

A NOTE ON THE NON-EQUIVALENCE OF  
A LOTKA-VOLTERRA MODEL AND  
A CONTINUOUS REPLICATOR

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**Abstract:** The equivalence of a continuous-time replicator equation for  $n$  strategies with a Lotka-Volterra equation for  $n - 1$  competing species, under a suitable transformation of variables, is disproven. The correction relates to the parametric conversion corresponding to a transformation of variables between these two models suggested widely in the literature of mathematical biology. An alternative approach shown here is purely algebraic instead of the heuristic calculus with which the earlier equivalence result was obtained. The particular and unavoidable non-linearity that arises to prevent the conversion is unambiguously identified. Consequently, it is shown that no such bridge exists between these foundational equations of evolutionary game theory and theoretical ecology, bearing on evolutionary properties of multi-species communities.

**AMS Subject Classification:** 92D40, 91A40

**Key Words:** evolutionary game theory, inter-species competition, predator-prey model

## 1. Introduction

Heuristic reasoning prevails on the bridge between theoretical population ecology, via the Lotka-Volterra model, and measures of the success of strategic fitness in evolutionary games, via the replicator dynamics. Replicator equations in continuous-time are essential to evolutionary game theory (see [1], [2], [3], [4]). A primer on modern

research in biological game-theoretic models, including replicator equations, is [5]. Inter-specific competition on species abundances is often assumed to be qualitatively equivalent to the dynamics of player strategies in evolutionary games. Evolutionary game theory posits the equivalence of these two foundational equations with respect to the broader scientific value of game-theoretical models ([6], [7], cf. [5]). A conversion was developed from the replicator equation to the formula that is a cornerstone in theoretical ecology due to Lotka [8] and Volterra [9]. This model has attracted research as an important idealization in ecosystem complexity science, see for example [10]. The transformation of variables considered here is the same one originally suggested [11] but the resultant parametric conversion is shown to be significantly non-linear; and this corrects a mainstream belief of formidable longevity; see Theorem 7.5.1 in [3], Theorem 4 in [12] Section 4.9.3 in [13], and [6]. Alternative generalizations consider a meta-population model for nested inter-specific competition within each sub-population ([14], [15], [16]). Their resultant dynamical systems synthesized the replicator and the Lotka-Volterra model to analyse *evolutionary ecological stability*. However, the focus here is the validity of direct translation from one model to the other under a change of variables.

Disproving the parametric conversion is shown directly with algebra that does not rely on the calculus of variations characterizing the heuristic proof of the equivalence. The mathematical definition of the model proceeds in Section 2 along with the derivation of the main non-equivalence result. The specific errors encountered in the earlier heuristic proof are described in Section 3.

## 2. Transformation of Relative and Absolute Abundances

A population of  $n$  players exists in relative frequencies defined on a simplex with  $(n - 1)$  degrees of freedom,  $\sum_{i=1}^n x_i = 1$ . Define the marginal payoff to the  $i$ -th strategy,  $f_i(\tilde{x}) = \sum_{j=1}^n a_{ij}x_j$ , where the payoff matrix between strategies is  $[a_{ij}]$ , for  $ij = 1, 2, \dots, n$ . The average payoff in the entire population is thus,

$$\varphi(\tilde{x}) = \sum_{i=1}^n x_i f_i(\tilde{x}) = \sum_{i=1}^n \left[ x_i \left( \sum_{j=1}^n x_j a_{ij} \right) \right].$$

Let the time derivative of frequencies be,  $dx_i/dt := \dot{x}_i$ . The evolutionary dynamics of  $\tilde{x}$  are determined by the *replicator equation*

$$\dot{x}_i = x_i (f_i(\tilde{x}) - \varphi(\tilde{x})). \quad (1.1)$$

The transformation of variables defines the frequencies  $\tilde{x} = (x_1, \dots, x_n)$  of the replicator equation in terms of species abundances  $\tilde{y} = (y_1, y_2, \dots, y_{n-1})$  in the

Lotka-Volterra equation; refer to (3.5). Thus,  $\tilde{x}$  and  $\tilde{y}$  describe relative and absolute abundances in the population, respectively. That is, let  $y = \sum_{j=1}^{n-1} y_j$ , then also let  $x_i = y_i/[1 + y]$ , for  $i = 1, 2, \dots, n - 1$ ; and  $x_n = 1/[1 + y]$ . The frequencies  $\tilde{x}$  describe a total of  $n$  strategies in the replicator equation, whereas the  $\tilde{y}$  in the Lotka-Volterra equation describe  $(n - 1)$  abundances

Differentiation yields, for  $i = 1, 2, \dots, n - 1$ ,

$$\dot{x}_i = \frac{\dot{y}_i}{1 + y} - \frac{y_i \dot{y}}{(1 + y)^2},$$

and

$$\dot{x}_n = \frac{-\dot{y}}{(1 + y)^2}. \tag{1.2}$$

Observe that  $\dot{y} \neq 0$  because constant population size does not hold in general as time evolves in the Lotka-Volterra model. Now, substitute the transformed variables (1.2) into the replicator equation (1.1) For  $i = 1, 2, \dots, n - 1$ ,

$$\begin{aligned} & \frac{\dot{y}_i}{1 + y} - \frac{y_i \dot{y}}{(1 + y)^2} \\ &= \frac{y_i}{1 + y} \left[ \sum_{j=1}^{n-1} \frac{y_j}{1 + y} a_{ij} + \frac{a_{in}}{1 + y} - \sum_{i=1}^{n-1} \frac{y_i}{1 + y} \left( \sum_{j=1}^{n-1} \frac{y_j}{1 + y} a_{ij} + \frac{a_{in}}{1 + y} \right) \right. \\ & \quad \left. - \frac{1}{1 + y} \left( \sum_{j=1}^{n-1} \frac{y_j}{1 + y} a_{nj} + \frac{a_{nn}}{1 + y} \right) \right]. \end{aligned} \tag{1.3}$$

The factor  $1/(1 + y)$  is cancelled out from both sides of the equation and further simplification of (1.3) yields,

$$\begin{aligned} \dot{y}_i \left( 1 - \frac{y_i}{1 + y} \right) &= y_i \left[ \frac{a_{in} + \sum_{j \neq i} \dot{y}_j}{1 + y} - \frac{a_{nn}}{(1 + y)^2} \right. \\ & \quad + \sum_{j=1}^{n-1} \frac{y_j a_{ij}}{1 + y} - \sum_{i=1}^{n-1} \frac{y_i}{1 + y} \sum_{j=1}^{n-1} \frac{y_j a_{ij}}{1 + y} \\ & \quad \left. - \sum_{i=1}^{n-1} \frac{y_i a_{in}}{(1 + y)^2} - \sum_{j=1}^{n-1} \frac{y_j a_{nj}}{(1 + y)^2} \right]. \end{aligned} \tag{1.4}$$

Collecting the coefficients of (1.4), and interchanging subscripts such that

$$\sum_{i=1}^{n-1} y_i \sum_{j=1}^{n-1} y_j a_{ij} = \sum_{j=1}^{n-1} y_j \sum_{i=1}^{n-1} y_i a_{ji},$$

$$\dot{y}_i = \left( \frac{y_i}{1 - \frac{y_i}{1+y}} \right) \left[ \frac{a_{in} + \sum_{j \neq i} \dot{y}_j}{1+y} - \frac{a_{nn}}{(1+y)^2} + \sum_{j=1}^{n-1} \frac{y_j}{1+y} \left( a_{ij} - \frac{a_{jn}}{1+y} - \frac{a_{nj}}{1+y} - \sum_{i=1}^{n-1} \frac{y_i a_{ji}}{1+y} \right) \right]. \quad (1.5)$$

Equation (1.5) does now vaguely resemble Lotka-Volterra form, although closer examination reveals incompatible non-linearity has arisen,

$$\dot{y}_i = \left( \frac{1+y}{1+y-y_i} \right) y_i \left[ r_i + \sum_{j=1}^{n-1} b_{ij} y_j \right], \quad (1.6)$$

where

$$r_i = \frac{a_{in} + \sum_{j \neq i} \dot{y}_j}{1+y} - \frac{a_{nn}}{(1+y)^2}$$

and

$$b_{ij} = \frac{1}{(1+y)^2} \left[ a_{ij} (1+y) - a_{jn} - a_{nj} - \sum_{i=1}^{n-1} y_i a_{ji} \right]. \quad (1.7)$$

This completes the proof.

More specifically, the non-linearity that arises in the conversion is three-fold:

(i)  $(1+y)y_i/(1+y-y_i)$  is a non-linear substitute for the usual  $y_i$  term in the Lotka-Volterra form;

(ii) the parameter  $r_i$  in (1.7) involves the derivatives  $\dot{y}_j$  and thus (1.6) is a recursive equation, which is not a feature of the usual Lotka-Volterra form;

(iii) there are  $y_i y_j^2$  and  $y_i^2 y_j$  terms of second degree on the right-hand side of (1.6) from the parameter  $b_{ij}$  in (1.7), which also violate the usual Lotka-Volterra form.

A clear presentation of the canonical Lotka-Volterra form as a foundational equation important to the development of mainstream theoretical ecology is given by [17]. In particular, the discussion on page 50 of that monograph, equation (3.9), in the sub-section *Predator-Prey Equations with Anti-Symmetry*. The next sub-section in May's landmark monograph is also relevant *Competition Equations with Symmetry* because point (iii) raised in the preceding paragraph holds under anti-symmetry. Under symmetry the corresponding  $a_{ij}$  and  $a_{ji}$  terms in (1.7) cancel out and so the alternative Lotka-Volterra form in that case is also violated by the transformation of variables between relative and absolute abundances.

### 3. Where Does the Standard Game-Theoretic Heuristic Proof Fail?

In matrix notation, the replicator equation (1.1), can be written

$$\frac{\dot{x}_i}{x_i} = (A\tilde{x})_i - \tilde{x}^T A \tilde{x} \quad (3.1)$$

for the payoff matrix  $A$ . That is, the relative rate of change of strategy  $i$  equals the fitness of strategy  $i$  minus the average fitness in the population. When the gain of one player is always the loss of its competitor a skew-symmetric payoff matrix results such that  $a_{ij} = -a_{ji}$ , of course in this case the diagonal entries  $a_{ii}$  must equal zero;  $i, j = 1, 2, \dots, n$ . This situation is known as a *zero-sum game* in evolutionary game theory. Alternatively, this situation also corresponds to zero average fitness of the population, which is obtained from the condition  $\tilde{x}^T A \tilde{x} = \sum_{i,j=1}^n a_{ij} x_i x_j = 0$

Thus, there is a convenient simplification to the replicator equation under the skew-symmetric payoff matrix, namely

$$\frac{\dot{x}_i}{x_i} = (A\tilde{x})_i, \quad (3.2)$$

where (3.2) is obtained from the definition of the replicator equation (3.1).

Now, consider the transformation of variables applied to the replicator equation. The derivation of the heuristic equivalence to a Lotka-Volterra equation proceeds from use of the quotient rule to obtain the identity of the derivative of absolute abundance for species  $i$ . Recall from Section 2 the relative frequency of strategies is given by the transformation from absolute to relative abundances,  $x_i = y_i/[1 + y]$ ;  $i = 1, 2, \dots, n-1$ , on the  $(n-1)$ -dimensional simplex such that  $x_n = 1 - \sum_{i=1}^{n-1} x_i$ . There is a loss of information when considering frequencies under this transformation, since without knowledge of the total population size  $y$  the reverse transformation is impossible. That is,  $y_i \neq x_i/x_n$ . The replacement of this heuristic reverse transformation is the first of two errors incurred when constructing the equivalence of the replicator to the Lotka-Volterra equation.

Applying the quotient rule to  $y_i = x_i/x_n$

$$\dot{y}_i = \frac{\dot{x}_i x_n - \dot{x}_n x_i}{x_n^2} = \frac{x_i}{x_n} \left[ \frac{1}{x_n} (A\tilde{x})_i - (A\tilde{x})_n \right], \quad (3.3)$$

where the second expression uses the substitution of the replicator equation (3.2). Expanding the right side of (3.3), and again using the reverse transformation,

$$\dot{y}_i = y_i \left[ \frac{1}{x_n} \sum_{j=i}^n a_{ij} x_j - \sum_{j=1}^n a_{nj} x_j \right]$$

$$= y_i \left[ a_{in} + \sum_{j=1}^{n-1} a_{ij} \frac{x_j}{x_n} - \sum_{j=1}^{n-1} a_{nj} x_j - a_{nn} x_n \right], \quad (3.4)$$

which yields the second error in the construction of the equivalence heuristic. If, instead the factor  $1/x_n$  was common to all terms in (3.4), for  $(A\tilde{x})_i$  and  $(A\tilde{x})_n$ , both replicators, then

$$\dot{y}_i = y_i \left[ a_{in} - a_{nn} + \sum_{j=i}^{n-1} (a_{ij} - a_{nj}) y_j \right]. \quad (3.5)$$

Equation (3.5) corresponds to the parametric conversions for heuristic equivalence such that  $r_i = a_{in} - a_{nn}$  and  $b_{ij} = a_{ij} - a_{nj}$ , which gives the canonical form of a *Lotka-Volterra* equation. The  $r_i$  parameter is a measure of the birth rate of species  $i$ ;  $i = 1, 2, \dots, n-1$ . The  $b_{ij}$  parameter is a measure of the competitive interaction of species  $i$  toward species  $j$ ;  $i, j = 1, 2, \dots, n-1$ . For  $b_{ij} > 0$  species  $j$  is predator to prey species  $i$ . For  $b_{ij} < 0$  species  $j$  is prey to predator species  $i$ . Observe that the resultant inter-specific competition matrix  $[b_{ij}]$  is neither necessarily symmetric nor skew-symmetric (otherwise known as anti-symmetric).

#### 4. Conclusion

By way of comparison with the heuristic parameter conversion [11], the direct algebra of Section 2 shows that  $r_i \neq a_{in} - a_{nn}$ , due to omitted terms and a common factor, and certainly  $b_{ij} \neq a_{ij} - a_{nj}$ . Furthermore, the case  $i = n$  of (1.1) is a corollary of the calculations above since the replicator equation is defined on an  $(n-1)$ -dimensional simplex. The particular varieties of non-linearity that arise under the translation from absolute to relative abundances of types in the population of interest are identified. Such non-linearity is shown to encompass three separate characteristics of the heuristic equivalence of a continuous replicator and a Lotka-Volterra equation. In Section 3, the calculations required to obtain the previous equivalence heuristic are explained.

The exposition of this note demonstrates a chasm of non-linearity exists between the inter-specific competition of the Lotka-Volterra equation and the continuous replicator of strategies in dynamic evolutionary games. By contrast, in the true Lotka-Volterra model the case of skew-symmetric interaction between species is equivalent to a predator-prey model on two trophic levels. Alternatively, also in the true Lotka-Volterra model the case of symmetric interaction between species is equivalent to inter-specific competition within a single trophic level. However, the results of this note demonstrate that such equivalences are confined to the Lotka-Volterra model itself and are unattainable from the continuous replicator dynamics of strategic interaction in evolutionary game theory.

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