes. This led to the concept of *kin selection* and *inclusive fitness*.

In order to incorporate kin selection into evolutionary game theory (Maynard Smith, 1974, 1982), Mirmirani & Oster (1978) proposed the following model. If $E(x, y)$ represents the payoff (i.e. change in classical fitness) to an

individual adopting strategy x against an opponent adopting strategy y , then the change in inclusive fitness (Hamilton, 1964a) of the individual adopting strategy x is supposed to be

$$E(x, y) + rE(y, x),$$

where r is a coefficient of relatedness. This model leads to a new payoff matrix, containing as entries changes in inclusive fitness instead of changes in classical fitness, and an evolutionarily stable strategy (ESS) can then be sought for this new payoff matrix by the usual method (Maynard Smith, 1982). However, Grafen (1979) pointed out that the model proposed by Mirmirani & Oster (1978) contains an apparent fallacy. Although $E(x, y) + rE(y, x)$ correctly measures the change in inclusive fitness of an x -strategist in a single contest against a y -strategist, an x -strategist is more likely than any other member of the population to play against an opponent adopting strategy x if the opponents are related. Grafen (1979) proposed the following model.

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Let $W(x)$ represent the change in *personal fitness* of an x -strategist and β be the mean strategy of the population. Then, we have

$$W(x) = rE(x, x) + (1 - r)E(x, \beta),$$

where r is the probability that an individual will meet an opponent adopting a strategy identical to its own because of genetical relationship. We emphasize that personal fitness modifies classical fitness by allowing for the effects that an individual's relatives will have on the number of its own offspring that survive, whereas inclusive fitness modifies classical fitness by allowing for the effects that an individual will have on the numbers of its relatives' offspring that survive (see also Hines & Maynard Smith, 1979; Hines, 1987). Following Grafen (1979), Hines & Maynard Smith (1979) investigated an asexual haploid model in which an individual plays against a member of its own clone with probability r and against a randomly chosen opponent with complementary probability $1 - r$. Their analysis shows that an evolutionarily stable strategy (ESS) under the definition of personal fitness, which was called a personal-fitness ESS corresponds to an ESS for the standard formulation, but with the payoff matrix \mathbf{A} replaced by $\mathbf{A} + r\mathbf{A}^T$ (where \mathbf{A}^T denotes the transpose of \mathbf{A}). Although this result seems to be in agreement with that suggested by the concept of inclusive fitness, where r is interpreted as Wright's (1922) coefficient of relationship, the attainment of an ESS (for $\mathbf{A} + r\mathbf{A}^T$) does not result in equal fitness for all strategies (Hines, 1987; Taylor, 1989; Vincent & Cressman, 2000).

The concept of partial change in the mean fitness of a population has been developed by Ewens (1989) in order to illustrate the general validity of Fisher's (1930) fundamental theorem of natural selection (FTNS). Ewens (1989) interprets the FTNS in the case of a population undergoing discrete, non-overlapping generations as follows: *the partial change in the mean fitness of the population is exactly equal to the ratio of the additive genetic variance in fitness over the mean fitness*. The partial change in the mean fitness is obtained by replacing the actual genotypic fitnesses by the corresponding additive values and by keeping these values fixed in the

change of the mean with respect to the changes in the genotypic frequencies (see also Ewens, 1992; Lessard & Castilloux, 1995; Castilloux & Lessard, 1995; and Lessard, 1997 for another interpretation). Recently, Tao & Lessard (2000) studied the partial changes in the phenotypic frequencies in the classical matrix game diploid model, i.e. the changes in the phenotypic frequencies due only to the changes in the genotypic frequencies, and investigated the relationship between the partial change in the mean fitness of the population and the partial changes in the phenotypic frequencies. Similarly to the partial change in the mean fitness of the population, the partial changes in the phenotypic frequencies are obtained by replacing the actual phenotypes of the individuals by the corresponding additive genetic values and by keeping these values fixed in the changes of the phenotypic frequencies with respect to the changes in the genotypic frequencies.

In this paper, a matrix game diploid model based on the definition of personal fitness in the case of pairwise contests between relatives is investigated. In this model, there are two phenotypes and they are determined by multiple alleles located at a single locus. We assume that mating is random and consider only kin selection effects between full sibs. Our main purpose is to develop the ESS theory in the context of frequency-dependent viability selection in family-structured populations. In Section 2, a definition of personal fitness for a diploid model is presented. This definition is a natural extension of the original definition of Hines & Maynard Smith (1979) for a haploid model. In Section 3, the conditions for an ESS in our model are deduced. For the classical two-phenotype matrix game diploid model, Lessard (1984) showed that there should be evolution, through mutations if necessary, to an ESS, which was then called *evolutionarily attractive*. For our model, a similar question is: should there be evolution to an ESS in family-structured populations? In Section 4, the relationship between an ESS when it exists and the partial changes in the phenotypic frequencies under the assumption of weak selection is analysed.

2. Model and Definitions

Consider an infinite diploid population undergoing non-overlapping, discrete generations in which there are two possible pure strategies, denoted by R_1 and R_2 . Suppose that n alleles G_1, G_2, \dots, G_n located at a single locus are responsible for the phenotypic determination such that an individual with genotype G_iG_j uses strategy R_1 with probability h_{ij} and strategy R_2 with complementary probability $1 - h_{ij}$ for $i, j = 1, 2, \dots, n$. For convenience, the phenotype of individuals with genotype G_iG_j is expressed as

$$\mathbf{h}_{ij} = (h_{ij}, 1 - h_{ij}) \tag{1}$$

for $i, j = 1, 2, \dots, n$. Of course, the pure strategies R_1 and R_2 can also be expressed as $R_1 = (1, 0)$ and $R_2 = (0, 1)$, respectively. All other phenotypes are called mixed strategies.

We assume that there is no fertility selection in the population, and that mating is random at the time of reproduction. Following Maynard Smith (1982) (see also Lessard, 1984, Hofbauer & Sigmund, 1988, 1998; Cressman, 1992), there are interactions between individuals before the time of reproduction and these are pairwise contests, whose outcomes affect the viability of the individuals. Let a_{kl} be the viability of an individual using strategy R_k in a contest against an opponent using strategy R_l for $k, l = 1, 2$. The viability payoff matrix is given by

$$\mathbf{A} = (a_{kl})_{k,l=1,2}, \tag{2}$$

where $a_{kl} \geq 0$ for all $k, l = 1, 2$.

In this paper, we consider only contests between either full sibs or unrelated opponents. We accept the basic definition of Hines & Maynard Smith (1979) for personal fitness (see also Hines, 1987). For a haploid model, Hines & Maynard Smith (1979) considered that an individual plays against a member of its own clone with probability r and against a randomly chosen opponent with complementary probability $1 - r$. For our diploid model, we make the following assumption.

Assumption. An individual plays against a randomly chosen member among its full sibs with probability r ($0 < r < 1$) and against a randomly

chosen opponent from the population with complementary probability $1 - r$.

Obviously, this assumption is a natural extension of the original assumption of Hines & Maynard Smith (1979). According to this assumption, the personal viability fitness of an individual adopting strategy \mathbf{h} is given by

$$r\mathbf{h} \cdot \mathbf{A}\bar{\mathbf{h}}_{sib} + (1 - r)\mathbf{h} \cdot \mathbf{A}\bar{\mathbf{h}}, \tag{3}$$

where $\bar{\mathbf{h}}_{sib}$ represents the average strategy of its sibs and $\bar{\mathbf{h}}$ represents the mean strategy of the population (for convenience, the personal viability fitness is called simply fitness in the following).

Let $2\tilde{P}_{ij}$ be the frequency of genotype G_iG_j if $i \neq j$ and \tilde{P}_{ii} be the frequency of genotype G_iG_i at the time of reproduction of the previous generation for $i, j = 1, 2, \dots, n$. Since there is no fertility selection and mating is random, the frequency of allele G_i at the beginning of the current generation, denoted by p_i , is

$$p_i = \sum_{j=1}^n \tilde{P}_{ij} \tag{4}$$

for $i = 1, 2, \dots, n$, and the frequency of phenotype R_1 at the beginning of the current generation, denoted by \bar{h} , is

$$\bar{h} = \sum_{i,j=1}^n p_i p_j h_{ij}. \tag{5}$$

If $\bar{\mathbf{h}}$ represent the mean strategy of the population, then we have

$$\begin{aligned} \bar{\mathbf{h}} &= (\bar{h}, 1 - \bar{h}) \\ &= \sum_{i,j=1}^n p_i p_j \mathbf{h}_{ij}. \end{aligned} \tag{6}$$

For the mating type $G_iG_k \times G_jG_l$ ($i, j, k, l = 1, 2, \dots, n$), the four possible genotypes G_iG_j, G_iG_l, G_jG_k and G_kG_l will have the same proportion in the offspring, which is $\frac{1}{4}$. Then, the average strategy of the offspring coming from the mating type $G_iG_k \times G_jG_l$ should be $(\mathbf{h}_{ij} + \mathbf{h}_{il} + \mathbf{h}_{jk} + \mathbf{h}_{kl})/4$. According to eqn (3), the

fitness of an offspring with genotype G_iG_j coming from the mating type $G_iG_k \times G_jG_l$ is

$$r\mathbf{h}_{ij} \cdot \mathbf{A} \left(\frac{\mathbf{h}_{ij} + \mathbf{h}_{il} + \mathbf{h}_{jk} + \mathbf{h}_{kl}}{4} \right) + (1-r)\mathbf{h}_{ij} \cdot \mathbf{A}\bar{\mathbf{h}}. \quad (7)$$

Note that, for a randomly chosen offspring with genotype G_iG_j , the probability that this offspring comes from the mating type $G_iG_k \times G_jG_l$ is

$$\frac{\tilde{P}_{ik}\tilde{P}_{jl}}{\sum_{k,l=1}^n \tilde{P}_{ik}\tilde{P}_{jl}} = \frac{\tilde{P}_{ik}\tilde{P}_{jl}}{p_i p_j}. \quad (8)$$

Thus, the expected fitness of an offspring with genotype G_iG_j , denoted by F_{ij} , is

$$F_{ij} = \sum_{k,l=1}^n \frac{\tilde{P}_{ik}\tilde{P}_{jl}}{p_i p_j} \left[r\mathbf{h}_{ij} \cdot \mathbf{A} \left(\frac{\mathbf{h}_{ij} + \mathbf{h}_{il} + \mathbf{h}_{jk} + \mathbf{h}_{kl}}{4} \right) + (1-r)\mathbf{h}_{ij} \cdot \mathbf{A}\bar{\mathbf{h}} \right], \quad (9)$$

for $i, j = 1, 2, \dots, n$.

3. Evolutionarily Stable Strategy

Maynard Smith (1982) pointed out that 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 our model, since the phenotypes are determined by alleles located at a single locus, we use the following definition.

Definition. A strategy \mathbf{h}^* (where $\mathbf{h}^* = (h^*, 1 - h^*)$) corresponding the genotype G^*G^* is an ESS if and only if allele G^* cannot be invaded by any mutant allele under the influence of natural selection when all members of the population have genotype G^*G^* . (An ESS for our model can also be called a personal-fitness ESS.)

This definition is identical to Maynard Smith's (1982) definition for the classical matrix game diploid model. In order to obtain the conditions for an ESS, suppose that there are only two alleles, G^* and G , in the population and that the frequency of allele G is small enough. This means that almost all G genes in the population will be carried by G^*G heterozygotes (rather than

by GG homozygotes). Let $1 - \varepsilon$ and ε be the frequencies of genotypes G^*G^* and G^*G , respectively, at the time of reproduction of the previous generation. Since the frequency of genotype G^*G is sufficiently small, mating between individuals with genotype G^*G can be ignored, i.e. almost all individuals with genotype G^*G will mate with individuals with genotype G^*G^* . Let $\mathbf{h} = (h, 1 - h)$ represent the phenotype of individuals with genotype G^*G . From eqn (9), the expected fitness of an offspring with genotype G^*G^* , denoted by $F_{\mathbf{h}^*}$, is approximated as

$$F_{\mathbf{h}^*}(\varepsilon) = r \left[(1 - \varepsilon)\mathbf{h}^* \cdot \mathbf{A}\mathbf{h}^* + \varepsilon\mathbf{h}^* \cdot \mathbf{A} \left(\frac{\mathbf{h}^* + \mathbf{h}}{2} \right) \right] + (1-r)\mathbf{h}^* \cdot \mathbf{A}\bar{\mathbf{h}} \quad (10)$$

and the expected fitness of an offspring with genotype G^*G , denoted by $F_{\mathbf{h}}$, is approximated as

$$F_{\mathbf{h}}(\varepsilon) = r\mathbf{h} \cdot \mathbf{A} \left(\frac{\mathbf{h}^* + \mathbf{h}}{2} \right) + (1-r)\mathbf{h} \cdot \mathbf{A}\bar{\mathbf{h}}, \quad (11)$$

where the mean strategy of the population, $\bar{\mathbf{h}}$, is approximated as

$$\bar{\mathbf{h}} = (1 - \varepsilon)\mathbf{h}^* + \varepsilon\mathbf{h}. \quad (12)$$

From the above definition, for \mathbf{h}^* to be an ESS, we must have

$$F_{\mathbf{h}^*}(\varepsilon) - F_{\mathbf{h}}(\varepsilon) > 0 \quad (13)$$

for all $\mathbf{h} \neq \mathbf{h}^*$.

Since ε is small enough, inequality (13) is equivalent to

$$\begin{aligned} F_{\mathbf{h}^*}(0) - F_{\mathbf{h}}(0) &= (\mathbf{h}^* - \mathbf{h}) \cdot \left(\mathbf{A} + \frac{r}{2}\mathbf{A}^T \right) \mathbf{h}^* \\ &\quad - \frac{r}{2}(\mathbf{h}^* - \mathbf{h}) \cdot \mathbf{A}(\mathbf{h}^* - \mathbf{h}) \\ &= (h^* - h)\mathbf{u} \cdot \left(\mathbf{A} + \frac{r}{2}\mathbf{A}^T \right) \mathbf{h}^* \\ &\quad - \frac{r}{2}(h^* - h)^2 a \\ &> 0, \end{aligned} \quad (14)$$

where

$$\mathbf{u} = (1, -1) \quad (15)$$

and

$$a = a_{11} - a_{12} - a_{21} + a_{22}, \tag{16}$$

or

$$\left(1 - \frac{r}{2}\right)(h^* - h)^2 a + r\mathbf{h} \cdot \mathbf{A}\mathbf{h}^* < 0 \tag{17}$$

if $F_{\mathbf{h}^*}(0) - F_{\mathbf{h}}(0) = 0$.

We consider two possible situations.

Case 1: $a \neq 0$. In this case, there cannot exist some h^* in the interval $(0, 1)$ such that $F_{\mathbf{h}^*}(0) - F_{\mathbf{h}}(0) = 0$ holds for all possible $\mathbf{h} \neq \mathbf{h}^*$. Moreover, for any h^* in the interval $(0, 1)$ which is such that $\mathbf{u} \cdot (\mathbf{A} + (r/2)\mathbf{A}^T)\mathbf{h}^* \neq 0$, it is always possible to find some h in the interval $(0, 1)$ such that $F_{\mathbf{h}^*}(0) - F_{\mathbf{h}} < 0$ holds.

On the other hand, if

$$\mathbf{u} \cdot \left(\mathbf{A} + \frac{r}{2}\mathbf{A}^T\right)\mathbf{h}^* = 0, \tag{18}$$

then

$$h^* = \frac{(a_{12} - a_{22}) + (r/2)(a_{21} - a_{22})}{(1 + (r/2))(a_{12} - a_{22} + a_{21} - a_{11})} \tag{19}$$

and inequality (14) holds for all $h \neq h^*$ if and only if $a < 0$.

It remains to consider $\mathbf{h}^* = R_1$ or R_2 , in the case where eqn (18) is not satisfied. We will consider without loss of generality (relabeling the phenotypes if necessary), only the case $\mathbf{h}^* = R_1$.

(i) If $a < 0$, a necessary and sufficient condition to have the inequality $F_{R_1}(0) - F_{\mathbf{h}}(0) > 0$ for all possible $\mathbf{h} \neq R_1$ is

$$\left(1 + \frac{r}{2}\right)a_{11} > \frac{r}{2}a_{12} + a_{21}. \tag{20}$$

(ii) If $a > 0$, a sufficient condition to have the inequality $F_{R_1}(0) - F_{\mathbf{h}} > 0$ for all possible $\mathbf{h} \neq R_1$ is

$$(a_{11} - a_{21}) > \frac{r}{2}(a_{22} - a_{21}). \tag{21}$$

If

$$(a_{11} - a_{21}) = \frac{r}{2}(a_{22} - a_{21}), \tag{22}$$

then the inequality $F_{R_1}(0) - F_{\mathbf{h}}(0) > 0$ holds only for all possible mixed strategies $\mathbf{h} \neq R_2$.

When $\mathbf{h} = R_2$, we have $F_{R_1}(0) - F_{R_2}(0) = 0$. But then, since $a > 0$, inequality (17) cannot be satisfied. Finally, if

$$(a_{11} - a_{21}) < \frac{r}{2}(a_{22} - a_{21}), \tag{23}$$

then there exists some \mathbf{h} such that $F_{R_1}(0) - F_{\mathbf{h}}(0) < 0$.

Case 2: $a = 0$. From the analysis of the standard two-phenotype matrix game model (Maynard Smith, 1982), there cannot exist a mixed strategy \mathbf{h}^* such that inequality (14) holds for all possible $\mathbf{h} \neq \mathbf{h}^*$. For the pure strategy $\mathbf{h}^* = R_1$, inequality (14) holds for all possible $\mathbf{h} \neq \mathbf{h}^*$ if and only if inequality (20) is satisfied, and similarly for the pure strategy $\mathbf{h}^* = R_2$.

Summarizing the above analysis, we have the following result.

Result. *A strategy \mathbf{h}^* which satisfies $\mathbf{u} \cdot (\mathbf{A} + (r/2)\mathbf{A}^T)\mathbf{h}^* = 0$ is an ESS if and only if $a < 0$. The pure strategy $\mathbf{h}^* = R_1$ that does not satisfy $\mathbf{u} \cdot (\mathbf{A} + (r/2)\mathbf{A}^T)\mathbf{h}^* = 0$ is an ESS if and only if*

$$\left(1 + \frac{r}{2}\right)a_{11} > \frac{r}{2}a_{12} + a_{21} \tag{24}$$

in the case $a \leq 0$, and if and only if

$$(a_{11} - a_{21}) > \frac{r}{2}(a_{22} - a_{21}) \tag{25}$$

in the case $a > 0$, and similarly for the pure strategy $\mathbf{h}^ = R_2$.*

The above result implies that, if a strategy \mathbf{h}^* is an ESS for the model at hand, then it must also be an ESS for the standard game model with the payoff matrix $\mathbf{A} + (r/2)\mathbf{A}^T$. This conclusion is similar to the one obtained by Hines & Maynard Smith (1979) for the haploid model. It is interesting to point out that, for our model, when $a > 0$, if both inequalities $(a_{11} - a_{21}) > (r/2)(a_{22} - a_{21})$ and $(a_{22} - a_{12}) > (r/2)(a_{11} - a_{12})$ are not satisfied, then no ESS can exist. This is different from the classical two-phenotype matrix game model, for which Maynard Smith (1982) showed that there is at least one ESS.

4. Analysis of Weak Selection

For the classical two-phenotype matrix game diploid model, Lessard (1984) showed that there should be evolution, through mutations if necessary, to an ESS, which was then called evolutionarily attractive. This means that the change in the phenotypic frequencies always tends to an ESS proportion. In this section, we study the relationship between the existence of an ESS and a partial change in the phenotypic frequencies in the model at hand (Tao & Lessard, 2000) under the assumption of weak selection.

We posit weak selection by assuming

$$h_{ij} = h + \delta_{ij}s, \quad (26)$$

i.e.

$$\mathbf{h}_{ij} = \mathbf{h} + \mathbf{u}\delta_{ij}s, \quad (27)$$

where h is in the interval $[0, 1]$ and s is positive and small enough. From eqns (5) and (6), the mean strategy in the population at the beginning of the current generation can be expressed as

$$\bar{\mathbf{h}} = \mathbf{h} + \mathbf{u}\bar{\delta}s, \quad (28)$$

where

$$\bar{\delta} = \sum_{i,j=1}^n p_i p_j \delta_{ij}. \quad (29)$$

For convenience, let

$$\delta_i = \sum_{j=1}^n p_j \delta_{ij} \quad (30)$$

for $i = 1, 2, \dots, n$, and define

$$\begin{aligned} \mathbf{h}_i &= \sum_{j=1}^n p_j \mathbf{h}_{ij} \\ &= \mathbf{h} + \mathbf{u}\delta_i s, \end{aligned} \quad (31)$$

which is the marginal phenotype of allele G_i for $i = 1, 2, \dots, n$.

Note that, under the assumption of weak selection as in Lessard (1997), the frequency of genotype $G_i G_j$ at the time of reproduction of the

previous generation can be approximated as

$$\tilde{P}_{ij} \approx p_i p_j \quad (32)$$

for $i, j = 1, 2, \dots, n$. Thus, the fitness of offspring with genotype $G_i G_j$, given in eqn (9), can be rewritten as

$$\begin{aligned} F_{ij} &= \sum_{k,l=1}^n p_k p_l \left[r \mathbf{h}_{ij} \cdot \mathbf{A} \left(\frac{\mathbf{h}_{ij} + \mathbf{h}_{il} + \mathbf{h}_{jk} + \mathbf{h}_{kl}}{4} \right) \right. \\ &\quad \left. + (1-r) \mathbf{h}_{ij} \cdot \mathbf{A}\bar{\mathbf{h}} \right] \\ &= \frac{r}{4} \mathbf{h}_{ij} \cdot \mathbf{A}(\mathbf{h}_{ij} + \mathbf{h}_i + \mathbf{h}_j) + \left(1 - \frac{3r}{4} \right) \mathbf{h}_{ij} \cdot \mathbf{A}\bar{\mathbf{h}} \\ &= \mathbf{h} \cdot \mathbf{A}\mathbf{h} + \mathbf{u} \cdot \mathbf{A}\mathbf{h}\delta_{ij}s \\ &\quad + \mathbf{u} \cdot \mathbf{A}^T \mathbf{h} \left[\frac{r}{4}(\delta_{ij} + \delta_i + \delta_j) + \left(1 - \frac{3r}{4} \right) \bar{\delta} \right] s \\ &\quad + a\delta_{ij} \left[\frac{r}{4}(\delta_{ij} + \delta_i + \delta_j) + \left(1 - \frac{3r}{4} \right) \bar{\delta} \right] s^2 \\ &= \mathbf{h} \cdot \mathbf{A}\mathbf{h} + \mathbf{u} \cdot \left(\mathbf{A} + \frac{r}{2} \mathbf{A}^T \right) \mathbf{h}\delta_{ij}s \\ &\quad + \mathbf{u} \cdot \mathbf{A}^T \mathbf{h} \left[\frac{r}{4}(\delta_i + \delta_j - \delta_{ij}) + \left(1 - \frac{3r}{4} \right) \bar{\delta} \right] s \\ &\quad + a\varphi_{ij}s^2, \end{aligned} \quad (33)$$

where

$$\varphi_{ij} = \delta_{ij} \left[\frac{r}{4}(\delta_{ij} + \delta_i + \delta_j) + \left(1 - \frac{3r}{4} \right) \bar{\delta} \right] \quad (34)$$

for $i, j = 1, 2, \dots, n$.

From eqn (33), the marginal fitness of allele G_i , denoted by F_i , is

$$\begin{aligned} F_i &= \sum_{j=1}^n p_j F_{ij} \\ &= \mathbf{h} \cdot \mathbf{A}\mathbf{h} + \mathbf{u} \cdot \left(\mathbf{A} + \frac{r}{2} \mathbf{A}^T \right) \mathbf{h}\delta_i s \\ &\quad + \left(1 - \frac{r}{2} \right) \mathbf{u} \cdot \mathbf{A}^T \mathbf{h}\bar{\delta}s + a\varphi_i s^2, \end{aligned} \quad (35)$$

where

$$\varphi_i = \sum_{j=1}^n p_j \varphi_{ij} \quad (36)$$

for $i = 1, 2, \dots, n$, and the mean fitness in the population, denoted by \bar{F} , is

$$\begin{aligned} \bar{F} &= \sum_{i,j=1}^n p_i p_j F_{ij} = \sum_{i=1}^n p_i F_i \\ &= \mathbf{h} \cdot \mathbf{A} \mathbf{h} + \mathbf{u} \cdot \left(\mathbf{A} + \frac{r}{2} \mathbf{A}^T \right) \mathbf{h} \bar{s} \\ &\quad + \left(1 - \frac{r}{2} \right) \mathbf{u} \cdot \mathbf{A}^T \mathbf{h} \bar{s} + a \bar{\varphi} s^2, \end{aligned} \quad (37)$$

where

$$\begin{aligned} \bar{\varphi} &= \sum_{i,j=1}^n p_i p_j \varphi_{ij} \\ &= \sum_{i=1}^n p_i \varphi_i. \end{aligned} \quad (38)$$

The frequency of allele G_i at the time of reproduction, denoted by p'_i , is

$$p'_i = \frac{p_i F_i}{\bar{F}} \quad (39)$$

for $i = 1, 2, \dots, n$. Since there is no fertility selection, the frequency of allele G_i at the beginning of the next generation is also equal to p'_i for $i = 1, 2, \dots, n$. Let Δp_i represent the change in frequency of allele G_i ($i = 1, 2, \dots, n$) from the time of conception to the beginning of the next generation. From eqns (35), (37) and (39), we have

$$\begin{aligned} \Delta p_i &= p'_i - p_i \\ &= p_i \frac{(F_i - \bar{F})}{\bar{F}} \\ &= \frac{p_i}{\bar{F}} \left[\mathbf{u} \cdot \left(\mathbf{A} + \frac{r}{2} \mathbf{A}^T \right) \mathbf{h} (\delta_i - \bar{\delta}) s + a (\varphi_i - \bar{\varphi}) s^2 \right] \end{aligned} \quad (40)$$

for $i = 1, 2, \dots, n$.

Note that \bar{h} is the mean of h_{ij} for $i, j = 1, 2, \dots, n$. From the classical population genetics theory (see, e.g., Crow & Kimura, 1970; Ewens,

1989), we define

$$\begin{aligned} b_i &= \sum_{j=1}^n \frac{p_i p_j (h_{ij} - h)}{p_i} \\ &= \sum_{j=1}^n \frac{p_i p_j (\delta_{ij} - \bar{\delta}) s}{p_i} \\ &= (\delta_i - \bar{\delta}) s \end{aligned} \quad (41)$$

as the average excess of allele G_i on phenotype R_1 for $i = 1, 2, \dots, n$. Then eqn (40) can be rewritten as

$$\Delta p_i = p_i \frac{[\mathbf{u} \cdot (\mathbf{A} + (r/2) \mathbf{A}^T) \mathbf{h} b_i + a (\varphi_i - \bar{\varphi}) s]^2}{\bar{F}} \quad (42)$$

for $i = 1, 2, \dots, n$. Since mating is random, the average effect of allele G_i on phenotype R_1 is also equal to b_i , and the additive genetic value of h_{ij} should be

$$\bar{h} + b_i + b_j \quad (43)$$

for all $i, j = 1, 2, \dots, n$. Thus, the additive genetic variance on phenotype R_1 , denoted by $\sigma_{R_1}^2$, is (Tao & Lessard, 2000).

$$\sigma_{R_1}^2 = a \sum_{i=1}^n p_i b_i^2. \quad (44)$$

Let P'_{ij} be the frequency of genotype $G_i G_j$ if $i \neq j$ and P'_{ii} be the frequency of genotype $G_i G_i$ at the time of reproduction for $i, j = 1, 2, \dots, n$. From eqns (33) and (37), we have

$$P'_{ij} = \frac{p_i p_j F_{ij}}{\bar{F}} \quad (45)$$

for $i, j = 1, 2, \dots, n$, and the frequency of the pure strategy R_1 at the time of reproduction, denoted by \bar{h}' , is

$$\bar{h}' = \sum_{i,j=1}^n P'_{ij} h_{ij}. \quad (46)$$

Let $\Delta \bar{h}$ represent the change in frequency of phenotype R_1 from the time of conception to the time of reproduction. From eqns (28), (33), (37),

(45) and (46), we have

$$\begin{aligned}
 \Delta \bar{h} &= \bar{h}' - \bar{h} \\
 &= \sum_{i,j=1}^n (P'_{ij} - p_i p_j) h_{ij} \\
 &= \frac{1}{\bar{F}} \sum_{i,j=1}^n p_i p_j (F_{ij} - \bar{F}) h_{ij} \\
 &= \frac{s}{\bar{F}} \sum_{i,j=1}^n p_i p_j (F_{ij} - \bar{F}) \delta_{ij} \\
 &= \frac{s}{\bar{F}} \sum_{i,j=1}^n p_i p_j \left[\mathbf{u} \cdot \left(\mathbf{A} + \frac{r}{2} \mathbf{A}^T \right) \mathbf{h} (\delta_{ij} - \bar{\delta}) s \right] \delta_{ij} \\
 &\quad + \frac{s}{\bar{F}} \sum_{i,j=1}^n p_i p_j \left[\frac{r}{4} \mathbf{u} \cdot \mathbf{A}^T \mathbf{h} (\delta_i + \delta_j - \delta_{ij} - \bar{\delta}) s \right. \\
 &\quad \left. + a(\varphi_{ij} - \bar{\varphi}) s^2 \right] \delta_{ij} \\
 &= \frac{V_{R_1}}{\bar{F}} \mathbf{u} \cdot \left(\mathbf{A} + \frac{r}{2} \mathbf{A}^T \right) \mathbf{h} + \frac{r}{4\bar{F}} (\sigma_{R_1}^2 - V_{R_1}) \mathbf{u} \cdot \mathbf{A}^T \mathbf{h} \\
 &\quad + \frac{as^3}{\bar{F}} \text{Cov}(\delta_{ij}, \varphi_{ij}), \tag{47}
 \end{aligned}$$

where

$$\begin{aligned}
 V_{R_1} &= \sum_{i,j=1}^n p_i p_j (h_{ij} - \bar{h})^2 \\
 &= \sum_{i,j=1}^n p_i p_j (\delta_{ij} - \bar{\delta})^2 s^2 \tag{48}
 \end{aligned}$$

is called the phenotypic variance on phenotype R_1 and

$$\begin{aligned}
 \text{Cov}(\delta_{ij}, \varphi_{ij}) &= \sum_{i,j=1}^n p_i p_j (\delta_{ij} - \bar{\delta})(\varphi_{ij} - \bar{\varphi}) \\
 &= \sum_{i,j=1}^n p_i p_j (\varphi_{ij} - \bar{\varphi}) \delta_{ij} \tag{49}
 \end{aligned}$$

is the covariance between δ_{ij} and φ_{ij} .

Since s is small enough, eqn (47) can be approximated as

$$\Delta \bar{h} = \frac{V_{R_1}}{\bar{F}} \mathbf{u} \cdot \left(\mathbf{A} + \frac{r}{2} \mathbf{A}^T \right) \mathbf{h} + \frac{r}{4\bar{F}} (\sigma_{R_1}^2 - V_{R_1}) \mathbf{u} \cdot \mathbf{A}^T \mathbf{h}. \tag{50}$$

When $r = 0$, we have

$$\Delta \bar{h} = \frac{V_{R_1}}{\bar{F}} \mathbf{u} \cdot \mathbf{A} \mathbf{h}. \tag{51}$$

Obviously, eqn (51) corresponds to Lessard's (1984) result for the classical two-phenotype matrix game diploid model.

For this model, Tao & Lessard (2000) defined the partial changes in the phenotypic frequencies as the changes in the phenotypic frequencies due only to the changes in the genotypic frequencies. The partial changes in the phenotypic frequencies are obtained by replacing the actual phenotypes of individuals by the corresponding genetic values and by keeping these values fixed in the changes of the phenotypic frequencies with respect to the changes in the genotypic frequencies (Ewens, 1989). According to this definition, the partial change in the frequency of phenotype R_1 from the time of conception to the time of reproduction, denoted by $\Delta_{\text{part}} \bar{h}$, is

$$\begin{aligned}
 \Delta_{\text{part}} \bar{h} &= \sum_{i,j=1}^n (P'_{ij} - p_i p_j) (\bar{h} + b_i + b_j) \\
 &= 2 \sum_{i=1}^n b_i \Delta p_i \\
 &= \frac{2 \sum_{i=1}^n p_i b_i^2}{\bar{F}} \mathbf{h} \cdot \left(\mathbf{A} + \frac{r}{2} \mathbf{A}^T \right) \mathbf{h} \\
 &\quad + \frac{2as^3}{\bar{F}} \sum_{i=1}^n p_i (\delta_i - \bar{\delta})(\varphi_i - \bar{\varphi}) \\
 &= \frac{\sigma_{R_1}^2}{\bar{F}} \mathbf{u} \cdot \left(\mathbf{A} + \frac{r}{2} \mathbf{A}^T \right) \mathbf{h} + \frac{2as^3}{\bar{F}} \text{Cov}(\delta_i, \varphi_i), \tag{52}
 \end{aligned}$$

where

$$\text{Cov}(\delta_i, \varphi_i) = \sum_{i=1}^n p_i (\delta_i - \bar{\delta})(\varphi_i - \bar{\varphi}) \tag{53}$$

is the covariance between δ_i and φ_i . It is necessary to point out that since we have

$$\begin{aligned}
 \sum_{i,j=1}^n (P'_{ij} - p_i p_j) (\bar{h} + b_i + b_j) &= \\
 \sum_{i,j}^n (p'_i p'_j - p_i p_j) (\bar{h} + b_i + b_j), \tag{54}
 \end{aligned}$$

$\Delta_{part}\bar{h}$ is also the partial change in frequency of phenotype R_1 from the time of conception to the beginning of the next generation.

Note that, if s is small enough, eqn (52) can be approximated as

$$\Delta_{part}\bar{h} = \frac{\sigma_{R_1}^2}{\bar{F}} \mathbf{u} \cdot \left(\mathbf{A} + \frac{r}{2} \mathbf{A}^T \right) \mathbf{h} \quad (55)$$

if $\mathbf{u} \cdot (\mathbf{A} + (r/2)\mathbf{A}^T)\mathbf{h} \neq 0$. As a consequence, the partial change in frequency of phenotype R_1 brings the population closer to an ESS for $\mathbf{A} + (r/2)\mathbf{A}^T$. As a matter of fact, if there exists some \mathbf{h}^* such that $\mathbf{u} \cdot (\mathbf{A} + (r/2)\mathbf{A}^T)\mathbf{h}^* = 0$ and \mathbf{h}^* is an ESS for $\mathbf{A} + (r/2)\mathbf{A}^T$, then $\Delta_{part}\bar{h} > 0$ if $h < h^*$ and $\Delta_{part}\bar{h} < 0$ if $h > h^*$; if \mathbf{h}^* satisfies $\mathbf{u} \cdot (\mathbf{A} + (r/2)\mathbf{A}^T)\mathbf{h}^* = 0$ but it is not an ESS for $\mathbf{A} + (r/2)\mathbf{A}^T$, then both pure strategies R_1 and R_2 are ESS strategies for $\mathbf{A} + (r/2)\mathbf{A}^T$ and $\Delta_{part}\bar{h} > 0$ if $h > h^*$ and $\Delta_{part}\bar{h} < 0$ if $h < h^*$; if no \mathbf{h}^* satisfies $\mathbf{u} \cdot (\mathbf{A} + (r/2)\mathbf{A}^T)\mathbf{h}^* = 0$, then $\Delta_{part}\bar{h} > 0$ if R_1 is an ESS for $\mathbf{A} + (r/2)\mathbf{A}^T$ and $\Delta_{part}\bar{h} < 0$ if R_2 is an ESS for $\mathbf{A} + (r/2)\mathbf{A}^T$.

In the case $a \leq 0$, a strategy which is an ESS for $\mathbf{A} + (r/2)\mathbf{A}^T$ is also an ESS for the model at hand, whereas in the case $a > 0$, if both inequalities $(a_{11} - a_{21}) > (r/2)(a_{22} - a_{21})$ and $(a_{22} - a_{12}) > (r/2)(a_{11} - a_{12})$ are not satisfied, then no ESS can exist for the model at hand. Thus, the partial change in the frequency of phenotype R_1 does not always bring the population closer to a personal-fitness ESS when $\mathbf{u} \cdot (\mathbf{A} + (r/2)\mathbf{A}^T)\mathbf{h} \neq 0$.

In the case where \mathbf{h} satisfies $\mathbf{u} \cdot (\mathbf{A} + (r/2)\mathbf{A}^T)\mathbf{h} = 0$, eqn (52) can be rewritten as

$$\Delta_{part}\bar{h} = \frac{2as^3}{\bar{F}} Cov(\delta_i, \varphi_i). \quad (56)$$

In this case, $\Delta_{part}\bar{h}$ may be positive or negative, the absolute value of $\Delta_{part}\bar{h}$ being small since s is assumed small.

5. Conclusion

Our main purpose was to develop the ESS theory for frequency-dependent viability selection in family-structured populations. Assuming that the phenotype of individuals is determined by alleles located at a single locus in a diploid population, a strategy corresponding to a homozygote genotype G^*G^* is an ESS if and

only if the allele G^* cannot be invaded by any mutant allele when all members of the population have genotype G^*G^* . This definition corresponds to Maynard Smith's (1982) definition for the classical matrix game diploid model.

Assuming two phenotypes and kin selection effects between full sibs, we have deduced necessary and sufficient conditions for an ESS and showed that if a strategy is an ESS for the model at hand, then it must also be an ESS under the standard game formulation with the matrix $\mathbf{A} + (r/2)\mathbf{A}^T$. This result is similar to a result obtained by Hines & Maynard Smith (1979) for the haploid model, but we have to emphasize that it is possible that no ESS exists in the model at hand. Assuming that selection is weak, we have showed that, in general, the partial change in phenotype frequencies brings to population toward an ESS for $\mathbf{A} + (r/2)\mathbf{A}^T$ when it exists. Note that if the partial change would be the total change, then the system could be said locally adaptive in Eshel's (1982) sense and, in particular, a mutant allele would be favoured if and only if it would tend to render the population strategy closer to an ESS, which is the evolutionary genetic stability (EGS) property in Eshel & Feldman's (1982) sense.

REFERENCES

- CASTILLOUX, A.-M. & LESSARD, S. (1995). The fundamental theorem of natural selection in Ewens' sense: case of many loci. *Theor. Popul. Biol.* **48**, 306–315.
- CRESSMAN, R. (1992). *The Stability Concept of Evolutionary Game Theory—A Dynamic Approach*, Lecture Notes in Biomathematics, Vol. 94. Berlin: Springer-Verlag.
- CROW, J. F. & KIMURA, K. (1970). *An Introduction to Population Genetics Theory*. New York: Harper & Row Publishers.
- ESHEL, I. (1982). Evolutionary stable strategies and viability selection in Mendelian populations. *Theor. Popul. Biol.* **22**, 204–217.
- ESHEL, I. & FELDMAN, M. (1982). On evolutionary genetic stability of the sex ratio. *Theor. Popul. Biol.* **21**, 430–439.
- EWENS, W. J. (1989). An interpretation and proof of the fundamental theorem of natural selection. *Theor. Popul. Biol.* **36**, 167–180.
- EWENS, W. J. (1992). An optimizing principle of natural selection in evolutionary population genetics. *Theor. Popul. Biol.* **42**, 333–346.
- FISHER, R. A. (1930). *The Genetic Theory of Natural Selection*. Oxford: Clarendon Press.
- GRAFEN, A. (1979). The hawk–dove game played between relatives. *Anim. Behav.* **27**, 905–907.
- HAMILTON, W. D. (1964a). The genetic evolution of social behaviour. *I. J. theor. Biol.* **7**, 1–16.

- HAMILTON, W. D. (1964b). The genetic evolution of social behaviour, **II**. *J. theor. Biol.* **7**, 17–25.
- HINES, W. G. S. (1987). Evolutionarily stable strategies: a review of basic theory. *Theor. Popul. Biol.* **31**, 195–272.
- HINES, W. G. S. & MAYNARD SMITH J. (1979). Games between relatives. *J. theor. Biol.* **79**, 19–30.
- HOFBAUER, J. & SIGMUND K. (1988). *Theory of Evolution and Dynamical Systems*. Cambridge: Cambridge University Press.
- HOFBAUER, J. & SIGMUND K. (1998). *Evolutionary Games and Population Dynamics*. Cambridge: Cambridge University Press.
- LESSARD, S. (1984). Evolutionary dynamics in frequency-dependent two-phenotype models. *Theor. Popul. Biol.* **25**, 210–234.
- LESSARD, S. (1997). Fisher's fundamental theorem of natural selection revisited. *Theor. Popul. Biol.* **52**, 119–136.
- LESSARD, S. & CASTILLOUX, A.-M. (1995). The fundamental theorem of natural selection in Ewens's sense: case of fertility selection. *Genetics* **141**, 733–742.
- MAYNARD SMITH, J. (1974). The theory of games and the evolution of animal conflicts. *J. theor. Biol.* **47**, 209–221.
- MAYNARD SMITH, J. (1982). *Evolution and the Theory of Games*. Cambridge, U.K.: Cambridge University Press.
- MIRMIRANI, M. & OSTER, G. (1978). Competition, kin selection, and evolutionarily stable strategies. *Theor. Popul. Biol.* **13**, 304–339.
- TAO Y. & LESSARD, S. (2000). Fundamental theorem of natural selection and frequency-dependent selection: analysis of the matrix game diploid model. *J. theor. Biol.* **206**, 17–25.
- TAYLOR, P. D. (1989). Evolutionary stability in one-parameter models under weak selection. *Theor. Popul. Biol.* **36**, 125–143.
- VINCENT, T. L. & CRESSMAN, R. (2000). An ESS maximum principle for matrix games. *Theor. Popul. Biol.* **58**, 173–186.
- WRIGHT, S. (1922). Coefficients of inbreeding and relationship. *Amer. Nat.* **56**, 330–338.