Replicator equation on time scale

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1 Introduction

The replicator equation describes the process of natural selection, i. e. the deterministic component of the biological evolution; for details see e.g. [2].

Let us assume that a population (biological community) is divided into n types (species, genotypes, phenotypes, traits etc.) E_1, E_2, … E_n with relative frequencies x_1, x_2, … x_n depending on time; the relative frequencies are non-negative values with the unity sum. The basic tenet of Darwinism states that

$$\text{change of } x_i \ = \ \text{fitness of } E_i \ - \ \text{average fitness.} \tag{1}$$

The fitness f_i of E_i depends on environment and the environment is formed by incidence of all of the types, i. e. $f_i = f_i(\boldsymbol{x})$, where $\boldsymbol{x} = (x_1, x_2, \ldots, x_n)^T$. The average fitness $\bar{f} = \bar{f}(\boldsymbol{x})$ equals $\sum_{i=1}^n x_i f_i(\boldsymbol{x})$. For technical reasons, we suppose that the frequencies x_1, x_2, …, x_n are differentiable functions of time t. Moreover, we consider the "change" appearing in the "equation" (1) to be relative. Hence, we have the system of ordinary differential equations

$$\frac{\dot{x}_i}{x_i} = f_i(\boldsymbol{x}) - \bar{f}(\boldsymbol{x}), \ i = 1, 2, \ldots, n.$$

Of particular interest is the case of linear f_i's, $f_i(\boldsymbol{x}) = \sum_{j=1}^n a_{ij} x_j$. There exists, then, an $n \times n$ real matrix $A = (a_{ij})$ such that $f_i(\boldsymbol{x}) = (A\boldsymbol{x})_i$ and $\bar{f}(\boldsymbol{x}) = \sum_{i=1}^n x_i (A\boldsymbol{x})_i = \boldsymbol{x}^T A\boldsymbol{x}$. The replicator equation takes the form

$$\dot{x}_i = x_i\big((A\boldsymbol{x})_i - \boldsymbol{x}^T A\boldsymbol{x}\big). \tag{2}$$

Now, the Darwinian "struggle for life" can be interpreted as a matrix game for players E_1, E_2, …, E_n and the fitness f_i of the player E_i as the payoff of the i-th pure strategy.

The replicator equation (2) was introduced by Taylor and Jonker [5] but it did not attract attention until Schuster and Sigmund [4] put it to point out an error in the famous book "The Selfish Gene" by Richard Dawkins. The important result by Hofbauer [3] states that the system (2) is topologically equivalent with the Lotka-Volterra equations

$$\dot{y}_j = y_j\big(r_j + (B\boldsymbol{y})_j\big), \ j = 1, 2, \ldots, n-1$$

for certain $(n-1) \times (n-1)$ matrix B and vector $\boldsymbol{r} = (r_1, r_2, \ldots, r_{n-1})^T$. In another words, the n-dimensional system with a cubic nonlinearity (2) can be transformed to $(n-1)$-dimensional system with a quadratic nonlinearity. Moreover, the result reveals a close link between evolution and ecology.

The aim of the presentation is to introduce a dynamic counterpart to the replicator equation (2); for survey of the dynamic equations theory and the underlying time scales calculus see [1].

Roughly speaking, a generalization of an differential equation to dynamic equation on time scale consists in replacing of the ordinary derivative $\dot{}$ by the Hilger derivative $^\Delta$ and in putting σ (forward jump operator) or a term multiplied by μ (graininess function) to proper places in right-hand side of the equation. However, such generalization should preserve representative qualitative properties of solutions. In our case, we require that the dynamic replicator equation admits a transformation to a dynamic counterpart of Lotka-Volterra system.

2 Main result

We start with some notation. Let $\operatorname{int} M$ be the interior of the set M, $\mathbb{R}_+$ be the set of non-negative reals, $S_n = \{(x_1, x_2, \ldots, x_n)^T \in \mathbb{R}_+^n : \sum_{i=1}^n x_i = 1\}$ be an n-dimensional simplex. Let further σ and $^\Delta$ denote forward jump operator and Hilger derivative, respectively, defined for a time scale $\mathbb{T}$; $\tilde{\sigma}$ and $^{\tilde{\Delta}}$ denote the ones for a time scale $\tilde{\mathbb{T}}$.

Theorem: Let $\mathbb{T} \subseteq \mathbb{R}$ be a time scale and $A = (a_{ij})$ be an $n \times n$ matrix such that the initial value problem for dynamic equation

$$\begin{array}{c} {x_i}^\Delta = x_i\big((A\boldsymbol{x}^\sigma)_i - \boldsymbol{x}^T A\boldsymbol{x}^\sigma\big), \quad i = 1, 2, \ldots, n \\ \boldsymbol{x}(t_0) \in \operatorname{int} S_n \end{array} \tag{3}$$

has the unique solution $\boldsymbol{x} : \mathbb{T} \to \operatorname{int} S_n$.

Then there exists time scale $\tilde{\mathbb{T}} \subseteq \mathbb{R}$, $(n-1) \times (n-1)$ matrix $B \in \mathbb{R}^{(n-1)\times(n-1)}$, vector $\boldsymbol{r} = (r_1, r_2, \ldots, r_{n-1})^T \in \mathbb{R}^{n-1}$ and invertible mappings $\varphi : \mathbb{T} \to \tilde{\mathbb{T}}$, $G : \operatorname{int} S_n \to \operatorname{int}\mathbb{R}_+^{n-1}$ such that $0 \in \tilde{\mathbb{T}}$ and the function $\boldsymbol{y} : \tilde{\mathbb{T}} \to \operatorname{int}\mathbb{R}_+^{n-1}$ defined by $\boldsymbol{y}(\tau) = G\Big(\boldsymbol{x}\big(\varphi^{-1}(\tau)\big)\Big)$ is the unique solution of the initial value problem

$$\begin{array}{c} {y_j}^{\tilde{\Delta}} = y_j\big(r_j + (B\boldsymbol{y}^{\tilde{\sigma}})_j\big), \quad j = 1, 2, \ldots, n-1 \\ \boldsymbol{y}(0) = G\big(\boldsymbol{x}(t_0)\big). \end{array} \tag{4}$$

For each solution $\boldsymbol{y} : \tilde{\mathbb{T}} \to \operatorname{int}\mathbb{R}_+^{n-1}$ of the initial value problem (4), the function $\boldsymbol{x} : \mathbb{T} \to \operatorname{int} S_n$ defined by $\boldsymbol{x}(t) = G^{-1}\Big(\boldsymbol{y}\big(\varphi(t)\big)\Big)$ is the unique solution of the initial value problem (3).

Sketch of proof: Let $\boldsymbol{x} = \boldsymbol{x}(t)$ be the unique solution of (3) and put

$$\tilde{\mathbb{T}} = \left\{ \int_{t_0}^{t} x_n(s)\Delta s : t \in \mathbb{T} \right\}, \quad \varphi(t) = \int_{t_0}^{t} x_n(s)\Delta s,$$
$$G = (g_1, g_2, \ldots, g_n)^T; \; g_j(\boldsymbol{\xi}) = g_j(\xi_1, \xi_2, \ldots, \xi_n) = \frac{\xi_j}{\xi_n}, j = 1, 2, \ldots, n-1,$$
$$r_j = a_{jn} - a_{nn}, \; b_{jl} = a_{jl} - a_{nl}, \; j, l = 1, 2, \ldots, n-1.$$

Using time scales calculus, in particular the chain rule [1, Theorem 1.93], we verify the both statements.

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References

[1] M. Bohner, A. Peterson. *Dynamic Equations on Time Scales. An Introduction with Applications,* Birkhäuser, Boston-Basel-Berlin, 2001.

[2] J. Hofbauer, K. Sigmund. *Evolutionary Games and Population Dynamics,* Cambridge University Press, Cambridge UK, 2002.

[3] J. Hofbauer. On the occurence of limit cycles in the Volterra-Lotka equation. *Nonlin. Analysis*, **5**:1003–1007, 1981.

[4] P. Schuster, K. Sigmund. Coyness, philandering and stable strategies. *Anim. Behavior*, **29**: 186–192, 1981.

[5] P. D. Taylor, L. Jonker. Evolutionary stable strategies and game dynamics. *Math. Biosci.*, **40**: 145–156, 1978.