Canadian Social Science Vol.4 No.6 December 2008

On the Causation of the Replicator Dynamics

DE LA CAUSALITÉ DE LA REPRODUCTION DE LA DYNAMIQUE

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Abstract: Here we demonstrate the models formation and research findings of the Replicator Dynamics that interpret the evolutionary process, also the discussion about problem with the models which are commonly used in evolutionary game theory, i.e. the difference between the fitness of population following a certain strategy and the average fitness of the entire population determine the change of population proportion following the strategy between generations, that is to say what happen after one bout are used to interpret the phenomena before the bout. As a modification, we construct a model directly with the numbers of the population following a certain strategy between generations, and prove the characteristics of its key can be discussed according to the model.

Key words: adaptation, evolutionary dynamics, Replicator Dynamics

Résumé: Ici, nous démontrons la formation des modèles et la conclusion de la recherche de la dynamique de la reproduction qui interprète le procès évolutionniste, et aussi la discussion sur le problème avec les modèles qui sont communément utilisés dans la théorie du jeu évolutionniste, c.-à-d. la différence entre l'aptitude de la population suivant une certaine stratégie et l'aptitude en moyenne de la toute la population déterminent le changement de la proportion de la population suivant la stratégie parmi les générations, c'est-à-dire ce qui se passe après un accès sont utilisé pour interpréter les phénomènes avant un accès. Comme une modification, nous construisons un modèle directement avec les nombres de la population selon une certaine stratégie parmi les générations, et prouvent que les caractéristiques de leur clé peuvent être discuté d'après le modèle.

Mots-Clés: adaptation, dynamique évolutionniste, dynamique de reproduction

1. INTRODUCTION

In R. A. Fisher's attempt [see *The Genetic Theory of Natural Selection* (1930)] to explain the approximate equality of the sex ratio in mammals, he found the "fixed point" that the

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* Received 16 October 2008; accepted 15 November 2008

evolutionary dynamics leads to a stable situation. Fisher's argument can be understood as the initial work of evolutionary game theory, but he did not state it in those terms. After that, there are two approaches to evolutionary game theory in generalized models structuring. One is Taylor and Jonker's (1978) Replicator Dynamical model (hereinafter referred to as RD). The other derives from the work of Maynard Smith and Price, i.e. the concept of an evolutionarily stable strategy. The latter focuses on stable conditions of dynamical process, while the former attempts to reveal the dynamical process of the evolutionary system that leads to a stable situation.

Taylor and Jonker's (1978) pioneering attempt stimulates widespread studies and applications of Replicator Dynamics and fitness in the framework of evolutionary economics. T. Day and P. D. Taylor (2003) followed Maynard Smith's (1982) approach to fitness, and applied it to their model of Replicator Dynamics. H. Gintis (1999) took a similar approach in his model. J. M. Alexander (2003) attempted to link ESS and Replicator Dynamics.

The aforesaid studies carry forward the thought of dynamical adaptation, and focus on the interpretation of dynamical evolution mechanism.

The clue of interpretation about the evolutionary mechanism must be the individual adaptation, but there have been long-standing debates over adaptation (Dobzhansky, 1977； Knoll and Niklas, 1987). Evolutionary biology makes it clear that whether adaptation is a process or a situation, the result should be an individul or a population's contrbution to the breeding of the population during the natural selection process, and hence the adaptive value or fitness in the environment can be obtained. Evolutionary game is first used to interpret the ecological phenomenon that individuals accept natural selection and adapt to their enviroment, and then it is referenced by economists in anlysing economic phenomena. The questions arise when we approach the Replicator Dynamics from the perspective of dynamical evolution:

1st. How does Replicator Dynamics reflect the dynamic nature of evolutionary adaptation in researchers' opinion when they use the model?

2nd. According to requirements of models interpreting dynamical mechanism, is the concept "fitness" [2] in Replicator Dynamics, methodologically valid?

3rd. Without applying the difference between the fitness of population (or expected payoff value) following a certain strategy and the average fitness of the entire population to Replicator Dynamics, can we discuss the characteristics of the equation's key?

Considering the questions raised, we review the models formation and research findings of the Replicator Dynamics that interpret the evolutionary process, also the discussion about the problem with the models which are commonly used in evolutionary game theory. We then directly construct a model with the numbers of the population following a certain strategy between generations, attempt to prove the characteristics of its key (the nature of evolutionary dynamics) which can be discussed according to the model instead of using the difference between the fitness of population following a certain strategy and the average fitness of the entire population that determines the change of population proportion following the strategy between generations.

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[2] Just talk about "the difference between the fitness of population following a certain strategy and the average fitness of the entire population".

2. REPLICATOR DYNAMICS AND ITS CONSECUTION IN METHODOLOGY

The formation of RD model symbolizes the shaping of evolutionary game theory. Many game theorists have made in-depth studies of the adjusting process of collective behavior, and constructed varying dynamical models from different perspectives, such as Weibull's (1995) Imitation Dynamics; Börgers and Sarin's (1995, 1997) Reinforcement Dynamics and so on. In fact the model that is widely accepted and applied is Taylor and Jonker's (1978) Replicator Dynamics. Up to the present, evolutionary game theorists have been inspired by the findings of Maynard Smith (1982), Taylor and Jonker (1978).[3]

2.1 Research and Review about RD

Paying particular attention to the standard criteria for evolutionary stability, T. Day and P. D. Taylor (2003) looked into similarities between discrete-trait games and continuous-trait games, and then attempted to show that the standard evolutionarily stable strategy conditions for discrete-trait games can be seen as a special case of the conditions employed in continuous-trait games. The general form (continuous-trait games) of adaptive dynamics is expressed as below:

$$\frac{d\bar{\mathbf{z}}}{dt} = \operatorname{cov}(\mathbf{z}, W(\mathbf{z}, \bar{\mathbf{z}})) \qquad (1)$$

Where $\bar{\mathbf{z}}$ denotes the population mean of traits, $\mathbf{z}$ denotes a one- or multi-dimensional quantitative trait,[4] $W(\mathbf{z}, \bar{\mathbf{z}})$ denotes the individual fitness.[5] RD is denoted in discrete-trait games as below:

$$\frac{d\bar{p}_i}{dt} = \bar{p}_i(w_i(\bar{\mathbf{p}}) - \overline{W}), \quad i = 1, \ldots, n \qquad (2)$$

where $\overline{W} = \sum_j \bar{p}_j w_j(\bar{\mathbf{p}})$ denotes the average fitness of the entire population, vectors of $\bar{\mathbf{p}}$ denote the proportions of different traits, $w_i(\bar{\mathbf{p}})$ denotes the fitness of individuals following strategy i, and take a_{ij} to be the fitness of an i-strategist against a j-opponent.

Much of the classical work in evolutionary game theory is based on this fundamental assumption, namely, the definition of fitness is just the number replicated. And this is the most significant difference between evolutionary games and dynamical games.

H. Gintis (1999) took a similar approach in his model

$$\dot{p}_i = p_i[w_i(t) - w(t)], \quad i = 1, \ldots, n \qquad (3)$$

where $w_i(t)$ denotes the fitness of individuals following one strategy, $w(t)$ denotes the average fitness of the entire population, p_i denotes the proportion following the strategy (E. S. Andersen, 1994 and R. A. Fisher, 1999 use the same description).

Gintis defines "fitness" as the expected number of offspring, and it depends on a single

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[3] The denotation in RD used in the literature is not consistent, here we adopt the common expression instead of giving a detailed description of each.

[4] $\mathbf{z}$ denotes the sector made up by the possibilities of individuals with continuous-trait(strategy).

[5] The definition of individual fitness adopts the doing of Maynard Smith (1982).

genetic locus.[6] Although his research was forward-looking at the time, his own idea is lacking when he incorporates the fitness in his model. He just follows his predecessors' thoughts: The change of proportion following one strategy depends on the distribution of fitness.

The aforementioned studies give *n* kinds of strategies (types or traits), we can conclude that they can be reduced to two strategies, which will not affect our discussion about dynamic process. Hence, we will discuss J. M. Alexander's (2003) study employing two strategies, typically called "Cooperate" and "Defect" (denoted as C and D). Alexander describes RD as below:

$$\frac{dp_c}{dt}=\frac{p_c(W_c-\overline{W})}{\overline{W}} \qquad (4)$$

where p_c denotes proportion following the strategy C, W_C denotes the fitness of cooperators, $\overline{W}$ denotes the average fitness of the entire population. It can be proved that the fitness here is just the number ratio between generations (see Part 3).[7] He used this model to explore whether there is constringency during the dynamical process and the influencing factors.

With regard to studies about dynamical models in the past 30 years, consensus reached in this field can be expressed as follows:

- Noticing that the transformation from (1) to (2) and the disposal with the right side of (3) and (4), we can see that the basic precondition of RD is that it take a_{ij} in the payoff matrix to be the fitness of an *i*-strategist against a *j*-opponent, also the number of individuals replicated in a bout.
- The principal notions of characterizing evolutionary mechanism by dynamical equation can be summarized as the following: The dynamical change of "the difference between the expected payoff value of population following a certain strategy and the average expected payoff value of the entire population" determines the change rate of population proportion following one strategy between generations. That is to say, the rate of change of population proportion following one strategy between generations depends on the distribution of "fitness".
- The introduction of "fitness" is a key factor, and fitness is assumed in most literature as the number of offspring that survives (or replicators), or the ratio of offspring that survives.
- Comparing the fitness of individuals following one strategy with that of the entire population, researchers discuss the fundamental question of dynamical model— whether or not there is the eventual constringency during the change between generations? It can also be understood that which equilibrium the system will be driven to depends on the original state of the system (just the path dependence), and whether the equilibrium is stable has something to do with the distribution of traits, proportion and payoff matrix.

Using the approach, researchers hope to interpret the dynamical process and evolutionary tendency between generations (bouts). And they assume that individuals' payoff just equals their growth ratio by replicating themselves after a bout, which implicitly describes a kind of learning mechanism. By using differential equation in mathematical technology, the widely used model RD which takes a_{ij} in the payoff matrix as the consequence misunderstands the

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[6] At a single genetic locus there are two genes (such creatures, which includes most of the "higher" plants and animals, are called diploid). Suppose there are n alternative types of genes (called alleles) at this genetic locus, which we label g_i, i=1, . . . , n. An individual whose gene pair is (g_i, g_j), whom we term an "*ij* -type," then has fitness w_{ij}, which is interpreted as being its probability of surviving to sexual maturity.

[7] Apparently, this is not in consistent in the context because of different definitions of "fitness". This also shows that the term is defined differently though it is applied widely.

concept "dynamics". In the model, the ratio of change of proportion during a bout depends on the result after a bout, which is used to explain the situation before the game.

2.2 Review of Methodology

Biological evolutionism is the source of the idea of evolutionary dynamics. In evolutionary game theory, it is assumed that individuals that have limited rationality are unable to respond rapidly and appropriately to the environmental change. Rather, individuals, through experimenting, imitating and learning, make decisions, which are also influenced by the environment. The evolutionary process of individual behavior is studied as an evolutionary system over time, so that researchers can interpret the complicated gradual process leading to equilibrium.

Causal interpretation is most frequently employed in the interpretation of evolutionary mechanism. Causal interpretation "interprets phenomena or events by pointing out how these phenomena or events happen" (J. J. Vromen, 1995). The situation before a bout (i.e. the cause) determines the result after the game when dynamical model is used to interpret evolutionary phenomenon. Consequently, we examine equation (2), (3) and (4) which are applied to explain evolution according to this principle: noticing the right side of (2), (3) and (4), we can find that they mean the same thing—difference between the expected payoff value of population following a certain strategy and the average expected payoff value of the entire population, or that of the "fitness", which determines the change of population proportion following the strategy between generations. Apparently, taking (4) as an example, we can see its right side is

$$\frac{W_c - \overline{W}}{\overline{W}}$$

which is the result individuals get after a bout. Evidently, the result can not explain the cause of the phenomenon. "It turns the thing upside down." as J. J. Vromen put it when he commented on the functional interpretation applied in the interpretation of biological evolution. A certain phenomenon can only be interpreted by its cause rather than its result. Therefore, we can say that the expositive model of RD transposes the cause and the result in the causal interpretation.

Finally, we explore the model in light of the three kinds of mechanism (inheritance, selection and mutation) in the natural selection. To all appearances, RD can not present all the three mechanisms in evolutionary process. Furthermore, the model does not distinguish different mechanisms in its interpretation. The prevalent approach is that individuals in a population will learn from those whose payoff goes above the average level of the population after a bout, and then the proportion of this type will grow during the process (vice versa). But RD confuses the two different processes of individual replication and environmental selection.

3. CONTRASTIVE ANALYSIS OF THE TWO MODELS

We now take the RD model presented by J. M. Alexander (2003) as an example in the discussion below:

He denotes the average fitness of cooperators and defectors as W_C and W_D respectively, and let $\overline{W}$ denote the average fitness of the entire population. The values of W_C, W_D and $\overline{W}$ can be expressed in terms of the population proportions and payoff values as follows:

$$\overline{W} = p_c W_C + p_d W_D \qquad (5)$$

$$W_C = F_0 + p_c \Delta F(C,C) + p_d \Delta F(C,D) \qquad (6)$$

$$W_D = F_0 + p_c \Delta F(D,C) + p_d \Delta F(D,D) \qquad (7)$$

After a bout, the change of proportions between generations can be expressed as below:

$$p_c' - p_c = \frac{p_c (W_C - \overline{W})}{\overline{W}} \qquad (8)$$

$$p_d' - p_d = \frac{p_d (W_D - \overline{W})}{\overline{W}} \qquad (9)$$

Assuming that the variation in the strategy frequency from one generation to another is small, these differences may be approximated by the differential equations

$$\frac{dp_c}{dt} = \frac{p_c (W_C - \overline{W})}{\overline{W}} \qquad (4)$$

$$\frac{dp_d}{dt} = \frac{p_d (W_D - \overline{W})}{\overline{W}} \qquad (10)$$

Since the matrix assumes that T > R and P > S, it follows that $W_D > W_C$, and hence WD > $\overline{W}$> WC. This means that

$$\frac{W_D - \overline{W}}{\overline{W}} > 0$$

and

$$\frac{W_C - \overline{W}}{\overline{W}} < 0$$

Since the strategy frequencies for Defect and Cooperate in the next generation are given by

$$p_d' = p_d \cdot \frac{W_D - \overline{W}}{\overline{W}} \qquad (11)$$

$$p_c' = p_c \cdot \frac{W_C - \overline{W}}{\overline{W}} \qquad (12)$$

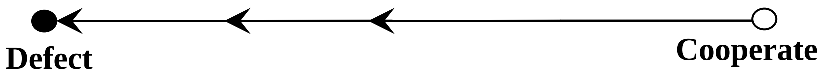

Figure 1. The Replicator Dynamical Model of the Prisoner's Dilemma

Over time the proportion of the population choosing the strategy Cooperate eventually becomes extinct. Figure 1 illustrates one way of representing the RD model of the prisoner's dilemma, known as a state-space diagram.

We can see from (4), (10) and the expression (5) and (6) of W_c and $\overline{W}$ in Part 2 that the core point still relates to the ideas of Taylor and Jonker who first proposed RD, which take a_{ij} to be the number replicated of an *i*-strategist against a *j*-opponent. Following this assumption, the change of proportion following one strategy in a population depends upon the distribution of the fitness of individual following this strategy, while the individual fitness is just the result of the game. Thus it can be seen that the dynamical equation is not tenable in causal relationship—it employs the result of evolutionary game to explain the phenomena of evolution.

Furthermore, since the two fundamental ESS conditions are valid in a broad sense, we have the following question in mind: if we do not use "the difference between the fitness of population following a certain strategy and the average fitness of the entire population" in Replicator Dynamics, can we discuss the characteristics of the equation's key (the proportion of individual following one strategy)?

It can be seen from (8) and (9) presented above that Alexander defines fitness W as

$$W_t = \frac{Q_{t+1}}{Q_t} \qquad (13)$$

where Q denotes the number of individuals. This is also the traditional approach of defining fitness in evolutionary biology. Then, according to Equation (5), (6), (7) and (13), Equation (8) can be rewritten as

$$\frac{p'_c - p_c}{p_c} = \frac{p_d Q_0 \left[\left(p_c \Delta F(C,C) + p_d \Delta F(C,D)\right) - \left(p_c \Delta F(D,C) + p_d \Delta F(D,D)\right)\right]}{Q_1}$$

(14)

where p_c and p_d denote the proportions of individuals following strategies C and D in current generation; p'_c and p'_d denote these proportions in the next generation respectively; Q_0, Q_{D0} and Q_{C0} respectively denote the numbers of the entire population, cooperators and defectors in the current generation; where Q_1, Q_{D1} and Q_{C1} denote these numbers in the next generation. Since $Q_1 = Q_{D1} + Q_{C1}$

$$= Q_{D0} + Q_{D0}\left(p_c \Delta F(D,C) + p_d \Delta F(D,D)\right) + Q_{C0} + Q_{C0}\left(p_c \Delta F(C,C) + p_d \Delta F(C,D)\right)$$

then Equation (14) can be rewritten as:

$$(p'_c - p_c) / \ p_c =$$

$$\frac{p_d Q_0 \left[\left(p_c \Delta F(C,C) + p_d \Delta F(C,D)\right) - \left(p_c \Delta F(D,C) + p_d \Delta F(D,D)\right)\right]}{Q_{D0} + Q_{D0}\left(p_c \Delta F(D,C) + p_d \Delta F(D,D)\right) + Q_{C0} + Q_{C0}\left(p_c \Delta F(C,C) + p_d \Delta F(C,D)\right)}$$

(15)

The left side of Model (15) is the rate of change of the proportion following the strategy Cooperate after a bout, while parameters on the right side are determined before the game. Therefore, Model (15) accords with the demand of dynamical equation—initial conditions and boundary conditions decide subsequent changes over generations.

Comparing Model (15) with the interpretation applying "the difference between the expected payoff value (or fitness) of population following a certain strategy and the average expected payoff value of the entire population", we now discuss how Model (15) describes the dynamical process and whether it can be used to analyze the stability of the key (i.e. the proportion of individual follow one strategy). In Model (8), the left side expresses the rate of change of the proportion following the strategy Cooperate after a bout, the right side includes two kinds of parameters determined before and after the bout. At the same time, the left side of Model (15) is the rate of change of the proportion follow the strategy Cooperate after a bout, while the parameters on the right side are determnied before the game. We can derive the fixed point from the differential equation of Model (15), and then discuss the stability of each fixed point with different parameters.

Taking the RD model of the Prisoner's Dilemma as follows:

$$\frac{p_c' - p_c}{p_c} = \frac{p_d\left[\left(p_c R + p_d S\right) - \left(p_c T + p_d P\right)\right]}{p_d + p_d\left(p_c T + p_d P\right) + p_c + p_c\left(p_c R + p_d S\right)} < 0$$

How will a population of individuals that repeatedly plays the Prisoner's Dilemma evolve? According to the model above, as the situation before a bout (at the right side of the equal mark) determines the rate of change of the proportion follow the strategy Cooperate after the bout (at the left side of the equal mark), we know that the proportion following the strategy Cooperate will decline over time, the proportion of the population choosing the strategy Cooperate eventually becomes extinct. Now we confirm that applying the change of number between generations to discuss the tendency and stability of the key (proportion) is feasible. In addition, there is no illogicality in this interpretation.

4. CONCLUSION

The assumption that taking a_{ij} to be the number replicated of strategist *i* against *j* opponent in a bout of game is the principal precondition of applying RD to the interpretation of evolutionary mechanism. The principal notions of interpreting evolutionary mechanism by dynamical equation can be reduced to the point that the dynamical change of “the difference between the expected payoff value of population following a certain strategy and the average expected payoff value of the entire population” determines the change rate of population proportion following one strategy (type or trait) between generations, i.e. the rate of change of population proportion following one strategy (type or trait) between generations depends on the distribution of “fitness”.

In fact, this approach misunderstands the essential concept of “dynamics” in evolution—the ratio of change of proportion during a bout depends on the result after a bout, which is used to explain the situation before the game.

We have pointed out that, instead of using the difference between the fitness of population (or expected payoff value) following a certain strategy and the average fitness of the entire population, it is logical to apply the change of number between generations to analyze the tendency and stability of the key (proportion).

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