

## Relative Advantage and Fundamental Theorems of Natural Selection

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**Summary.** According to the tenet of Darwinian selection, a phenotype will spread only if its fitness is greater than the mean fitness of the entire population. It is, therefore, natural to introduce the notion of relative advantage of a replicator, which is defined as the expected fitness of this replicator minus the average fitness of the entire replicator population. For the general replicator dynamics, it is shown that the relative advantage of an offspring population over its parent population is proportional to the variance in fitness. The relationship between the proposed and earlier versions of the fundamental theorem of natural selection is also discussed.

**Key words:** Fitness variance, fundamental theorem of natural selection, relative advantage, replicator dynamics.

### 6.1 Introduction

In this chapter, we consider a sufficiently large population in which the individual phenotypes are uniquely determined genetically. We consider only the frequency-dependent selection process.

This chapter is centered around the following question: what function is optimized during natural selection such that its rate of increase equals the variance of the fitnesses?

Fisher's fundamental theorem of natural selection states that "*the rate of increase in the average fitness of a population is equal to the genetic variance of that population*" [5]. This theorem has been the subject of controversy and exegesis.<sup>1</sup> For instance, this theorem does not hold in evolutionary game theory where genotypic fitness is frequency dependent. For example, infanticide is a successful evolutionary strategy among lions and langurs [9]. This kind of phenotype, obviously, decreases the mean fitness of the population.

Ewens [3] redrafted the fundamental theorem of natural selection in the following way: *the partial change in mean fitness is equal to the additive genetic variance in*

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<sup>1</sup> The historical details of this controversy can be traced from the references in [2,4,13,14].

*fitness divided by the mean fitness* (see also [13]). Ewens has substituted the average fitness by the partial change in the mean fitness.

The aim of this chapter is to reveal the relationship between selection and variance in a replicator population. We will see the simplest version of a fundamental theorem of natural selection which can be given in terms of the relative advantage. Moreover, in special cases we also see the connection between one version of Fisher's theorem and the proposed theorem, and that the notion of the partial change in mean fitness contains the notion of the relative advantage.

For this purpose, we have to recall the dynamics of the selection of proper replicators. Let us consider  $n$  different types of a given proper replicator. A replicator is proper if the principle of "*i-type from an i-type*" is valid. In other words, for the production of an  $i$ -type replicator the contribution of a parent  $i$ -type replicator is a must. Here we can think about an asexual population without mutation or a sexual diploid population where two alleles at a single locus determine the individual fitness and there is no mutation, either. In both cases replication is proper. Consider, for example, the first situation. Now the gamete distributions are the same as the allele distributions, and the gamete dynamics is nothing else than the replicator dynamics of the alleles. This is no surprise, because now each individual only reproduces its parental gametes.

Denote by  $F_i(x)$  the frequency-dependent fitness of an  $i$ -replicator and by  $F(x) := (F_1(x), F_2(x), \dots, F_n(x))$  the fitness vector of the population in state  $x \in S_n$ .<sup>2</sup> Using this notation, the average fitness of the population is  $x F(x) = \sum_{i=1}^n x_i F_i(x)$ , where  $x_i$  is the frequency of the  $i$ -replicator.

AU: Is  $x_i$  here OK?

In the course of selection, the frequencies of the replicators will change. This change can be given by the *replicator dynamics* [10] formulated in discrete time as

$$x_i(t+1) = x_i \frac{F_i(x)}{x F(x)}, \quad (6.1)$$

and in continuous time as

$$\dot{x}_i = x_i (F_i(x) - x F(x)). \quad (6.2)$$

We have to emphasise that these dynamics are strictly based on proper replicators. This explains that the right-hand side of dynamics (6.1) and (6.2) are linearly proportional to the relative frequency of the replicator.

Now let us recall the definition of the relative advantage function [11]. According to the classical Darwinian theory, a phenotype will spread if it has greater fitness than the others. Based on this, the definition of *relative advantage function* for a proper replicator population is the following:

$$A : S_n \times S_n \rightarrow R, \quad A(y, z) := y F(z) - z F(z). \quad (6.3)$$

This function describes the relative advantage of state  $y$  over state  $z$ , since it is positive only if the average fitness of a subpopulation,  $y F(z)$ , in which the distribution of replicators is  $y$ , is greater than the average fitness of the whole population with distribution

<sup>2</sup>  $S_n$  denotes the standard simplex of the  $n$ -dimensional space.

$z, zF(z)$ . This implies that the frequency of subpopulation  $y$  increases.<sup>3</sup> Finally, observe that the right-hand side of the replicator dynamics (6.2) is the frequency of the  $i$ -replicator multiplied by their relative advantage.

## 6.2 The Fundamental Theorem of Natural Selection Based on Relative Advantage

We are in a position to formulate a new and the simplest possible fundamental theorem of natural selection. First, let us consider proper replicators.

### 6.2.1 Discrete Case

Assume that we have a discrete time scale. In this case, we have the following statement: *the relative advantage of the offspring generation over its parent generation is always positive and is proportional to the variance of the fitness of its parent population*. Indeed, according to the discrete replicator dynamics (6.1), after the operation of selection, in the offspring generation the distribution of the replicator can be given by

$$x(t+1) = \left( \frac{x_1(t)F_1(x(t))}{x(t)F(x(t))}, \frac{x_2(t)F_2(x(t))}{x(t)F(x(t))}, \dots, \frac{x_n(t)F_n(x(t))}{x(t)F(x(t))} \right).$$

We have to assume that the number of offspring of an  $i$ -replicator, i.e.,  $F_i(x(t))$  is positive to avoid division by zero. Now the relative advantage of the offspring generation over its parental one can be calculated as

$$\begin{aligned} (x(t+1) - x(t))F(x(t)) &= \sum_{i=1}^n \frac{x_i(t)F_i(x(t))}{x(t)F(x(t))} F_i(x(t)) - \sum_{i=1}^n x_i(t)F_i(x(t)) \\ &= \frac{1}{x(t)F(x(t))} \left[ \sum_{i=1}^n x_i(t) (F_i(x(t)))^2 - (x(t)F(x(t)))^2 \right] \\ &= \frac{\text{Var}(F(x(t)))}{x(t)F(x(t))}. \end{aligned} \quad (6.4)$$

In particular, in an asexual population offspring are fitter than their parents when competing against the parents' state.

### 6.2.2 Continuous Case

The above statement is true for the continuous-time version of the replicator dynamics as well. More specifically, we claim an analogue of the fundamental theorem for the

<sup>3</sup> The relative advantage can be used in evolutionary game theory to define an evolutionarily stable state (ESS): an  $x^* \in S_n$  is an ESS if and only if  $A(x^*, x) = x^*F(x) - xF(x) > 0$  for all  $x^* \in S_n, x^* \neq x$  near  $x^*$  [16]. Let us observe that the relative advantage of an ESS as a function of its second variable attains a local minimum at  $x^*$ , the ESS.

continuous-time version of the replicator dynamics (6.2): *the instantaneous rate of increase in the population's relative advantage over its current state is equal to the variance of the replicators' fitnesses.*<sup>4</sup> Indeed, for a fixed  $z$  and time-dependent  $x$ ,

$$\frac{d}{dt}A(x, z) = \dot{x}F(z).$$

Putting  $z = x$

$$\begin{aligned} \dot{x}F(z)|_{z=x} &= \sum_{i=1}^n x_i [F_i(x) - xF(x)] F_i(x) \\ &= \sum_{i=1}^n x_i [F_i(x) - xF(x)]^2 = \text{Var}(F(x)). \end{aligned} \quad (6.5)$$

The above two arguments are obviously true for the evolutionary matrix game, the classical Fisher's selection model and the single autosomal locus model when the individual's fitness can be given by an evolutionary game-theoretical model. In the third model, the fitness of  $A_i$  allele  $F_i(x) := \sum_j p_j \sum_{k,l} a_{ij,kl} p_k p_l$ , where  $p_i$  is the frequency of allele  $A_i$  and  $a_{ij,kl}$  is the  $A_i A_j$  zygote's pay-off when it interacts with  $A_k A_l$  zygote [7]. We emphasise that in all models it is supposed that there is no mutation during the selection process, and this is why the replicators are proper in these examples.

### 6.2.3 General Replicators with Panmixis

To see that the above reasoning can be extended beyond proper replicator, let us consider  $n$  different types of a given general replicator. A replicator is general if the principle of  $i$ -type from an  $i$ -type does not hold. Let us consider a sufficiently large, panmictic diploid sexual population where the phenotypes are genetically determined by multiple loci with recombination and/or mutation between existing alleles. Recombination produces chromosomes different from those in parental zygotes. Moreover, mutation injures the principle of  $i$ -types gamete from  $i$ -types gamete.

Now we introduce some notation. Let  $x_i$  be the relative frequency of the  $G_i$  gamete types. Let  $w_{ij}(x)$  be an arbitrary frequency-dependent fitness (viability) function of zygote  $G_i G_j$  ( $i, j = 1, 2, \dots, n$ ),  $m_{i,kl}$  be the probability that zygotes  $G_k G_l$  produce gamete  $G_i$ . Of course,  $\sum_i m_{i,kl} = 1$  for all zygotes  $G_k G_l$ . Since we assume that the population is panmictic, the relative frequency of the ordered genotype  $G_i G_j$  is  $x_i x_j$ . Thus, we get the following discrete gamete dynamics:

$$x_i(t+1) = \frac{\sum_{k,l} m_{i,kl} w_{kl}(x(t)) x_k(t) x_l(t)}{\sum_i \sum_{k,l} m_{i,kl} w_{kl}(x(t)) x_k(t) x_l(t)}$$

<sup>4</sup> This statement is a generalization of an earlier result [8]: the relative advantage of an ESS decreases in the course of replicator selection and the rate of decrease is proportional to the variance of the fitnesses of the replicators.

$$= \frac{\sum_{k,l} m_{i,k,l} w_{kl}(x(t)) x_k(t) x_l(t)}{\sum_{k,l} w_{kl}(x(t)) x_k(t) x_l(t)}. \quad (6.6)$$

For continuous time we have the following dynamics:

$$\dot{x}_i = x_i \sum_{k,l} m_{i,k,l} w_{kl}(x) x_k x_l - x_i \sum_{k,l} w_{kl}(x) x_k x_l. \quad (6.7)$$

In general, such an equation describes a multiplication process in which a replicator may also be produced by a replicator of a different type [1, 12, 17].

For the generalization of the concept of fitness, it is suitable to introduce the notation of *production rate* of a gamete type present in the parental population. Let the production rate of an  $i$ -gamete be the number of  $i$ -gametes in the offspring generation divided by the number of  $i$ -gametes in the parental generation. Formally, for all  $x \in S_n$  and  $i = 1, 2, \dots, n$  with  $x_i > 0$ , we define the production rate of the  $i$ -gamete as

$$f_i(x(t)) = \frac{\sum_{k,l} m_{i,k,l} w_{kl}(x(t)) x_k(t) x_l(t)}{x_i(t)}. \quad (6.8)$$

Observe in the definition of production rate that the assumption of a large enough population is important. If we have a small population and a huge number of different gamete types then all possible gamete types cannot exist at any point of time, thus  $x_i(t) = 0$  may occur. Moreover, if the population is small then genetic drift can mask the effect of selection.

Using the production rate, we rewrite the dynamics (6.6) and (6.7) as follows:

$$x_i(t+1) = x_i(t) \frac{f_i(x(t))}{\sum_k x_k(t) f_k(x(t))}. \quad (6.9)$$

For the continuous-time scale, we have the following dynamics:

$$\dot{x}_i = x_i \left( f_i(x) - \sum_k x_k f_k(x) \right). \quad (6.10)$$

Based on the notion of production rate, the relative advantage function for a gamete population can be defined as

$$A : S_n \times S_n \rightarrow \mathbb{R}, \quad A(y, z) := yf(z) - zf(z). \quad (6.11)$$

Using the notion of production rate, the fundamental theorems of natural selection proposed in (6.4) and (6.5) are valid without any change for general replicators, as well.

### 6.3 Connection to Fisher's Theorem

In order to see the connection between Fisher's fundamental theorem of natural selection and the one proposed here (6.5), we have to recall the well-known proof of the

continuous version of Fisher's theorem (see, e.g., [10]). Let us consider the classical Fisher's selection model, which considers a diploid, panmictic sexual population, in which abiotic selection takes place at the zygotic level. The marginal fitness of alleles is given by  $F_i(x) := (Ax)_i$ , where the viability matrix  $A$  is symmetric (i.e.,  $a_{ij} = a_{ji}$  for all  $i, j$ ) and  $(Ax)_i$  denotes the  $i$ th coordinates of vector  $Ax$ . Using these notions, the average fitness of the allele population is given by  $xAx$  and the replicator dynamics (6.2) is rewritten as

$$\dot{x}_i = x_i((Ax)_i - xAx). \quad (6.12)$$

In this case, the average fitness is a Lyapunov function with respect to Fisher's selection model, and its derivative with respect to Fisher's selection equation (6.12) is the variance of the marginal fitness of alleles. Indeed, since the viability matrix  $A$  is symmetric, the gradient of the average fitness is  $\text{grad } xAx = 2((Ax)_1, (Ax)_2, \dots, (Ax)_n)$ . Thus, its derivative with respect to dynamics (6.12) is

$$\begin{aligned} (\text{grad } xAx)\dot{x} &= 2 \sum_i x_i((Ax)_i - xAx)(Ax)_i = 2 \sum_i x_i((Ax)_i - xAx)^2 \\ &= 2\text{Var}(Ax). \end{aligned} \quad (6.13)$$

If the viability matrix  $A$  is not symmetric then this proof does not work.

Now, let us compare (6.5) and the above proof of Fisher's fundamental theorem (6.13). We recognize first that the proposed version of the fundamental theorem is based strictly on Fisher's theorem, since the proof of the proposed version is part of the proof of Fisher's theorem. Second, observe that  $\sum_i x_i((Ax)_i - xAx)(Ax)_i$  is, in essence, the relative advantage of the offspring generation over its parents. Indeed, according to the dynamics (6.3),  $x_i(t + \Delta t) - x_i(t) \approx \Delta t x_i((Ax)_i - xAx)$ , thus the relative advantage in  $\Delta t$  is  $\sum_i (x_i(t + \Delta t) - x_i(t))(Ax)_i \approx \Delta t \sum_i x_i((Ax)_i - xAx)(Ax)_i$ .

## 6.4 Relative Advantage Versus Partial Change in Mean Fitness

Here the connection between the proposed fundamental theorem (6.4) and Ewens's theorems will be investigated. We will do this in three steps. First, we recall the concept of partial change in mean fitness. Second, we will study the residual of average effects. Third, we will see that the notion of partial change of mean fitness "contains" the concepts of relative advantage.

### 6.4.1 Ewens's Concept

To get insight into the connection between the partial change in mean fitness and the relative advantage we have to recall the notion of partial change in mean fitness. We will follow the derivation of Ewens's version of the fundamental theorem for one locus [3] and briefly recall all points of [3] used here. Let  $p_i$  denote the frequency of allele

$A_i$ , and  $P_{ij}$  denote the frequency and  $w_{ij}$  the fitness (viability) of zygote  $A_i A_j$  ( $i, j = 1, 2, \dots, n$ ). Ewens [3] considered Mendelian systems, thus  $w_{ij} = w_{ji}$ . The current frequency of allele  $A_i$  is

$$p_i = \sum_j P_{ij} \quad (6.14)$$

and, in the next generation, this frequency

$$p'_i = \frac{\sum_j P_{ij} w_{ij}}{w(p)}, \quad (6.15)$$

where  $\bar{w}(P) = \sum_{i,j} P_{ij} w_{ij}$  is the mean fitness of the population. Using this notation, Ewens [3] introduced the following notions, based on [6, 15]. The *average excess* of allele  $A_i$  is defined by

$$a_i(p) = \frac{\sum_j P_{ij}(w_{ij} - \bar{w}(P))}{p_i}. \quad (6.16)$$

In Ewens's version of the fundamental theorem, even more important is the notion of the average effect of allele  $A_i$  which is defined by a least squares procedure. Let  $\alpha_i$  denote the *average effect* of allele  $A_i$ . Then  $\alpha_1, \alpha_2, \dots, \alpha_n$  are chosen so as to minimize

$$\sum_{i,j} P_{ij}(w_{ij} - \bar{w}(P) - \alpha_i - \alpha_j)^2, \quad (6.17)$$

subject to

$$\sum_j p_j \alpha_j = 0. \quad (6.18)$$

Of course, the average effect depends on the parental allele distribution. Moreover, Ewens [3] noted that if  $P_{ij} = p_i p_j$  then the average effect and the average excess are equal.

Now we are at the basic concept of the Ewens version, namely the concept of the *partial change in mean fitness* which is defined as follows:

$$\sum_{i,j} P_{ij}(\bar{w}(P) + \alpha_i + \alpha_j). \quad (6.19)$$

The additive genetic variance is given by Ewens as

$$\sigma^2 = 2 \sum_i p_i a_i \alpha_i = 2 \bar{w}(P) \sum_i (\Delta p_i) \alpha_i,$$

where  $\Delta p_i = p_i(t+1) - p_i(t)$ . Ewens' version of the fundamental theorem reads

$$\begin{aligned}
\sum_{i,j} (P'_{ij} - P_{ij})(\bar{w}(P) - \alpha_i - \alpha_j) &= 2 \sum_i \alpha_i \sum_j (P'_{ij} - P_{ij}) \\
&= 2 \sum_i (\Delta p_i) \alpha_i = \frac{\sigma^2}{w(p)}. \quad (6.20)
\end{aligned}$$

This says that the *partial change in mean fitness is proportional to the fitness variance of the alleles*.

In what follows we make a few remarks on the average effect and partial change in the mean fitness.

#### 6.4.2 Residual of Average Effect

To demonstrate the background of the average effect let us see a case where the minimization problem defined by (6.17), (6.18) is without residual for all allele distributions. Function (6.17) is equal to zero if and only if  $w_{ij} = \bar{w}(P) + \alpha_i + \alpha_j$  for all  $i, j$ . This equality means that the fitness components of the alleles are additive.<sup>5</sup> The widely used fitness additivity condition is rather restrictive since it reduces the degree of freedom of the symmetric fitness matrix and excludes, for instance, the case of overdominance. Moreover, in this additive case the fitness of an allele is  $w_i(p) = \bar{w}(P) + \alpha_i$ , so the relative advantage of an allele (i.e.,  $w_i(p) - \bar{w}(P) = \alpha_i$ ) does not depend on the allele distribution, which is a very special frequency dependence. Thus, the minimization problem defined by (6.17), (6.18) is with residual in general.

Let us consider a panmictic but non-additive case, where the residual of (6.17) is given in the following.

*Remark 1* When  $P_{ij} = p_i p_j$  using the previous notation and observation (recall  $P_{ij} = p_i p_j$  implies  $\alpha_i = a_i(p) = w_i(p) - \bar{w}(P)$  for all  $i = 1, 2, \dots, n$ ) it is not hard to see that (6.17) becomes

$$\begin{aligned}
&\sum_{i,j} P_{ij} (w_{ij} - \bar{w}(P) - \alpha_i - \alpha_j)^2 \\
&= \sum_{i,j} P_{ij} (w_{ij} - \bar{w}(P))^2 - 2 \sum_{i,j} p_i (w_i(p) - \bar{w}(P))^2. \quad (6.21)
\end{aligned}$$

This means that the residual of (6.17) for the minimizing values of  $\alpha_i$  under the constraint (6.18) can be given as a difference of the fitness variance at the zygote level and two times the fitness variance at the allelic level. To my knowledge, the residual of the minimalization problem of (6.17), (6.18) is not given in the literature.

Observe that optimization model (6.17), (6.18) is an additive estimation of the effects of alleles, which is surprising, since it is unusual to base a theoretical setup on a statistical approach. In my view, the intuitive strength of the optimization model (6.17), (6.18) is that it provides a fundamental theorem in a general genetic situation. Then the question is what the theoretical interpretation of constraint (6.18) is in the case of non-additive fitness.

AU: Is (6.18) corect in footnote 5?

<sup>5</sup> An easy calculation shows that the constraint (6.18) must hold in this case.

## 6.5 Connection Between Partial Change and Relative Advantage

In this subsection, we will see a possible interpretation of partial change in mean fitness. For this purpose, we will see first, in Remarks 2 and 3, two important connections between the notions of relative advantage and of partial change in mean fitness.

*Remark 2* Let us assume that  $w_{ij} = \alpha_i + \alpha_j$  for all  $i, j = 1, 2, \dots, n$ . Then we have

$$\sum_{i,j} (P'_{ij} - P_{ij})(\bar{w}(P) + \alpha_i + \alpha_j) = \sum_{i,j} (P'_{ij} - P_{ij})(\alpha_i + \alpha_j) = \sum_{i,j} (P'_{ij} - P_{ij})w_{ij}, \quad (6.22)$$

so the partial change in the mean fitness is equal to the relative advantage of the offspring zygote population over the parent zygote population.

*Remark 3* Let us assume  $P_{ij} = p_i p_j$ . Then the average excess of allele  $A_i$  is, apart from the multiplication by 2, equal to the relative advantage of allele  $A_i$  over the population  $p$ . Formally,  $A_i$  is identified with the  $i$ -replicator and  $F_i(p) = w_i(p) = \sum_j w_{ij} p_j$  denotes the fitness of allele  $A_i$ . Using  $P_{ij} = p_i p_j$  and  $\bar{w}(p) = \sum_{i,j} w_{ij} p_j$  we get the definition of average excess rewritten as follows:

$$\begin{aligned} a_i(p) &= \sum_j \frac{p_i p_j (w_{ij} - \sum_{k,l} w_{kl} p_k p_l)}{p_i} = \sum_j p_j \left( w_{ij} - \sum_{k,l} w_{kl} p_k p_l \right) \\ &= w_i(p) - \bar{w}(p). \end{aligned} \quad (6.23)$$

Moreover, under the condition that  $P_{ij} = p_i p_j$ , we already know that the average effect and the average excess are equal; thus, the average effect and the relative advantage are equal as well. Therefore, for the partial change in mean fitness we obtain

$$\begin{aligned} &\sum_{i,j} (P'_{ij} - P_{ij})(\bar{w}(p) + \alpha_i + \alpha_j) \\ &= \sum_{i,j} (p'_i p'_j - p_i p_j)(\bar{w}(p) + w_i(p) - \bar{w}(p) + w_j(p) - \bar{w}(p)) \\ &= \sum_{i,j} (p'_i p'_j - p_i p_j)(w_i(p) + w_j(p)) = 2 \sum_{i,j} (p'_i - p_i)w_i(p). \end{aligned} \quad (6.24)$$

Thus, apart from the multiplication by 2, the partial change in mean fitness is equal to the relative advantage of the offspring generation of alleles over its parental allele population. Thus, Ewens's version and the proposed version of the fundamental theorem are essentially the same under random mating.

Based on Remarks 2 and 3 it is intuitively clear that there is a deep connection between the partial change in mean fitness and the relative advantage. Now, from the viewpoint of the notion of relative advantage, a possible interpretation of partial change in the mean fitness is given. In the definition of Ewens's partial change in the mean fitness, there are two points.

1. What is the connection between the average fitness of the whole population and the average effects of alleles? We have the following:

$$\bar{w}(P) = \sum_{i,j} P_{ij} w_{ij} = \sum_{i,j} P_{ij} (\bar{w}(P) + \alpha_i + \alpha_j) = \bar{w}(P) + 2 \sum_i p_i \alpha_i. \quad (6.25)$$

Thus, equality (6.25) strictly depends on constraint (6.18). It seems that this is the only biological relevance of constraint (6.18).

2. The second point concerns the relative advantage of the offspring zygote generation over its parents,  $\sum_{i,j} (P'_{ij} - P_{ij}) w_{ij}$ . Similarly to (6.25), if  $w_{ij}$  is replaced by  $\bar{w}(P) + \alpha_i + \alpha_j$ , then we get the concept of Ewens's formula (6.19). In other words, if we take the relative advantage of zygotes but we approximate fitness with the average effects, then we obtain the partial change in mean fitness. In this sense, the notion of partial change in mean fitness includes that of relative advantage. In general, however, we have

$$\sum_{i,j} P_{ij} (\bar{w}(P) + \alpha_i + \alpha_j) \neq \sum_{i,j} (P'_{ij} - P_{ij}) w_{ij}, \quad (6.26)$$

due to the residual of the average effect (see Remark 1).

Let us observe that Ewens's approach is "zygote centered," as was the original concepts of Fisher, in the sense that the definition of partial change in the mean fitness is based on the relative frequencies of the zygotes.

There is, however, another possibility. Let us consider Fisher's selection equation (6.12), which is "allele centered," in the sense that the state of the population is described in terms of the allele distribution. If we try to follow Ewens's setup but at the level of alleles we need neither the average excess nor the average effect of alleles, since in Fisher's selection equation (6.12) the allelic fitness determines the whole process of selection. Following Ewens's setup, the partial change in mean fitness at the allelic level could be defined as  $\sum_{i,j} (p'_i - p_i) w_i(p)$  which is nothing else than the relative advantage of the offspring allele generation over its parental population (cf. second point above).

Summing up, the notion of partial change of the zygote mean fitness contains the notion of relative advantage of the offspring allele population over its parent one. Furthermore, Ewens's version is "zygote centered" while the proposed version is "allele centered."

## 6.6 Summary

In this chapter, the simplest fundamental theorem of natural selection is given: the relative advantage of the offspring generation over its parent generation is always positive and is proportional or equal to the variance of fitness in the parent population in the discrete- or continuous-time model, respectively.

Now a game-theoretical interpretation of this statement is given. During Darwinian selection, a phenotype will spread only if its fitness is greater than the mean fitness of

the whole population. Thus, it is natural to ask: What kind of improvement can happen during natural selection? Now let us consider a frequency-dependent individual fitness. In this chapter, we see that from generation to generation, the offspring generation is better against its parental population than the parental population against itself. In this sense, natural selection improves competition ability from generation to generation. Moreover, we also see that this improvement is proportional to the variance of the marginal fitness of replicators.

Moreover, we have shown that the relative advantage plays an important role in Fisher's (see Section 6.3) and Ewens's version (see Section 6.4) of the fundamental theorems of natural selection, as well.

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