

Analytic Solutions to a Family of Lotka-Volterra Related Differential Equations

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An initial formal analysis of the analytic solution [C. M. Evans and G. L. Findley, *J. Math. Chem.*, in press] to the Lotka-Volterra dynamical system is presented. A family of first-order autonomous ordinary differential equations related to the LV system is derived, and the analytic solutions to these systems are given. Invariants for the latter systems are introduced, and a simple transformation which allows these systems to be reduced to Hamiltonian form is provided.

I. INTRODUCTION

The Lotka-Volterra (LV) problem, originally introduced in 1920 by A. Lotka [1] as a model for undamped oscillating chemical reactions, and later applied by V. Volterra [2] to predator-prey interactions, consists of the following pair of first-order autonomous ordinary differential equations:

$$\begin{aligned}\dot{x}_1 &= a x_1 - b x_1 x_2 \\ \dot{x}_2 &= -c x_2 + b x_1 x_2,\end{aligned}\quad (1)$$

where $x_1(t)$ and $x_2(t)$ are real functions of time, $\dot{x}_i = dx_i/dt$, and a, b, c are positive real constants. Since that time, the LV model has been applied to problems in population biology [3], chemical kinetics [4], neural networks [5] and epidemiology [6], and has become a classic example for nonlinear dynamical systems [7,8]. In the 1960s, E. H. Kerner [10] showed that the dynamical invariant, known since the original publication by Lotka [1] and having the form,

$$\Lambda = b x_1 + b x_2 - c \ln x_1 - a \ln x_2, \quad (2)$$

could reduce eq. (1), by means of a logarithmic transformation, to a Hamiltonian system. This initial discovery has been expanded by E. H. Kerner [10,11] and M. Plank [12] to multi-dimensional Lotka-Volterra equations, and R. Dutt [13] has analyzed the Hamiltonian form of eq. (2) using Hamilton-Jacobi theory.

Recently, eq. (1) was shown [14] to have the solution

$$\begin{aligned}x_1 &= \frac{1}{b} (a \alpha w + \dot{w}) \\ x_2 &= \frac{1}{b} (a w - \dot{w}),\end{aligned}\quad (3)$$

where $a \alpha = c$ and w is given by the solution to

$$\begin{aligned}\ddot{w} - \dot{w}^2 - a(\alpha - 1)(w - 1)\dot{w} \\ + a^2 \alpha w (w - 1) = 0.\end{aligned}\quad (4)$$

With the use of eq. (2), eq. (4) can be written as

$$\begin{aligned}\ddot{w} - a(1 - \alpha)\dot{w} - a^2 \alpha w \\ - k^2 \left[\frac{1}{b} (a \alpha w + \dot{w}) \right]^{1-\alpha} e^{(\alpha+1)w} = 0,\end{aligned}\quad (5)$$

where $k^2 = -b^2 e^{-\Lambda/a}$. In [14] we showed that the formal analytic solution to eq. (5) is

$$t - t_0 = \int_{w_0}^w [a \alpha (e^{\rho} - w')]^{-1} dw', \quad (6)$$

where e^{ρ} solves

$$\begin{aligned}b a (\alpha + 1) w' e^{\alpha \rho} - b \alpha a e^{(\alpha+1)\rho} \\ + k^2 \left(\frac{b}{a \alpha} \right)^{\alpha} e^{(\alpha+1)w'} = 0.\end{aligned}\quad (7)$$

Eq. (6) represents a complete reduction of the LV problem to an integral quadrature which, however, is not reducible to elementary functions. The purpose of the present paper is to begin an exploration of this quadrature.

In Section 2, we provide an initial analysis of eq. (5) [and, therefore, of eq. (6)] by means of a power series expansion of the exponential $e^{(\alpha+1)w}$, for small integer values of α ($\alpha = 1, 2, 3$). Moreover, for the case $\alpha = 1$, the relationship of the solutions provided by eq. (6) to the family of elliptic functions will be explored. In Section 3, an inverse transformation of eq. (3), along with the solutions to eq. (5) provided in Section 2, is used to develop a family of LV related first-order autonomous ordinary differential equations, and the dynamical invariant for each of these systems is derived. Finally, a simple transformation of these invariants which permits each system to be placed into Hamiltonian form is presented.

II. POWER SERIES ANALYSIS

Our analysis begins by expanding the exponential term in eq. (5) in a power series to give

$$\begin{aligned} \ddot{w} - a(1 - \alpha)\dot{w} - a^2\alpha w \\ - k^2 \left[\frac{1}{b} (a\alpha w + \dot{w}) \right]^{1-\alpha} \\ \times \sum_{m=0}^{\infty} \frac{1}{m!} (\alpha + 1)^m w^m = 0, \end{aligned} \quad (8)$$

Truncation of the power series in eq. (8) gives approximate solutions to the LV problem (cf. Fig. 1). As will be shown below, the truncation of eq. (8) leads to a family of differential equations, each seemingly more complex than the original LV problem, which can be solved in terms of known functions. For finite integer n , eq. (8) can be approximated as

$$\begin{aligned} \ddot{w} - a(1 - \alpha)\dot{w} - a^2\alpha w \\ - k^2 \left[\frac{1}{b} (a\alpha w + \dot{w}) \right]^{1-\alpha} \\ \times \sum_{m=0}^n \frac{1}{m!} (\alpha + 1)^m w^m = 0, \end{aligned} \quad (9)$$

which has the solution

$$t - t_0 = \int^w [a\alpha(\rho - w')]^{-1} dw', \quad (10)$$

where ρ is given by the solution to

$$\begin{aligned} (n+1)! \left[-b a \alpha \rho^{\alpha+1} \right. \\ \left. + b a (\alpha + 1) w' \rho^\alpha + k^2 \left(\frac{b}{a\alpha} \right)^\alpha \right. \end{aligned} \quad (11)$$

$$\left. \times \sum_{m=0}^{n+1} \frac{1}{m!} (\alpha + 1)^m w'^m \right] = 0.$$

When α is an integer, eq. (11) reduces to an $\alpha + 1$ degree polynomial which can be solved in terms of radicals for $\alpha \leq 3$ with the aid of a symbolic processor [15].

For $\alpha = 1$, the solution to eq. (11) is

$$\rho = w' \pm \frac{1}{a} \left[a^2 w'^2 + k^2 \sum_{m=0}^{n+1} \frac{2^m}{m!} w'^m \right]^{1/2},$$

which, when substituted into eq. (10), gives the solution

$$\begin{aligned} t - t_0 = \pm \int^w \left[a^2 w'^2 \right. \\ \left. + k^2 \sum_{m=0}^{n+1} \frac{2^m}{m!} w'^m \right]^{-1/2} dw'. \end{aligned} \quad (12)$$

With the use of a symbolic processor [15,16], eq. (12) can be integrated in terms of known functions for $n \leq 3$; these solutions are given in Table 1. The solutions for $n = 0$ and $n = 1$ are exponential, although the solution for $n = 1$ can become periodic when $a^2 < 2k^2$. When $n = 2$ or $n = 3$, the solutions are elliptic functions of the first kind [17].

When $\alpha = 2$, the solution of eq. (11) leads to three values for p which can then be substituted into eq. (10) to yield the analytic solutions

$$t - t_0 = \int \left[\frac{1}{2} p_2^{1/3} + 2a^2 w'^2 p_2^{-1/3} - a w' \right]^{-1} dw'$$

and

$$t - t_0 = \int \left[-\frac{1}{4} (1 \pm i\sqrt{3}) p_2^{1/3} - a^2 (1 \mp i\sqrt{3}) w'^2 p_2^{-1/3} - a w' \right]^{-1} dw',$$

where p_2 is defined as

$$p_2 = 8a^3 w'^3 + 4k^2 b \sum_{m=0}^{n+1} \frac{3^m}{m!} w'^m + 4 \left[b k^2 \sum_{m=0}^{n+1} \frac{3^m}{m!} w'^m \left(4a^3 w'^3 + \frac{3^m}{m!} b k^2 w'^m \right) \right]^{1/2}.$$

Substituting the four solutions of eq. (11) when $\alpha = 3$ into eq. (10) gives the analytic solutions

$$t - t_0 = \int \left[-2a w' \pm 12a^3 w'^3 (3b^2 k^2 S p_3^{-1/3} - p_3^{1/3} - 6a^2 w'^2)^{-1/2} + \frac{\sqrt{6}}{6} [(3b^2 k^2 S p_3^{-1/3} - p_3^{1/3} - 6a^2 w'^2)^{1/2} \pm (3b^2 k^2 S p_3^{-1/3} - p_3^{1/3} - 12a^2 w'^2)]^{-1} \right] dw'$$

and

$$t - t_0 = \int \left[-2a w' \pm 12a^3 w'^3 (3b^2 k^2 S p_3^{-1/3} - p_3^{1/3} - 6a^2 w'^2)^{-1/2} - \frac{\sqrt{6}}{6} [(3b^2 k^2 S p_3^{-1/3} - p_3^{1/3} - 6a^2 w'^2)^{1/2} \mp (3b^2 k^2 S p_3^{-1/3} - p_3^{1/3} - 12a^2 w'^2)]^{-1} \right] dw'$$

where

$$p_3 = 3k^2 b^2 S [-9a^2 w'^2 + (3k^2 b^2 S + 81a^4 w'^4)^{1/2}]$$

and

$$S = \sum_{m=0}^{n+1} \frac{4^m}{m!} w'^m.$$

TABLE 1. Analytic Solutions to Eq. (12) of Text for $\alpha = 1$ and $n \leq 3$

n	Solution
0	$w(t) = \frac{1}{2a} e^{\pm a(t-t_0)} + \frac{k^2}{2a^2} (k^2 - a) e^{\mp a(t-t_0)} - \frac{k^2}{a^2}$
1	$w(t) = \frac{1}{2\lambda} e^{\pm \lambda(t-t_0)} + \frac{k^2}{2\lambda^2} (k^2 - \lambda) e^{\mp \lambda(t-t_0)} - \frac{k^2}{\lambda^2}$ where $\lambda = \sqrt{a^2 + 2k^2}$
2	$\pm \frac{\sqrt{3}}{3} k \sqrt{\beta_1 - \beta_3} (t - t_0) = F \left(\sin^{-1} \left(\frac{w - \beta_3}{\beta_2 - \beta_3} \right)^{1/2}, \frac{\beta_2 - \beta_3}{\beta_1 - \beta_3} \right)$ where F is an elliptic function of the first kind ^a and $\beta_1 = -\frac{1}{4} \frac{a^2 + 2k^2}{k^2} - \frac{1}{8} (1 + i\sqrt{3}) k^{-2} p_2^{1/3} - \frac{1}{8} (1 - i\sqrt{3}) k^{-2} (a^4 + 4a^2k^2 - 4k^4) p_2^{-1/3}$ $\beta_2 = -\frac{1}{4} \frac{a^2 + 2k^2}{k^2} - \frac{1}{8} (1 - i\sqrt{3}) k^{-2} p_2^{1/3} - \frac{1}{8} (1 + i\sqrt{3}) k^{-2} (a^4 + 4a^2k^2 - 4k^4) p_2^{-1/3}$ $\beta_3 = -\frac{1}{4} \frac{a^2 + 2k^2}{k^2} - \frac{1}{4} k^{-2} p_2^{1/3} - \frac{1}{4} k^{-2} (a^4 + 4a^2k^2 - 4k^4) p_2^{-1/3}$ with p_2 defined as $p_2 = -a^6 - 6a^4k^2 - 8k^6 + 4\sqrt{3a^2k^2(5a^2 - 4k^2) + k^3(3a^6 + 8k^3)}$

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When $\alpha > 3$, the polynomial can no longer be solved in terms of radicals.

The solutions of eq. (9) represent analytic solutions to a family of first-order autonomous ordinary differential equations. The next Section develops this family of differential equations from an inverse transformation of eq. (3) coupled with the knowledge of eq. (9).

III. SYSTEMS OF LV RELATED DIFFERENTIAL EQUATIONS

In this Section, an inverse transformation of eq. (3) is used to develop the family of first-order autonomous ordinary differential equations which are equivalent to eq. (9). Eq. (10) represents the analytic solutions to this family of equations which, as shown in Section 2, can be solved in terms of known functions for $\alpha = 1$ and $n \leq 3$. The phase space trajectories (cf. Fig. 1) indicate that these systems are conservative since closed orbits exist. Later in this Section, the constant of the motion for each

TABLE 1. continued

n	Solution
3	$\frac{\sqrt{6}}{2} k [(\beta_2 - \beta_4)(\beta_1 - \beta_3)]^{1/2} (t - t_0) = F \left(\sin^{-1} \left(\frac{(\beta_2 - \beta_4)(w - \beta_1)}{(\beta_1 - \beta_4)(w - \beta_2)} \right)^{1/2}, \frac{(\beta_1 - \beta_4)(\beta_2 - \beta_3)}{(\beta_1 - \beta_3)(\beta_2 - \beta_4)} \right)$ <p style="text-align: center;">where</p> $\beta_1 = -\frac{1}{2} + \frac{\sqrt{2}}{4} k^{-1} [p_3^{1/3} + (a^2 + 2k^2)^2 p_3^{-1/3} - 2(a^2 + k^2)]^{1/2}$ $+ \frac{\sqrt{2}}{4} k^{-1} \left[p_3^{1/3} + (a^2 + 2k^2)^2 p_3^{-1/3} + 4(a^2 + k^2) \right. \\ \left. + 2\sqrt{2} k (2k^2 - 3a^2) [p_3^{1/3} + (a^2 + 2k^2)^2 p_3^{-1/3} - 2(a^2 + k^2)]^{-1/2} \right]^{1/2}$ $\beta_2 = -\frac{1}{2} + \frac{\sqrt{2}}{4} k^{-1} [p_3^{1/3} + (a^2 + 2k^2)^2 p_3^{-1/3} - 2(a^2 + k^2)]^{1/2}$ $- \frac{\sqrt{2}}{4} k^{-1} \left[p_3^{1/3} + (a^2 + 2k^2)^2 p_3^{-1/3} + 4(a^2 + k^2) \right. \\ \left. + 2\sqrt{2} k (2k^2 - 3a^2) [p_3^{1/3} + (a^2 + 2k^2)^2 p_3^{-1/3} - 2(a^2 + k^2)]^{-1/2} \right]^{1/2}$ $\beta_3 = -\frac{1}{2} - \frac{\sqrt{2}}{4} k^{-1} [p_3^{1/3} + (a^2 + 2k^2)^2 p_3^{-1/3} - 2(a^2 + k^2)]^{1/2}$ $+ \frac{\sqrt{2}}{4} k^{-1} \left[p_3^{1/3} + (a^2 + 2k^2)^2 p_3^{-1/3} + 4(a^2 + k^2) \right. \\ \left. + 2\sqrt{2} k (2k^2 - 3a^2) [p_3^{1/3} + (a^2 + 2k^2)^2 p_3^{-1/3} - 2(a^2 + k^2)]^{-1/2} \right]^{1/2}$ $\beta_4 = -\frac{1}{2} - \frac{\sqrt{2}}{4} k^{-1} [p_3^{1/3} + (a^2 + 2k^2)^2 p_3^{-1/3} - 2(a^2 + k^2)]^{1/2}$ $- \frac{\sqrt{2}}{4} k^{-1} \left[p_3^{1/3} + (a^2 + 2k^2)^2 p_3^{-1/3} + 4(a^2 + k^2) \right. \\ \left. + 2\sqrt{2} k (2k^2 - 3a^2) [p_3^{1/3} + (a^2 + 2k^2)^2 p_3^{-1/3} - 2(a^2 + k^2)]^{-1/2} \right]^{1/2}$ <p style="text-align: center;">with p defined by</p> $p_3 = a^6 + 6a^4 k^2 - 24k^4 a^2 - 4k^6 + 2k^2 \sqrt{72a^4 k^4 - 12k^8 - 114a^6 k^2 - 18a^8}$

^aM. Abramowitz and I. A. Stegun, *Handbook of Mathematical Functions*, Dover, New York, 1965.

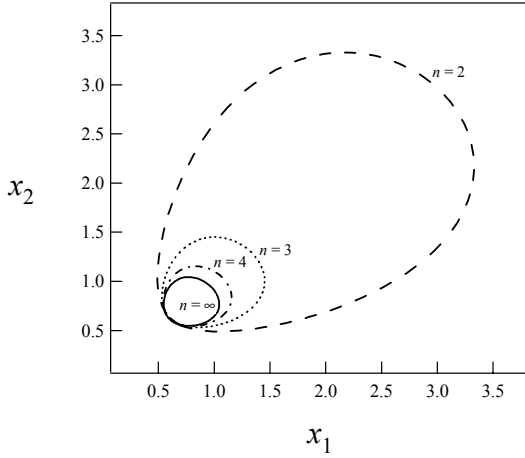


Fig. 1. Phase-plane plot of eq. (3) obtained by a fourth-order Runge-Kutta solution to eq. (8) for $n = 2$ (—), $n = 3$ (---), $n = 4$ (.....) and $n = \infty$ (·—) when $a = c = 1.00$ and $b = 1.30$. Initial data for these trajectories are $x_1(t = 0) = 0.7000$ and $x_2(t = 0) = 0.5556$. The phase-plane trajectory for $n = 1$ is not shown since the trajectory is exponential for the initial conditions chosen.

system will be derived, and a transformation will be presented which allows this family of equations to be placed into Hamiltonian form.

The inverse transformation of eq. (3) is given by

$$w = \frac{b}{a} (\alpha + 1)^{-1} (x_1 + x_2) \quad (13)$$

$$\dot{w} = b (\alpha + 1)^{-1} (x_1 - \alpha x_2).$$

Substituting obtained from eq. (9) into the time derivative of eq. (3), and employing the transformation given by eq. (13) yields the following system of first-order autonomous ordinary differential equations:

$$\begin{aligned} \dot{x}_1 &= a x_1 + \frac{k^2}{b} x_1^{1-\alpha} \\ &\times \sum_{m=0}^n \frac{1}{m!} \left(\frac{b}{a} \right)^m (x_1 + x_2)^m \end{aligned} \quad (14)$$

$$\begin{aligned} \dot{x}_2 &= -a \alpha x_2 - \frac{k^2}{b} x_1^{1-\alpha} \\ &\times \sum_{m=0}^n \frac{1}{m!} \left(\frac{b}{a} \right)^m (x_1 + x_2)^m. \end{aligned}$$

Although these equations appear to be more complicated than the original LV system given in eq. (1), eq. (14) can be solved analytically in terms of known functions for $\alpha = 1$ and $n \leq 3$. When $n = 2$ and $\alpha = 1$, eq. (14) has the quadratic coupling term which appears in the LV predator-prey model [i.e., eq. (1)] as well as quadratic terms dependent only on x_1 and x_2 (which is reminiscent of the LV competition model [18]).

The phase space trajectories of eq. (14) are determined by

$$\begin{aligned} \frac{dx_1}{dx_2} &= \left[a x_1 + \frac{k^2}{b} x_1^{1-\alpha} \right. \\ &\times \left. \sum_{m=0}^n \frac{1}{m!} \left(\frac{b}{a} \right)^m (x_1 + x_2)^m \right] / \end{aligned} \quad (15)$$

$$\left[-a \alpha x_2 - \frac{k^2}{b} x_1^{1-\alpha} \right]$$

$$\times \sum_{m=0}^n \frac{1}{m!} \left(\frac{b}{a} \right)^m (x_1 + x_2)^m \Big]$$

which can be integrated to give

$$I_n = a x_1^\alpha x_2 + k^2 \times \sum_{m=1}^{n+1} \frac{1}{m!} a^{1-m} b^{m-2} (x_1 + x_2)^m. \quad (16)$$

That I_n is an invariant for the system, thereby explaining the closed-orbit nature of the phase-space trajectories of Fig. 1, may be shown by induction as follows.

The condition that I_n be constant is

$$\frac{dI_n}{dt} = \partial_1 I_n \dot{x}_1^{(n)} + \partial_2 I_n \dot{x}_2^{(n)} = 0, \quad (17)$$

where $\partial_i I_n = \partial I_n / \partial x_i$ and $\dot{x}_i^{(n)} = \dot{x}_i$, for some specific value of n . For $n=0$, eq. (17) becomes

$$\begin{aligned} \frac{dI_0}{dt} &= \left(a \alpha x_1^{\alpha-1} x_2 + \frac{k^2}{b} \right) \left(a x_1 + \frac{k^2}{b} x_1^{1-\alpha} \right) \\ &+ \left(a x_1^\alpha + \frac{k^2}{b} \right) \left(-a \alpha x_2 - \frac{k^2}{b} x_1^{1-\alpha} \right), \end{aligned}$$

which simplifies to

$$\frac{dI_0}{dt} = 0.$$

When $n = j + 1$, eq. (14) can be written recursively as

$$\begin{aligned} \dot{x}_1^{(j+1)} &= \dot{x}_1^{(j)} + [(j+1)!]^{-1} \\ &\times k^2 b^j a^{-j-1} x_1^{1-\alpha} (x_1 + x_2)^{j+1} \\ \dot{x}_2^{(j+1)} &= \dot{x}_2^{(j)} - [(j+1)!]^{-1} \\ &\times k^2 b^j a^{-j-1} x_1^{1-\alpha} (x_1 + x_2)^{j+1}, \end{aligned} \quad (18)$$

and I_{j+1} [eq. (16)] can be rewritten as

$$I_{j+1} = I_j + [(j+2)!]^{-1} \times k^2 b^j a^{-j-1} (x_1 + x_2)^{j+2}. \quad (19)$$

Substituting eq. (18) and the derivatives of eq. (19) into eq. (17) and rearranging gives

$$\begin{aligned} \frac{dI_{j+1}}{dt} &= \left(\partial_1 I_j \dot{x}_1^{(j)} + \partial_2 I_j \dot{x}_2^{(j)} \right) \\ &+ [(j+1)!]^{-1} k^2 (x_1 + x_2)^{j+1} b^j a^{-j-1} \\ &\times \left[x_1^{1-\alpha} \left(\partial_1 I_j - \partial_2 I_j \right) + \left(\dot{x}_1^{(j)} + \dot{x}_2^{(j)} \right) \right]. \end{aligned}$$

Since $\partial_1 I_j \dot{x}_1^{(j)} + \partial_2 I_j \dot{x}_2^{(j)} = 0$ by assumption, dI_{j+1}/dt reduces to

$$\begin{aligned} \frac{dI_{j+1}}{dt} &= [(j+1)!]^{-1} k^2 b^j a^{-j-1} (x_1 + x_2)^{j+1} \\ &\times \left[x_1^{1-\alpha} \left(a \alpha x_1^{\alpha-1} x_2 - a x_1^\alpha \right) \right. \\ &\left. + \left(a x_1 - a \alpha x_2 \right) \right], \end{aligned}$$

which simplifies to $dI_{j+1}/dt = 0$, thus completing the proof.

The invariant of eq. (16) can be written in Hamiltonian form by introducing (q, p) variables

$$q = x_1 \quad \text{and} \quad p = x_1^{\alpha-1} x_2. \quad (20)$$

This transformation allows the system represented by eqs. (14) and (16) to be written as

$$\begin{aligned} \dot{q} &= a q + k^2 q^{1-\alpha} \\ &\times \sum_{m=0}^n \frac{1}{m!} a^{-m} b^{m-1} (q + p q^{1-\alpha})^m \end{aligned} \quad (21)$$

$$\begin{aligned} \dot{p} &= -a p - k^2 [1 + (1 - \alpha) p q^{-\alpha}] \\ &\times \sum_{m=0}^n \frac{1}{m!} a^{-m} b^{m-1} (q + p q^{1-\alpha})^m, \end{aligned}$$

with the function

$$\begin{aligned} H_n &= a q p + k^2 \\ &\times \sum_{m=1}^{n+1} \frac{1}{m!} a^{1-m} b^{m-2} (q + p q^{1-\alpha})^m. \end{aligned} \quad (22)$$

serving as a Hamiltonian, which may be shown simply as follows. The derivatives of eq. (22) with respect to q and p are

$$\begin{aligned} \frac{\partial H_n}{\partial p} &= a q + k^2 q^{1-\alpha} \\ &\times \sum_{m=0}^n \frac{1}{m!} a^{-m} b^{m-1} (q + p q^{1-\alpha})^m \end{aligned} \quad (23)$$

$$\begin{aligned} \frac{\partial H_n}{\partial q} &= a p + k^2 [1 + (1 - \alpha) p q^{-\alpha}] \\ &\times \sum_{m=0}^n \frac{1}{m!} a^{-m} b^{m-1} (q + p q^{1-\alpha})^m. \end{aligned}$$

Directly comparing eq. (23) with eq. (21) gives

$$\frac{\partial H_n}{\partial p} = \dot{q} \quad \text{and} \quad \frac{\partial H_n}{\partial q} = -\dot{p},$$

which are, of course, Hamilton's equations.

IV. CONCLUSION

In this paper, we have presented an initial analysis of the analytic solution [14] to the Lotka-Volterra problem and have shown, for the special case of $\alpha = 1$, the relationship between this solution and the family of elliptic functions. We also have provided the form of the integral quadrature [eq. (6)] for the cases of $\alpha \leq 3$. The truncation of the power series used in our analysis of the analytic solution has been shown to lead to a new family of LV related differential equations which, for $\alpha = 1$ and $n \leq 3$, can be solved in terms of known functions. The constant of the motion for this family was given, and a simple transformation was found to take this invariant into Hamiltonian form.

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