



Fundamental Theorem of Natural Selection and Frequency-dependent Selection: Analysis of the Matrix Game Diploid Model

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Following Ewens' interpretation about Fisher's fundamental theorem of natural selection, the matrix game model for diploid populations undergoing non-overlapping, discrete generations is investigated. The total genetic variance is decomposed and it is shown that the partial change in the mean fitness, which is equal to the additive genetic variance over the mean fitness, can be thought of as a change due only to the partial changes in the phenotypic frequencies.

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1. Introduction

Ewens (1989), following Price (1972), pointed out that Fisher's (1930) fundamental theorem of natural selection (FTNS) about the increase in mean fitness is of general validity without any restrictive assumptions on the mating system, the fitness parameters, or the genes involved, but that this theorem concerns only a partial change in mean fitness. Mating does not have to be random, the fitness parameters frequency-independent and the genes restricted in numbers of loci or allelic forms. Ewens (1989) interprets the FTNS in the case of discrete non-overlapping generations as follows: *a partial change in the mean fitness of a 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 genetic values and by keeping these values fixed

in the change of the mean with respect to the changes in the genotypic frequencies. This interpretation of the FTNS, first proposed in the context of the Malthusian parameter as fitness in continuous-time models with overlapping generations (Price, 1972), has been checked to hold in the case of viability selection from conception to maturity [Ewens (1989); see also Ewens (1992) and Castilloux & Lessard (1995) for corrections] and in the case of fertility selection from the time of mating to the time of reproduction (Lessard & Castilloux, 1995) for populations undergoing discrete, non-overlapping generations.

An alternate interpretation, closer to Fisher's (1941) own explanations, has been proposed (Lessard, 1997). The partial change is obtained by considering only the changes in the genotypic frequencies directly consequent on the changes in gene frequencies, the fitness parameters being kept constant.

In the classical theory of natural selection developed by Fisher and Wright, the viability of an individual is assumed to be completely

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determined by its genotype. However, it has long been recognized that, in practice, these viabilities are not constant but are affected by such factors as the current frequencies of other genotypes in the population, the total population size, external environment changes, etc. In order to explain the evolution of genetically determined social behaviours within a single animal species, Maynard Smith (1982) developed the evolutionary game theory and the ESS (evolutionarily stable strategy) concept. In this theory, the fitness of an individual is not only determined by its own phenotype (strategy) but also depends on the other individuals' phenotypes in the population, i.e. selection is phenotypically frequency-dependent. In this context, an ESS is supposed to represent a strategy that is uninvadable by any mutant once fixed in the population.

In order to understand how the partial change in the mean fitness is affected by the changes in the phenotypic frequencies under frequency-dependent selection, we will investigate a matrix game model for diploid populations. It is well known that the matrix game model developed by Maynard Smith (1982) 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 may be an important source of ideas and principles that provide some insights on intra-specific selection. In the matrix game model, the fitness of an individual is a linear function of the phenotypic frequencies in the population. This means that any change in the mean fitness is based essentially on changes in the phenotypic frequencies. In this paper, our main purpose is to give the relationship between the partial change in the mean fitness and the changes in the phenotypic frequencies in the matrix game model for one-locus multi-allele diploid populations undergoing non-overlapping, discrete generations.

Our motivation is to make precise the status of the FTNS in frequency-dependent selection models. For such models, it is well known that the mean fitness does not necessarily increase and, therefore, evolution to a maximum point of the mean fitness does not necessarily occur. Assuming a 2×2 matrix game in a one-locus multi-allele diploid population, Lessard (1984) showed

that there should be evolution, through mutations if necessary, to an ESS, which was then called evolutionarily attractive. Considering an $n \times n$ matrix game and a two-locus model, Hammerstein (1994) proved that the only fixation states that can resist invasion by a large class of mutants correspond to ESS states. Then he introduced an evolutionary principle intended to replace the FTNS, called the streetcar theory of evolution, which states that the final stop of evolution as mutant genes are introduced sequentially must be an ESS. Since an ESS is a static ecological concept depending only on phenotypes, it is tempting to conclude that genetics does not count in predicting the results of evolution.

On the other hand, Ewens (1989) proposed that the FTNS concerns not the total change in the mean fitness but only a partial change which makes sense also under frequency-dependent selection. Therefore, two questions arise: what does this partial change correspond to in the matrix game model? and does this partial change depend on the underlying genetics? We will try to answer these questions.

2. Basic Model and Definitions

Consider an infinite diploid population undergoing non-overlapping, discrete generations in which there are m possible phenotypes (pure strategies), S_1, S_2, \dots, S_m . Suppose that n alleles A_1, A_2, \dots, A_n located at a single locus are responsible for the phenotypic determination such that an individual with genotype $A_i A_j$ expresses phenotype S_k with probability $v_{ij}^{(k)}$ where $\sum_{k=1}^m v_{ij}^{(k)} = 1$ for $i, j = 1, 2, \dots, n$. Then, the vector $(v_{ij}^{(1)}, v_{ij}^{(2)}, \dots, v_{ij}^{(m)})$ represents the strategy of the individual whose genotype is $A_i A_j$ for $i, j = 1, 2, \dots, n$. For $k = 1, 2, \dots, m$, the symmetric matrix $[v_{ij}^{(k)}]_{i,j=1,2,\dots,n}$ represents a strategy determination matrix.

The frequency of genotype $A_i A_j$ at the beginning of the current generation is denoted by $2P_{ij}$ when $i \neq j$ (precisely, if the order of genotypes is considered, the frequencies of genotypes $A_i A_j$ and $A_j A_i$ should be denoted by P_{ij} and P_{ji} , respectively, and $P_{ij} = P_{ji}$ for all $i \neq j$) and P_{ii} when $i = j$. The frequency of allele A_i is then given by $p_i = \sum_{j=1}^n P_{ij}$ for $i = 1, 2, \dots, n$. Throughout this

paper, we do not assume that mating is random. The frequency of phenotype S_k is given by

$$x_k = \sum_{i,j=1}^n P_{ij} v_{ij}^{(k)} \quad (1)$$

for $k = 1, 2, \dots, m$.

Following Maynard Smith (1982) (see also Lessard, 1984; Hofbauer & Sigmund, 1988; Cressman, 1992; Cressman *et al.*, 1996), we assume that the individuals compete randomly in pairwise contests, and that the outcome of the contest affects the viability of the individuals. Let η_{kl} be the viability of an individual exhibiting phenotype S_k in a contest against an opponent exhibiting phenotype S_l . The viability matrix $[\eta_{kl}]_{k,l=1,2,\dots,m}$ satisfies $\eta_{kl} \geq 0$ for $k, l = 1, 2, \dots, m$ and is not necessarily symmetric. The fitness of phenotype S_k is given by

$$f_k = \sum_{l=1}^m x_l \eta_{kl} \quad (2)$$

for $k = 1, 2, \dots, m$.

From the above assumptions and definitions, the fitness of genotype $A_i A_j$ is

$$w_{ij} = \sum_{k=1}^m v_{ij}^{(k)} f_k \quad (3)$$

for $i, j = 1, 2, \dots, n$, where w_{ij} is interpreted as the probability of survival from the time of conception to the time of reproduction. Obviously, the mean fitness in the population is

$$\bar{f} = \sum_{i,j=1}^n P_{ij} w_{ij} = \sum_{k=1}^m x_k f_k. \quad (4)$$

Equations (2)–(4) show clearly that the genotypic fitnesses and the mean fitness in the population are functions only of the phenotypic frequencies.

Under the above assumptions, the frequency of genotype $A_i A_j$ at the time of reproduction is

$$P'_{ij} = \frac{P_{ij} w_{ij}}{\bar{f}} \quad (5)$$

for $i, j = 1, 2, \dots, n$, and the frequency of gene A_i at the time of reproduction is

$$p'_i = \sum_{j=1}^n P'_{ij} = \sum_{j=1}^n \frac{P_{ij} w_{ij}}{\bar{f}} \quad (6)$$

for $i = 1, 2, \dots, n$. It is necessary to point out that in general $2P'_{ij}$ (or P'_{ii}) is not the frequency of genotype $A_i A_j$ for all $i \neq j$ (or for all $i = j$) at the beginning of the next generation, but if all individuals have the same fecundity and segregation is Mendelian, p'_i will be equal to the frequency of gene A_i at the beginning of the next generation for $i = 1, 2, \dots, n$ for all mating schemes that do not affect gene frequencies.

3. Changes in Gene Frequencies

Let us consider the changes in gene frequencies from the time of conception to the time of reproduction. If Δp_i represents the change in the frequency of gene A_i , then, from eqn (6), we have

$$\begin{aligned} \Delta p_i &= p'_i - p_i \\ &= \sum_{j=1}^n \frac{P_{ij}(w_{ij} - \bar{f})}{\bar{f}} \end{aligned} \quad (7)$$

for $i = 1, 2, \dots, n$. From the classical population genetics theory, we know that the average excess of gene A_i on fitness is defined by

$$a_i = \sum_{j=1}^n \frac{P_{ij}(w_{ij} - \bar{f})}{p_i} \quad (8)$$

for $i = 1, 2, \dots, n$ (Crow & Kimura, 1970; see also Ewens, 1989). On the other hand, since we always have

$$w_{ij} - \bar{f} = \sum_{k=1}^m (v_{ij}^{(k)} - x_k) f_k \quad (9)$$

for $i, j = 1, 2, \dots, n$, and x_k is the mean value of $v_{ij}^{(k)}$ ($i, j = 1, 2, \dots, n$) in the population, we can also define

$$b_i^{(k)} = \sum_{j=1}^n \frac{P_{ij}(v_{ij}^{(k)} - x_k)}{p_i} \quad (10)$$

as the average excess of gene A_i on phenotype S_k for $i = 1, 2, \dots, n$ and $k = 1, 2, \dots, m$, and we have

$$a_i = \sum_{k=1}^m b_i^{(k)} f_k \quad (11)$$

for $i = 1, 2, \dots, n$. Thus, the change in the frequency of gene A_i can be expressed in the form

$$\begin{aligned} \Delta p_i &= \frac{p_i a_i}{\bar{f}} \\ &= \sum_{k=1}^m \frac{p_i b_i^{(k)} f_k}{\bar{f}} \end{aligned} \quad (12)$$

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

4. Average Effects of Genes on Phenotype and Fitness

The concept of the average effects of genes on fitness is one of the most important theoretical concepts in the population genetics theory. For the matrix game diploid model, since the fitness of any individual in the population is a linear function of the phenotypic frequencies only, we need first to consider the average effects of genes on phenotype. We will also discuss the relationship between the average effects of genes on phenotype and the average effects of genes on fitness.

4.1. AVERAGE EFFECT ON PHENOTYPE

Similar to the concept of average effect on fitness (Crow & Kimura, 1970; see also Ewens, 1989), if the probability $v_{ij}^{(k)}$ that the individual with genotype $A_i A_j$ ($i, j = 1, 2, \dots, n$) expresses phenotype S_k can be written in the form

$$v_{ij}^{(k)} = x_k + \beta_i^{(k)} + \beta_j^{(k)} \quad (13)$$

and

$$\sum_{i=1}^n p_i \beta_i^{(k)} = 0, \quad (14)$$

then the effect on phenotype S_k of any individual whose genotype contains an A_j gene of replacing

that gene by an A_i gene should be $\beta_i^{(k)} - \beta_j^{(k)}$. If a randomly chosen gene in the population is replaced by gene A_i , the average effect on phenotype S_k of the individual carrying the replaced gene is

$$\beta_i^{(k)} - \sum_{j=1}^n p_j \beta_j^{(k)} = \beta_i^{(k)}. \quad (15)$$

Thus, when $v_{ij}^{(k)}$ can be expressed as in eqn (13), we call $\beta_i^{(k)}$ the average effect of gene A_i on phenotype S_k . Of course, in general, $v_{ij}^{(k)}$ cannot be written directly as in eqn (13), and $\beta_i^{(k)}$ must be defined by the standard least-squares method under condition (14) (Crow & Kimura, 1970; see also Ewens, 1989). This means that the quadratic form

$$\sum_{i,j=1}^n P_{ij} (v_{ij}^{(k)} - x_k - \beta_i^{(k)} - \beta_j^{(k)})^2 \quad (16)$$

is minimized with respect to $\beta_1^{(k)}, \beta_2^{(k)}, \dots, \beta_n^{(k)}$ under condition (14), and $\beta_i^{(k)}$ ($i = 1, 2, \dots, n$) is given implicitly as the solution of the equation

$$p_i \beta_i^{(k)} + \sum_{j=1}^n P_{ij} \beta_j^{(k)} = p_i b_i^{(k)}. \quad (17)$$

Obviously, if $P_{ij} = p_i p_j$ for $i, j = 1, 2, \dots, n$ (which will be the case after one generation if there is random mating), then eqn (17) shows that $\beta_i^{(k)} = b_i^{(k)}$ for $i = 1, 2, \dots, n$. From the least-squares method, we also know that the additive genetic variance in phenotype S_k , denoted by $\sigma_{\beta^{(k)}}^2$ and defined by

$$\sigma_{\beta^{(k)}}^2 = \sum_{i,j=1}^n P_{ij} (\beta_i^{(k)} + \beta_j^{(k)}),$$

is given by

$$\sigma_{\beta^{(k)}}^2 = 2 \sum_{i=1}^n p_i b_i^{(k)} \beta_i^{(k)} \quad (18)$$

for $k = 1, 2, \dots, m$.

4.2. AVERAGE EFFECT ON FITNESS

For a given genotype $A_i A_j$ ($i, j = 1, 2, \dots, n$), if $v_{ij}^{(k)}$ is replaced by $x_k + \beta_i^{(k)} + \beta_j^{(k)}$ for

$k = 1, 2, \dots, m$, then the fitness of genotype $A_i A_j$ can be expressed in the form

$$w_{ij} = \bar{f} + \sum_{k=1}^m (\beta_i^{(k)} + \beta_j^{(k)}) f_k, \quad (19)$$

and we always have $\sum_{i=1}^n p_i \sum_{k=1}^m \beta_i^{(k)} f_k = 0$. From the definition of average effect on fitness (Crow & Kimura, 1970; see also Ewens, 1989), we know that

$$\alpha_i = \sum_{k=1}^m \beta_i^{(k)} f_k \quad (20)$$

is the average effect of gene A_i on fitness, and from eqns (11) and (17), the solution of the equation

$$p_i \alpha_i + \sum_{j=1}^n P_{ij} \alpha_j = p_i a_i \quad (21)$$

for $i = 1, 2, \dots, n$. Equation (21) implies that the additive genetic variance in fitness, denoted by σ_{α}^2 and defined by

$$\sigma_{\alpha}^2 = \sum_{i,j=1}^n P_{ij} (\alpha_i + \alpha_j)^2,$$

is given by

$$\begin{aligned} \sigma_{\alpha}^2 &= 2 \sum_{i=1}^n p_i a_i \alpha_i \\ &= 2 \sum_{i=1}^n p_i \left(\sum_{k=1}^m b_i^{(k)} f_k \right) \left(\sum_{l=1}^m \beta_i^{(l)} f_l \right) \\ &= 2 \sum_{i=1}^n p_i \left(\sum_{k=1}^m b_i^{(k)} \beta_i^{(k)} f_k^2 \right. \\ &\quad \left. + \sum_{k=1}^m \sum_{l=1, l \neq k}^m b_i^{(k)} \beta_i^{(l)} f_k f_l \right) \\ &= \sum_{k=1}^m f_k^2 \left(2 \sum_{i=1}^n p_i b_i^{(k)} \beta_i^{(k)} \right) \\ &\quad + 2 \sum_{k=1}^m \sum_{l=1, l \neq k}^m f_k f_l \left(\sum_{i=1}^n p_i b_i^{(k)} \beta_i^{(l)} \right) \end{aligned}$$

$$\begin{aligned} &= \sum_{k=1}^m \sigma_{\beta^{(k)}}^2 f_k^2 \\ &\quad + 2 \sum_{k=1}^m \sum_{l=1, l \neq k}^m \text{cov}(b^{(k)}, \beta^{(l)}) f_k f_l, \quad (22) \end{aligned}$$

where

$$\text{cov}(b^{(k)}, \beta^{(l)}) = \sum_{i=1}^n p_i b_i^{(k)} \beta_i^{(l)} \quad (23)$$

is the covariance between the average excess on phenotype S_k and the average effect on phenotype S_l for $k, l = 1, 2, \dots, m$ but $k \neq l$.

Equation (22) clearly shows the relationship between the additive genetic variances in fitness and in phenotype.

5. Changes in Frequencies of Phenotypes

For a given phenotype S_k ($k = 1, 2, \dots, m$), the change of its frequency from the time of conception to the time of reproduction is

$$\begin{aligned} \Delta x_k &= x'_k - x_k \\ &= \sum_{i,j=1}^n (P'_{ij} - P_{ij}) v_{ij}^{(k)} \\ &= \sum_{i,j=1}^n \frac{P_{ij} (w_{ij} - \bar{f}) v_{ij}^{(k)}}{\bar{f}} \\ &= \frac{1}{\bar{f}} \sum_{i,j=1}^n P_{ij} \left[\sum_{l=1}^m (v_{ij}^{(l)} - x_l) f_l \right] v_{ij}^{(k)} \\ &= \frac{1}{\bar{f}} \sum_{l=1}^m f_l \sum_{i,j=1}^n P_{ij} (v_{ij}^{(l)} - x_l) (v_{ij}^{(k)} - x_k) \\ &= \frac{\sigma_{S_k}^2 f_k}{\bar{f}} + \sum_{l=1, l \neq k}^m \frac{\text{cov}(S_k, S_l) f_l}{\bar{f}}, \quad (24) \end{aligned}$$

where

$$\sigma_{S_k}^2 = \sum_{i,j=1}^n P_{ij} (v_{ij}^{(k)} - x_k)^2 \quad (25)$$

is the total genetic variance in phenotype S_k and

$$\text{cov}(S_k, S_l) = \sum_{i,j=1}^n P_{ij} (v_{ij}^{(k)} - x_k) (v_{ij}^{(l)} - x_l) \quad (26)$$

is the covariance between phenotypes S_k and S_l for $k \neq l$.

The total genetic variance in phenotype S_k can be decomposed as

$$\begin{aligned}\sigma_{S_k}^2 &= \sum_{i,j=1}^n P_{ij} [v_{ij}^{(k)} - x_k - (\beta_i^{(k)} + \beta_j^{(k)}) + (\beta_i^{(k)} + \beta_j^{(k)})]^2 \\ &= \sum_{i,j=1}^n P_{ij} [v_{ij}^{(k)} - x_k - (\beta_i^{(k)} + \beta_j^{(k)})]^2 \\ &\quad + 2 \sum_{i,j=1}^n P_{ij} [v_{ij}^{(k)} - x_k - (\beta_i^{(k)} + \beta_j^{(k)})] (\beta_i^{(k)} + \beta_j^{(k)}) \\ &\quad + \sum_{i,j=1}^n P_{ij} (\beta_i^{(k)} + \beta_j^{(k)})^2.\end{aligned}\quad (27)$$

From eqns (10) and (17), we find that

$$\sum_{i,j=1}^n P_{ij} [v_{ij}^{(k)} - x_k - (\beta_i^{(k)} + \beta_j^{(k)})] (\beta_i^{(k)} + \beta_j^{(k)}) = 0.$$

Therefore,

$$\sigma_{S_k}^2 = \sigma_{\beta^{(k)}}^2 + \sigma_{R-S_k}^2, \quad (28)$$

where $\sigma_{\beta^{(k)}}^2$ is the additive genetic variance in phenotype S_k and

$$\sigma_{R-S_k}^2 = \sum_{i,j=1}^n P_{ij} [v_{ij}^{(k)} - x_k - (\beta_i^{(k)} + \beta_j^{(k)})]^2 \quad (29)$$

is the residual variance in phenotype S_k .

From eqn (28), the change in the frequency of phenotype S_k can be rewritten as

$$\begin{aligned}\Delta x_k &= \frac{\sigma_{\beta^{(k)}}^2 f_k}{\bar{f}} + \frac{\sigma_{R-S_k}^2 f_k}{\bar{f}} \\ &\quad + \sum_{l=1, l \neq k}^m \frac{cov(S_k, S_l) f_l}{\bar{f}}.\end{aligned}\quad (30)$$

From Ewens (1989), the partial change in the mean fitness is obtained by replacing the actual genotypic fitness by the corresponding additive genetic values and by keeping these values fixed

in the change of the mean with respect to changes in genotypic frequencies. In our model, for a given genotype $A_i A_j$ ($i, j = 1, 2, \dots, n$), the fitness of genotype $A_i A_j$, w_{ij} , will be replaced by its additive genetic value $\bar{f} + \alpha_i + \alpha_j$ if the strategy associated with genotype $A_i A_j$, $\{v_{ij}^{(k)}\}_{k=1,2,\dots,m}$, is replaced by $\{x_k + \beta_i^{(k)} + \beta_j^{(k)}\}_{k=1,2,\dots,m}$ [see eqns (13), (19) and (20)]. Notice that, for a given phenotype S_k ($k = 1, 2, \dots, m$), the additive genetic value of genotype $A_i A_j$ on S_k is $x_k + \beta_i^{(k)} + \beta_j^{(k)}$ [see eqn (13)]. Thus, similar to the definition of the partial change in the mean fitness, if the probability $v_{ij}^{(k)}$ that an individual with genotype $A_i A_j$ expresses phenotype S_k is replaced by $x_k + \beta_i^{(k)} + \beta_j^{(k)}$ for $i, j = 1, 2, \dots, n$ and if these values are kept constant, then the partial change in the frequency of phenotype S_k , denoted by $\Delta_{part} x_k$, will be

$$\begin{aligned}\Delta_{part} x_k &= \sum_{i,j=1}^n (P'_{ij} - P_{ij}) (x_k + \beta_i^{(k)} + \beta_j^{(k)}) \\ &= 2 \sum_{i=1}^n \beta_i^{(k)} \sum_{j=1}^n (P'_{ij} - P_{ij}) \\ &= 2 \sum_{i=1}^n \beta_i^{(k)} (\Delta p_i) \\ &= \frac{2}{\bar{f}} \sum_{i=1}^n p_i \beta_i^{(k)} \sum_{l=1}^m b_i^{(l)} f_l \\ &= \frac{\sigma_{\beta^{(k)}}^2 f_k}{\bar{f}} + 2 \sum_{l=1, l \neq k}^m \frac{cov(b^{(l)}, \beta^{(k)}) f_l}{\bar{f}}.\end{aligned}\quad (31)$$

Obviously, the partial changes in the phenotypic frequencies should be thought of as the changes in the phenotypic frequencies due only to the changes in the genotypic frequencies when the actual phenotypes of the genotypes are replaced by the corresponding additive genetic values and these additive genetic values are kept constant.

6. Change in Mean Fitness

The total change in the mean fitness of the population from the time of conception to the time of reproduction, denoted by $\Delta \bar{f}$, can be

decomposed as

$$\begin{aligned}
\Delta\bar{f} &= \bar{f}' - \bar{f} \\
&= \sum_{k=1}^m (x'_k f'_k - x_k f_k) \\
&= \sum_{k=1}^m [(x'_k - x_k) f_k + x'_k (f'_k - f_k)] \\
&= \sum_{k=1}^m (\Delta x_k) f_k + \sum_{k=1}^m x'_k (\Delta f_k), \tag{32}
\end{aligned}$$

where $\Delta f_k = f'_k - f_k$ is the change in the fitness of phenotype S_k ($k = 1, 2, \dots, m$). The first term on the right-hand side in eqn (32) can be thought of as a change in the mean fitness due only to changes in the phenotypic frequencies but not to changes in the fitnesses of the phenotypes. Note that

$$\sum_{k=1}^m (\Delta x_k) f_k = \sum_{i,j=1}^n \frac{P_{ij}(w_{ij} - \bar{f})^2}{\bar{f}} \geq 0 \tag{33}$$

so that any possible decrease in the mean fitness is necessarily due to changes in the fitnesses of the phenotypes. In fact, just as pointed out by Lessard (1997), eqn (33) exactly corresponds to Li's (1955) simplified version of Fisher's fundamental theorem of natural selection.

In eqn (33), the term $\sum_{i,j=1}^n P_{ij}(w_{ij} - \bar{f})^2$ is the total genetic variance in fitness, denoted by σ_T^2 . From Castilloux & Lessard (1995), σ_T^2 can be decomposed as

$$\sigma_T^2 = \sigma_\alpha^2 + \sigma_{R-f}^2, \tag{34}$$

where

$$\sigma_{R-f}^2 = \sum_{i,j=1}^n P_{ij} [w_{ij} - \bar{f} - (\alpha_i + \alpha_j)]^2 \tag{35}$$

is the residual variance in fitness. This residual variance can be decomposed as follows:

$$\begin{aligned}
\sigma_{R-f}^2 &= \sum_{i,j=1}^n P_{ij} [w_{ij} - \bar{f} - (\alpha_i + \alpha_j)]^2 \\
&= \sum_{i,j=1}^n P_{ij} \left\{ \sum_{k=1}^m [v_{ij}^{(k)} - x_k - (\beta_i^{(k)} + \beta_j^{(k)})] f_k \right\}^2
\end{aligned}$$

$$\begin{aligned}
&= \sum_{i,j=1}^n P_{ij} \sum_{k=1}^m [v_{ij}^{(k)} - x_k - (\beta_i^{(k)} + \beta_j^{(k)})]^2 f_k^2 \\
&\quad + \sum_{i,j=1}^n P_{ij} \sum_{k=1}^m \sum_{l=1, l \neq k}^m [v_{ij}^{(k)} - x_k \\
&\quad - (\beta_i^{(k)} + \beta_j^{(k)})][v_{ij}^{(l)} - x_l - (\beta_i^{(l)} + \beta_j^{(l)})] f_k f_l \\
&= \sum_{k=1}^m f_k^2 \sum_{i,j=1}^n P_{ij} [v_{ij}^{(k)} - x_k - (\beta_i^{(k)} + \beta_j^{(k)})]^2 \\
&\quad + 2 \sum_{k=1}^m \sum_{l=1, l \neq k}^m f_k f_l \sum_{i=1}^n \beta_i^{(l)} \\
&\quad \times \sum_{j=1}^n P_{ij} (\beta_i^{(l)} + \beta_j^{(l)}) \\
&\quad - 4 \sum_{k=1}^m \sum_{l=1, l \neq k}^m f_k f_l \sum_{i=1}^n \beta_i^{(k)} \sum_{j=1}^n P_{ij} (v_{ij}^{(l)} - x_l) \\
&\quad + \sum_{k=1}^m \sum_{l=1, l \neq k}^m f_k f_l \\
&\quad \times \sum_{i,j=1}^n P_{ij} (v_{ij}^{(k)} - x_k)(v_{ij}^{(l)} - x_l) \\
&= \sum_{k=1}^m \sigma_{R-S_k}^2 f_k^2 \\
&\quad + \sum_{k=1}^m \sum_{l=1, l \neq k}^m cov(S_k, S_l) f_k f_l \\
&\quad - 2 \sum_{k=1}^m \sum_{l=1, l \neq k}^m cov(b^{(k)}, \beta^{(l)}) f_k f_l. \tag{36}
\end{aligned}$$

Therefore, using eqns (22) and (36), σ_T^2 can be expressed in the form

$$\begin{aligned}
\sigma_T^2 &= \sum_{k=1}^m \sigma_{\beta^{(k)}}^2 f_k^2 + \sum_{k=1}^m \sigma_{R-S_k}^2 f_k^2 \\
&\quad + \sum_{k=1}^m \sum_{l=1, l \neq k}^m cov(S_k, S_l) f_k f_l. \tag{37}
\end{aligned}$$

Equation (37) shows that the total genetic variance in fitness is not affected by the covariance between the average excess on phenotype S_k and

the average effect on phenotype S_i , $cov(b^{(k)}, \beta^{(l)})$, for all $k, l = 1, 2, \dots, m$ but $k \neq l$. It depends only on the additive genetic variances, the residual variances and the covariances in phenotype.

From Ewens (1989), the partial change in the mean fitness of the population, denoted by $\Delta_{part}\bar{f}$, is given by

$$\begin{aligned}\Delta_{part}\bar{f} &= \sum_{i,j=1}^n (P'_{ij} - P_{ij})(\bar{f} + \alpha_i + \alpha_j) \\ &= 2 \sum_{i=1}^n \alpha_i(\Delta p_i) \\ &= \frac{\sigma_\alpha^2}{\bar{f}}.\end{aligned}\quad (38)$$

From eqns (22) and (31), we find immediately that the partial change in the mean fitness can be also expressed in the form

$$\Delta_{part}\bar{f} = \sum_{k=1}^m (\Delta_{part}x_k) f_k. \quad (39)$$

Equation (39) shows that, for the matrix game model, the partial change in the mean fitness can be thought of as a linear function of the partial changes in the phenotypic frequencies with the phenotypic fitnesses as coefficients. In other words, the partial change in the mean fitness of the population should be thought of as a change in the mean fitness due only to the partial changes in the phenotypic frequencies. This property not only corresponds to the general principle of the fundamental theorem of natural selection (Ewens, 1989, 1992; Castilloux & Lessard, 1995; Lessard & Castilloux, 1995; Lessard, 1997), but also it should be thought of as an important characteristic of the matrix game model for the relationship between the partial change in the mean fitness and the changes in the phenotypic frequencies.

7. Summary

Ewens (1989) emphasized that Fisher's fundamental theorem of natural selection about the

increase in mean fitness is of general validity without any restrictive assumptions on the mating system, the fitness parameters, or the number of loci and alleles involved, but that it concerns only a partial change in mean fitness. We agree with Ewens' interpretation about the fundamental theorem of natural selection.

As a classical frequency-dependent selection model, the matrix game model may be an important source of ideas and principles that provide some insights on intra-specific selection. As pointed out in Section 1, the change in the mean fitness must be based on the changes in the phenotypic frequencies. In order to understand the relationship between the partial change in the mean fitness and the changes in the phenotypic frequencies, the concepts of average excess and average effect on phenotype are defined in Sections 3 and 4. In Section 5, the concept of the partial change in the phenotypic frequencies is presented. In Section 6, we further illustrate that, for the matrix game diploid model, the partial change in the mean fitness can be thought of as a change in the mean fitness due only to the partial changes in the phenotypic frequencies. Although the genetics seems to count, it does not really.

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