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A Note on Constants of Motion for the Lotka-Volterra and Replicator Equations

Ryusuke Kon

ABSTRACT. This paper considers constants of motion for the Lotka-Volterra and replicator equations. It is known that these two equations are topologically equivalent. By using this property, we obtain new constants of motion for the two equations. These constants of motion provide conservation law for the special cases of the predator-prey population dynamics and the rock-scissors-paper game dynamics.

1. Introduction

In this paper, by focusing on the equivalence between Lotka-Volterra and replicator equations, we will obtain new constants of motion for these equations.

The Lotka-Volterra equation is one of the most fundamental models representing population dynamics of interacting species and is defined as follows:

$$\dot{x}_i = x_i(r_i + \sum_{j=1}^{n} a_{ij}x_j), \quad i = 1, 2, \ldots, n, \tag{1}$$

where $\dot{x}_i = dx_i/dt$. The variables $x_i(t)$, $i = 1, 2, \ldots, n$ denote the population densities of species i at time t. We can easily see that the non-negative cone $\mathbb{R}^n_+ := \{\mathbf{x} \in \mathbb{R}^n_+ : x_1 \geq 0, x_2 \geq 0, \ldots, x_n \geq 0\}$ is forward invariant. The parameters r_i are intrinsic growth (or decay) rates and a_{ij} describe the effect of species j upon the growth of species i. The $n \times n$ matrix $A = (a_{ij})$ is called the interaction matrix.

On the other hand, the replicator equation, which describes the evolution of the frequencies of strategies in a population, is defined as follows:

$$\dot{y}_i = y_i((B\mathbf{y})_i - \mathbf{y} \cdot B\mathbf{y}), \quad i = 0, 1, \ldots, n, \tag{2}$$

where $\dot{y}_i = dy_i/dt$, $\mathbf{y} = (y_0, y_1, \ldots, y_n)^\top$, $B = (b_{ij})$ is an $(n+1) \times (n+1)$ matrix, $(B\mathbf{y})_i = \sum_{j=0}^{n} b_{ij}y_j$ and "$\cdot$" indicates an inner product. The variables y_i, $i = 0, 1, \ldots, n$ denote the frequencies of strategy i in a population at time t. So, y_i should be in the interval $[0, 1]$ and $y_0 + y_1 + \cdots + y_n = 1$. We can easily see that the simplex $\mathbb{S}_{n+1} := \{\mathbf{y} \in \mathbb{R}^{n+1}_+ : y_0 + y_1 + \cdots + y_n = 1\}$ is forward invariant. Therefore, as long as the initial values are on the simplex $\mathbb{S}_{n+1}$, $y_0 + y_1 + \cdots + y_n = 1$ remains unity and each y_i is non-negative. The parameters b_{ij} represents the expected payoff of an individual player with pure strategy i when the player meets a player with pure strategy j. The $(n+1) \times (n+1)$ matrix $B = (b_{ij})$ is called the payoff matrix.

It is known that these two equations, the Lotka-Volterra and replicator equations, are topologically equivalent in the following sense:

Theorem 1.1 ([1] and [2], Theorem 7.5.1)**.** *There exists a differentiable, invertible map ψ from $\widehat{S}_{n+1} = \{\mathbf{y} \in \mathbb{S}_{n+1} : y_0 > 0\}$ onto $\mathbb{R}^n_+$ mapping the orbits of the replicator equation* (2) *onto the orbits of the Lotka-Volterra equation* (1) *with $r_i = b_{i0}$ and $a_{ij} = b_{ij} - b_{0j}$.*

The map $\psi : \widehat{\mathbb{S}}_{n+1} \to \mathbb{R}^n_+$ is given by

$$\psi(\mathbf{y}) = \left(\frac{y_1}{y_0}, \frac{y_2}{y_0}, \dots, \frac{y_n}{y_0} \right),$$

whose inverse is

$$\psi^{-1}(\mathbf{x}) = \left(\frac{x_0}{\sum_{i=0}^n x_i}, \frac{x_1}{\sum_{i=0}^n x_i}, \dots, \frac{x_n}{\sum_{i=0}^n x_i} \right),$$

where $x_0 = 1$. From these results, it is ensured that if the Lotka-Volterra equation (1) has a constant of motion, then the replicator equation (2) does and vice versa. In this paper, by using this property, we will obtain new constants of motion for (1) and (2).

In Section 2, we review the known results on constants of motion for (1) and (2). In Section 3, by using the results in Section 2, we obtain new constants of motion and illustrates some examples, which include a predator-prey population dynamics and a rock-scissors-paper game dynamics.

2. The Known Results on Constants of Motion

2.1. The Lotka-Volterra equations

In this subsection, we introduce a result of Volterra [4, 5], which gives a constant of motion for the Lotka-Volterra equation (1) (see also Scudo and Ziegler [3] for a re-edition of classic papers of Vito Volterra). Volterra [4, 5] obtained a constant of motion under the assumption that the interaction matrix A can be transformed into an anti-symmetric matrix in the following sense:

(H1) : There exists a diagonal matrix $D = \mathrm{diag}\{d_1, d_2, \dots, d_n\}$, $d_i > 0$, $i = 1, 2, \dots, n$ such that DA is anti-symmetric, i.e., $DA = -(DA)^\top$.

This assumption implies that there are no intra-specific competition since $a_{ii} = 0$ for all $i = 1, 2, \dots, n$ and all interactions between two species are of predator-prey type since $a_{ij}a_{ji} \le 0$ for all $i, j = 1, 2, \dots, n$. Under this assumption, the Lotka-Volterra equation (1) has a constant of motion as follows:

Theorem 2.1 ([3], p.130, and [2], Exercise 15.3.7)**.** *Suppose that* (H1) *holds and* (1) *has an interior equilibrium* $\mathbf{p} = (p_1, p_2, \ldots, p_n) \in \mathrm{int}\mathbb{R}^n_+$. *Then every solution* $\mathbf{x}(t)$ *with* $\mathbf{x}(0) \in \mathrm{int}\mathbb{R}^n_+$ *satisfies*

$$V_1(\mathbf{x}) := \sum_{i=1}^{n} d_i(p_i \ln x_i - x_i) = C,$$

where C *is a constant dependent of the initial value* $\mathbf{x}(0)$.

2.2. The replicator equations

In this subsection, we introduce a constant of motion for the replicator equation (2). It is well known that the replicator equation (2) has a constant of motion if an interior equilibrium $\mathbf{q} \in \mathrm{int}\mathbb{S}_{n+1}$ exists and the payoff matrix B is anti-symmetric (the game with an anti-symmetric payoff matrix is called a zero-sum game)(see Hofbauer and Sigmund [2], Exercise 7.4.3). This well-known result can be generalized by using the following feature of the replicator equation (2):

- The application of the projective transformation $\mathbf{y} \to \mathbf{z}$ with
$$z_i = \frac{y_i/m_i}{\sum_{j=0}^{n} y_j/m_j}, \quad m_j > 0,$$
transforms (2) into the replicator equation with the payoff matrix $BM = (a_{ij}m_j)$ (see Hofbauer and Sigmund [2], Exercise 7.1.3).

By using this feature, we can show that the replicator equation (2) has a constant of motion even if the payoff matrix B is not anti-symmetric but can be transformed into an anti-symmetric matrix in the following sense:

(H2) : There exists a diagonal matrix $M = \mathrm{diag}\{m_0, m_2, \ldots, m_n\}$, $m_i > 0$, $i = 0, 1, \ldots, n$ such that BM is anti-symmetric, i.e., $BM = -(BM)^\top$.

In fact, we have the following theorem:

Theorem 2.2. *Suppose that* (H2) *holds and the replicator equation* (2) *has an interior equilibrium* $\mathbf{q} \in \mathrm{int}\mathbb{S}_{n+1}$. *Then every solution* $\mathbf{y}(t)$ *with* $\mathbf{y}(0) \in \mathrm{int}\mathbb{S}_{n+1}$ *satisfies*

$$P_1(\mathbf{y}) := \prod_{i=0}^{n} \left(\frac{y_i/m_i}{\sum_{j=0}^{n} y_j/m_j} \right)^{\frac{q_i/m_i}{\sum_{j=0}^{n} q_j/m_j}} = C,$$

where C *is a constant dependent of the initial value* $\mathbf{y}(0)$.

Proof. Since $\mathbf{q}$ is an interior equilibrium of (2), we have

$$(B\mathbf{q})_i - \mathbf{q} \cdot B\mathbf{q} = 0, \quad i = 0, 1, \ldots, n. \tag{3}$$

If we multiply both sides of the equation by $w_i = (q_i/m_i)/\sum_{j=0}^{n}(q_j/m_j)$ and sum over i, then we have

$$\mathbf{w} \cdot BM\mathbf{w} \sum_{j=0}^{n} (q_j/m_j) - \mathbf{q} \cdot B\mathbf{q} = 0,$$

where $\mathbf{w} = (w_0, w_1, \ldots, w_n)^\top$. Since BM is anti-symmetric, we have

$$\mathbf{w} \cdot BM\mathbf{w} = \mathbf{q} \cdot B\mathbf{q} = 0$$

and (3) implies

$$(BM\mathbf{w})_0 = (BM\mathbf{w})_1 = \cdots = (BM\mathbf{w})_n = \mathbf{w} \cdot BM\mathbf{w} = 0. \tag{4}$$

Hereafter, we show that $\dot{P}_1 = 0$ holds. Since $P_1 = \prod_{i=0}^{n} z_i^{w_i}$, we have

$$\dot{P}_1 = P_1 \sum_{i=0}^{n} w_i \frac{1}{z_i} \frac{dz_i}{dt}.$$

Furthermore, since

$$\dot{z_i} = z_i \{(BM\mathbf{z})_i - \mathbf{z} \cdot BM\mathbf{z}\}(\sum_{j=0}^{n} y_j/m_j),$$

we have

$$\begin{aligned} \dot{P}_1 &= P_1 \sum_{i=0}^{n} w_i ((BM\mathbf{z})_i - \mathbf{z} \cdot BM\mathbf{z})(\sum_{j=0}^{n} y_j/m_j) \\ &= -P_1 \sum_{i=0}^{n} z_i (BM\mathbf{w})_i (\sum_{j=0}^{n} y_j/m_j) = 0, \end{aligned}$$

where the anti-symmetry of BM and (4) are used. □

Remark: If (H2) holds, every diagonal element of the matrix B is zero. We can assume it without loss of generality since the replicator equation (2) does not change on $\mathbb{S}_{n+1}$ even if we add a constant c_j to the j-th column of B (see Hofbauer and Sigmund [2], Exercise 7.1.2).

3. The Constants of Motion Derived from Topologically Equivalent Equations

3.1. The Lotka-Volterra equations

In this subsection, by using Theorems 1.1 and 2.2, we obtain a new constant of motion for the Lotka-Volterra equation (1). Since the Lotka-Volterra equation (1) and the replicator equation (2) are equivalent, the constant of motion P_1 for the replicator equation (2) can be transformed into the one for the Lotka-Volterra equation (1) through the map ψ. Therefore, the following theorem is an immediate consequence of Theorems 1.1 and 2.2:

Theorem 3.1. *Suppose that* (H2) *holds and the replicator equation* (2) *has an interior equilibrium* $\mathbf{q} \in \mathrm{int}\mathbb{S}_{n+1}$. *Then the Lotka-Volterra equation* (1) *with* $r_i = b_{i0}$

and $a_{ij} = b_{ij} - b_{0j}$, $i, j = 1, 2, \ldots, n$, has an interior equilibrium $\mathbf{p} \in \mathrm{int}\mathbb{R}^n_+$ and every solution of (1) with $\mathbf{x}(0) \in \mathrm{int}\mathbb{R}^n_+$ satisfies

$$V_2(\mathbf{x}) := \prod_{i=0}^{n} \left(\frac{x_i/m_i}{\sum_{j=0}^{n} x_j/m_j} \right)^{\frac{p_i/m_i}{\sum_{j=0}^{n} p_j/m_j}} = C,$$

where C is a constant dependent of the initial value $\mathbf{x}(0)$ and $x_0 = p_0 = 1$.

Example (the rock-scissors-paper game). Let us consider the replicator equation with the following payoff matrix:

$$B = \begin{pmatrix} 0 & -\beta_1 & b_2 \\ b_0 & 0 & -\beta_2 \\ -\beta_0 & b_1 & 0 \end{pmatrix}, \tag{5}$$

where b_i, $\beta_i > 0$, $i = 1, 2, 3$. The game with this payoff matrix is called the general rock-scissors-paper game (see Hofbauer and Sigmund [2], §7.7). We can easily see that the replicator equation (2) with (5) always has an interior equilibrium

$$\mathbf{q} = \frac{1}{\Sigma}(b_1 b_2 + b_1\beta_2 + \beta_2\beta_1, \quad b_2 b_0 + b_2\beta_0 + \beta_0\beta_2, \quad b_0 b_1 + b_0\beta_1 + \beta_0\beta_1),$$

where

$$\Sigma = \beta_0\beta_1 + \beta_0\beta_2 + \beta_1\beta_2 + \beta_1 b_0 + \beta_2 b_1 + b_0 b_1 + \beta_0 b_2 + b_0 b_2 + b_1 b_2 > 0.$$

It is known that every solution in $\mathrm{int}\mathbb{S}_3$ of the replicator equation (2) with (5) converges to $\mathbf{q}$ or the boundary of $\mathbb{S}_3$ if $b_0 b_1 b_2 \neq \beta_1\beta_2\beta_3$ (see Hofbauer and Sigmund [2], Theorem 7.7.2 and its proof). So, in order to obtain a constant of motion, we assume the following

(H2)$'$: $\beta_0\beta_1\beta_2 = b_0 b_1 b_2 > 0$ holds.

Then it is seen that $BM = -(BM)^\top$ holds for the diagonal matrix

$$M = \mathrm{diag}\{1, b_0/\beta_1, (b_0 b_1)/(\beta_1\beta_2)\}.$$

Hence, by Theorem 2.2, we have a constant of motion P_1 for the replicator equation. Fig.1(b) illustrates this constant of motion for the case where $b_i = \beta_i = 1$, $i = 0, 1, 2$, and then

$$P_1(\mathbf{y}) = y_1^{\frac{1}{3}} y_2^{\frac{1}{3}} y_3^{\frac{1}{3}}.$$

By Theorem 3.1, under the assumption (H2)$'$, we can obtain a constant of motion V_2 for the following Lotka-Volterra equation

$$\begin{cases} \dot{x}_1 &= x_1\{b_0 + \beta_1 x_1 - (\beta_2 + b_2)x_2\}, \\ \dot{x}_2 &= x_2\{-\beta_0 + (\beta_1 + b_1)x_1 - b_2 x_2\}. \end{cases}$$

The interaction matrix A is

$$A = \begin{pmatrix} \beta_1 & -\beta_2 - b_2 \\ \beta_1 + b_1 & -b_2 \end{pmatrix}$$

Note that this matrix does not satisfy the assumption (H1) since the diagonal elements are not zero. Since the off-diagonal elements have opposite signs, the interaction between species 1 and 2 is of predator-prey type (species 1 is a prey of species 2). However, notice that this equation is strange in the sense that the intra-specific density effect for species 1 is positive, which means that the higher the density of species 1 becomes, the more efficiently species 1 reproduces. Fig.1(a) illustrates the constant of motion for this equation with $\beta_i = b_i = 1$, $i = 0, 1, 2$, and then

$$V_2(\mathbf{x}) = \frac{x_1^{\frac{1}{3}} x_2^{\frac{1}{3}}}{1 + x_1 + x_2}.$$

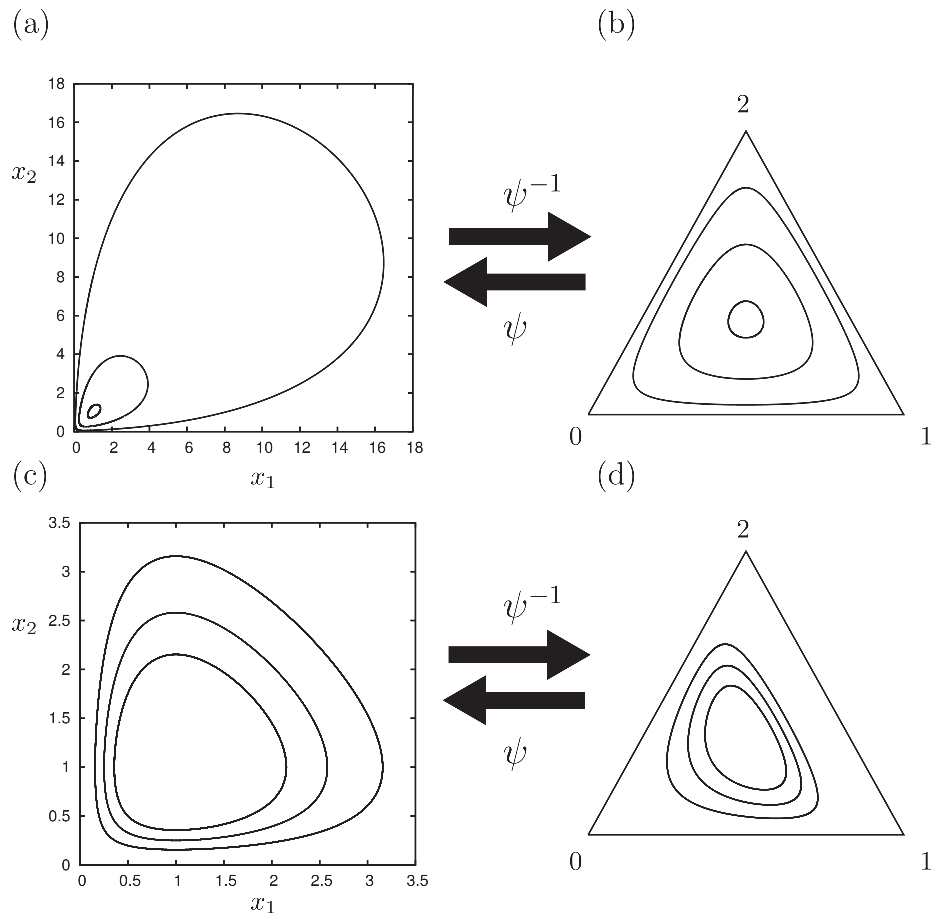

FIGURE 1. (a), (b), (c) and (d) illustrate the constants of motion V_2, P_1, V_1 and P_2, respectively.

3.2. The replicator equations

In this subsection, by using Theorems 1.1 and 2.1, we obtain a new constant of motion for the replicator equation (2). Since the Lotka-Volterra equation (1) and the replicator equation (2) are equivalent, the constant of motion V_1 for the Lotka-Volterra equation (1) can be transformed into the one for the replicator equation (2) through the map ψ^{-1}. Therefore, the following theorem is an immediate consequence of Theorems 1.1 and 2.1:

Theorem 3.2. *Suppose that* (H1) *holds and the Lotka-Volterra equation* (1) *has an interior equilibrium* $\mathbf{p} \in \mathrm{int}\mathbb{R}_n$. *Then the replicator equation* (1) *with* $b_{0j} = 0$, $b_{i0} = r_i$, $b_{ij} = a_{ij}$, $i, j = 1, 2, \dots, n$ *has an interior equilibrium* $\mathbf{q} \in \mathrm{int}\mathbb{S}_{n+1}$ *and every solution of* (2) *with* $\mathbf{y}(0) \in \mathrm{int}\mathbb{S}_{n+1}$ *satisfies*

$$P_2(\mathbf{y}) := \sum_{i=1}^{n} d_i \left(\frac{q_i}{q_0} \ln \frac{y_i}{y_0} - \frac{y_i}{y_0} \right) = C,$$

where C is a constant dependent of the initial value $\mathbf{y}(0)$.

Example (the predator-prey model). Let us consider the following classic Lotka-Volterra equation for predator-prey type interaction:

$$\begin{cases} \dot{x}_1 &= x_1(r_1 - a_{12}x_2), \\ \dot{x}_2 &= x_2(-r_2 + a_{21}x_1), \end{cases} \tag{6}$$

where x_1 and x_2 denote the population densities of prey and predator species, respectively, and r_1, r_2, a_{12} and a_{21} are positive. This equation has an interior equilibrium $\mathbf{p} = (r_2/a_{21}, r_1/a_{12})$. It is seen that $DA = -(DA)^\top$ holds for the diagonal matrix

$$D = \mathrm{diag}\{a_{21}, a_{12}\}.$$

Hence, by Theorem 2.1, this Lotka-Volterra equation has a constant of motion V_1. Fig.1(c) illustrates this constant of motion for the case where $a_{12} = a_{21} = 1$ and $r_1 = r_2 = 1$, and then

$$V_1(\mathbf{x}) = \ln(x_1 x_2) - x_1 - x_2.$$

By Theorem 3.2, we can obtain a constant of motion P_2 for the replicator equation (2) with the following payoff matrix

$$B = \begin{pmatrix} 0 & 0 & 0 \\ r_1 & 0 & -a_{12} \\ -r_2 & a_{21} & 0 \end{pmatrix}.$$

Note that the game with this payoff matrix is not a zero-sum game and does not satisfy the assumption (H2). However, by Theorem 3.2, we can construct a constant of motion P_2.

Fig.1(d) illustrates the constant of motion P_2 for the case where $a_{12} = a_{21} = 1$ and $r_1 = r_2 = 1$, and then

$$P_2(\mathbf{y}) = \ln \frac{y_1 y_2}{y_0^2} - \frac{y_1}{y_0} - \frac{y_2}{y_0}.$$

4. Discussion

In this paper, by using the topological equivalence between the Lotka-Volterra and replicator equations, we obtained new constants of motion for these equations (Theorems 3.1 and 3.2). As illustrations, we gave two examples. In the first example, we investigated the Lotka-Volterra equation that is associated with the replicator equation for the rock-scissors-paper game by the map ψ. This investigation showed that the Lotka-Volterra equation of predator-prey type can have a constant of motion even if the intra-specific density dependence is present in both populations (cf. Eq.(6)) though it involves a strange property in the sense that the population density of the prey accelerates the increase of itself. In the second example, we investigated the replicator equation that is associated with the classic Lotka-Volterra equation of predator-prey type, i.e., Eq.(6). This investigation showed that the replicator equation for the rock-scissors-paper game (i.e., Eq.(2) with (5)) can have a constant of motion even if $\beta_0\beta_1\beta_2 = b_0b_1b_2 = 0$.

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References

[1] Hofbauer, J. (1981): On the occurrence of limit cycles in the Volterra-Lotka equation, Nonlinear Analysis **5**, 1003–1007

[2] Hofbauer, J. and Sigmund, K. (1998): *Evolutionary games and population dynamics*, Gambridge, Cambridge University Press

[3] Scudo, F. M. and Ziegler J. R. (1978): The golden age of theoretical ecology: 1923–1940, A collection of works by V. Volterra, V. A. Kostitzin, A. J. Lotka and A. N. Kolmogoroff. *Lecture Notes in Biomathematics* 22, Springer-Verlag, Berlin

[4] Volterra, V. (1931): *Leş sur la théorie mathematique de la lutte pour la vie* (Redigees par M. Brolot), Gauthier-Villars, Paris

[5] Volterra, V. (1937): Principes de biologie mathématique, *Acta Biotheoretica* **3**, 1–36

Ryusuke Kon
Faculty of Mathematics, Kyushu University
Hakozaki 6-10-1, Higashi-ku, Fukuoka 812-8581, Japan
E-mail address: kon-r@math.kyushu-u.ac.jp