

**A CLASS OF GENERALIZATIONS OF THE
LOTKA-VOLTERRA PREDATOR-PREY
EQUATIONS HAVING EXACTLY
SOLUBLE SOLUTIONS**

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ABSTRACT. We consider a number of ordinary differential equations which may be used to model predator-prey (P-P) interactions. All of these equations are generalization of the standard Lotka-Volterra equations. However, the new equations have the important feature that they can be explicitly solved in terms of elementary functions. We also discuss the general mathematical restrictions which need to be placed on the various terms in the P-P equations for valid models to exist. The results are extended to the more realistic case where the prey population has more complex population dynamics.

Keywords and phrases: Lotka-Volterra equations; Population models; Ordinary differential equations; Exact solutions

AMS numbers: 34A 05, 34A 30, 92D 25, and 92D 40.

1. INTRODUCTION

The Lotka-Volterra (L-V) equations provides a foundational model for predator-prey (P-P) interactions [1, 2]. In spite of its fundamental and historical significance, in general, the model does not provide an accurate representation of real data [1]. However, it gives many important insights into interacting populations dynamics and is a valuable learning tool for introducing those new to the field. One key difficulty is that the standard L-V equations

$$\frac{dx}{dt} = ax - bxy, \quad \frac{dy}{dt} = -cy + dxy \quad (1.1)$$

can not be solved in terms of the elementary functions; however, this problem holds for essentially all interacting population mathematical models [1, 2].

Received by the editors March 02, 2017; Revised: April 04, 2017; Accepted: April 05, 2017

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The main goals of this paper are, first, to provide a new class of P-P ordinary differential equation models and demonstrate that they can be solved exactly in terms of elementary functions, i.e., exponential and trigonometric functions. To construct these models, information is needed on the possible mathematical structures of the various growth, death, and interaction terms appearing in the differential equations and we provide a brief discussion of such functions.

This paper is organized as following: Section 2 gives the general mathematical structures of the terms in a P-P model. Section 3 presents four new P-P models based on direct modifications of the standard L-V equations. In section 4, we select one of the models given in the previous section and calculate its exact solution. The final section include a summary of our results and an extension to the case where the prey population has more complex population dynamics.

2. RESTRICTIONS ON PREDATOR-PREY MODELS

Let $x(t)$ and $y(t)$ denote, respectively, the prey and predator populations at time t . In the following discussion, the parameters, (a, b, λ) , are taken to be non-negative. A general P-P model has the structure

$$\frac{dx}{dt} = F_1(x) - G(x, y), \quad \frac{dy}{dt} = -F_2(y) + \lambda G(x, y) \quad (2.1)$$

where

(a) $F_1(x)$ represents the rate of growth of the prey in the absence of the predator;

(b) $F_2(y)$ is the rate of decline of the predator if no prey are available and the assumption is made that the only food source is the prey;

(c) $G(x, y)$ is the death rate of the prey in the presence of the predator;

(d) λ is a parameter related to the conversion of the prey into nutrition for the predator.

In order to have a valid P-P model, these functions must have the following mathematical properties [1, 2].

$$(i) F_1(x) : F_1(0) = 0; F_1(x) > 0, \quad x > 0; F_1(x_1) > F_1(x_2), \quad x_1 > x_2. \quad (2.2)$$

$$(ii) \ F_2(y) : F_2(0) = 0; \ F_2(y) > 0, y > 0; \quad F_2(y_1) > F_2(y_2), \ y_1 > y_2. \quad (2.3)$$

$$(iii) \ G(x, y) : G(0, 0) = 0; \ G(x, y) > 0, \ x > 0, y > 0;$$

$$G(x_1, y) > G(x_2, y), \ x_1 > x_2;$$

$$G(x, y_1) > G(x, y_2), \quad y_1 > y_2; \quad (2.4)$$

Note that for the standard L-V model, we have

$$F_1(x) = ax, \quad F_2(y) = cy, \quad G(x, y) = bxy, \quad \lambda = \frac{d}{b}. \quad (2.5)$$

Also, observe that the conditions of Eq. (2.2) imply that the prey population, in and of itself, can increase without limits. In section 5, we indicate how this can be modified to include a finite carrying capacity for the prey population. More complex functions can be selected for $F_1(x)$, $F_2(x)$, and $G(x, y)$ [1].

3. GENERALIZATIONS OF THE LOTKA-VOLTERRA EQUATIONS

Consider the following expressions for the three functions given on the right-sides of Eq. (2.1):

$$F_1(x) : \quad x, \sqrt{x}; \quad (3.1)$$

$$F_2(y) : \quad y, \sqrt{y}; \quad (3.2)$$

$$G(x, y) : \quad \sqrt{x}\sqrt{y}. \quad (3.3)$$

Inspection shows that all three functions satisfy the restrictions given in Eqs. (2.2), (2.3), and (2.4). From these forms, four P-P models can be constructed; they are

$$\frac{dx}{dt} = a_1\sqrt{x} - b_1\sqrt{x}\sqrt{y}, \quad \frac{dy}{dt} = -c_1\sqrt{y} + d_1\sqrt{x}\sqrt{y}, \quad (3.4)$$

$$\frac{dx}{dt} = a_2x - b_2\sqrt{x}\sqrt{y}, \quad \frac{dy}{dt} = -c_2y + d_2\sqrt{x}\sqrt{y}, \quad (3.5)$$

$$\frac{dx}{dt} = a_3x - b_3\sqrt{x}\sqrt{y}, \quad \frac{dy}{dt} = -c_3\sqrt{y} + d_3\sqrt{x}\sqrt{y}, \quad (3.6)$$

$$\frac{dx}{dt} = a_4\sqrt{x} - b_4\sqrt{x}\sqrt{y}, \quad \frac{dy}{dt} = -c_4y + d_4\sqrt{x}\sqrt{y}. \quad (3.7)$$

Using the transformation of variables

$$u = \sqrt{x}, \quad v = \sqrt{y}, \quad (3.8)$$

the Eqs. (3.4)-(3.7) become, respectively,

$$\frac{du}{dt} = \bar{a}_1 - \bar{b}v, \quad \frac{dv}{dt} = -\bar{c}_1 + \bar{d}_1u, \quad (3.9)$$

$$\frac{du}{dt} = \bar{a}_2u - \bar{b}v, \quad \frac{dv}{dt} = -\bar{c}_2v + \bar{d}_2v, \quad (3.10)$$

$$\frac{du}{dt} = \bar{a}_3u - \bar{b}v, \quad \frac{dv}{dt} = -\bar{c}_3 + \bar{d}_3u, \quad (3.11)$$

$$\frac{du}{dt} = \bar{a}_4 - \bar{b}v, \quad \frac{dv}{dt} = -\bar{c}_4v + \bar{d}_4u, \quad (3.12)$$

where, in general, a barred parameter \bar{p} is $\bar{p} = \frac{p}{2}$.

Observe that all four pairs of equations are first-order, linear, constant coefficients differential equations and, consequently, can be solved exactly using elementary techniques from differential equations [3, 4].

We illustrate this methodology in the next section by calculating the full analytical solutions for Eq. (3.9). Thus, given $u(t)$ and $v(t)$, the corresponding solutions for Eq. (3.4) are given by the relations

$$x(t) = [u(t)]^2, \quad y(t) = [v(t)]^2. \quad (3.13)$$

An important feature of the result of Eq. (3.13) is that the prey and predator solutions satisfy a condition of positivity, i.e.,

$$x(0) > 0, y(0) > 0 \implies x(t) > 0, y(t) > 0, t > 0. \quad (3.14)$$

4. SOLUTIONS TO EQ. (3.4)

For convenience, we write Eq. (3.9) here, again, i.e.,

$$\frac{du}{dt} = \bar{a}_1 - \bar{b}_1 v, \quad \frac{dv}{dt} = -\bar{c}_1 + \bar{d}_1 u. \quad (4.1)$$

The fixed-point, equilibrium or constant solution are

$$u^* = \frac{\bar{c}_1}{\bar{d}_1} = \frac{c_1}{d_1}, \quad v^* = \frac{\bar{a}_1}{\bar{b}_1} = \frac{a_1}{b_1}, \quad (4.2)$$

and these translate into the following values for x^* and y^*

$$x^* = \left(\frac{c_1}{d_1} \right)^2, \quad y^* = \left(\frac{a_1}{b_1} \right)^2. \quad (4.3)$$

If the first of Eqs. (4.1) is solved for $v(t)$ and then substituted into the second of Eq. (4.1), the following second-order ODE is obtained for $u(t)$

$$\frac{d^2 u}{dt^2} + \left(\frac{b_1 d_1}{4} \right) u = \frac{b_1 c_1}{4}, \quad (4.4)$$

and its general solution is

$$u(t) = A \cos(\Omega t) + B \sin(\Omega t) + \frac{c_1}{d_1}, \quad (4.5)$$

where A and B are arbitrary constants and

$$\Omega = \sqrt{\frac{b_1 d_1}{4}}. \quad (4.6)$$

Since $v(t)$ is given by the expression

$$v(t) = \left(\frac{1}{\bar{b}_1} \right) \left[\bar{a}_1 - \frac{du}{dt} \right], \quad (4.7)$$

we have

$$v(t) = \left(\frac{a_1}{b_1} \right) + \left(\sqrt{\frac{d_1}{b_1}} \right) A \sin(\Omega t) - \left(\sqrt{\frac{d_1}{b_1}} \right) B \cos(\Omega t). \quad (4.8)$$

For the initial conditions

$$x(0) = x_0 > 0, \quad y(0) > 0, \quad (4.9)$$

it follows that

$$u_0 = \sqrt{x_0}, \quad v_0 = \sqrt{y_0}. \quad (4.10)$$

Evaluating Eqs. (4.5) and (4.8), at $t = 0$, gives two linear equations for A and B, and these may be solved to obtain

$$A = \sqrt{x_0} - \sqrt{x^*}, \quad B = \left(\frac{b_1}{d_1}\right)^{\frac{1}{2}} [\sqrt{y_0} - \sqrt{y^*}]. \quad (4.11)$$

Note that x^* and y^* are the fixed-points or equilibrium solutions; see Eq. (4.3).

Putting all this together gives for $u(t)$ and $v(t)$ the expressions

$$x(t) = \left\{ \left(\sqrt{x_0} - \sqrt{x^*} \right) \cos(\Omega t) - \left(\frac{b_1}{d_1} \right)^{\frac{1}{2}} \left(\sqrt{y_0} - \sqrt{y^*} \right) \sin(\Omega t) + \sqrt{x^*} \right\}^2, \quad (4.12)$$

$$y(t) = \left\{ \left(\frac{d_1}{b_1} \right)^{\frac{1}{2}} \left(\sqrt{x_0} - \sqrt{x^*} \right) \sin(\Omega t) + \left(\sqrt{y_0} - \sqrt{y^*} \right) \cos(\Omega t) + \sqrt{y^*} \right\}^2. \quad (4.13)$$

5. DISCUSSION

A detailed examination of Eqs. (4.12) and (4.13) allows the following conclusions to be reached:

(1) Given the initial-values, $x(0) = x_0 > 0$ and $y(0) = y_0 > 0$, Eqs. (4.12) and (4.13) are the solutions to the generalized L-V model of Eq. (3.4).

(2) The equilibrium solutions or fixed-points are given by the results in Eq. (4.3). If $x_0 = x^*$, $y_0 = y^*$, then

$$x(t) = x^*, \quad y(t) = y^* \quad (5.1)$$

(3) For $x_0 > 0$ and $y_0 > 0$, then $x(t) > 0$ and $y(t) > 0$.

(4) Note, Eq.(3.4) also has the solutions $x(t) = 0$ and $y(t) = 0$. These solutions are not contained in the analytic expressions given by Eqs. (4.12) and (4.13).

(5) All solutions with $x_0 > 0$ and $y_0 > 0$ are periodic with period T given by

$$T = \frac{2\pi}{\Omega} = \frac{4\pi}{\sqrt{b_1 d_1}}. \quad (5.2)$$

(6) For $0 < x_0 < \infty$, and $0 < y_0 < \infty$, all solutions are bounded.

The above results may be generalized if more complex prey population dynamics is included. For example, consider only the prey population and take its evolution to be determined by the relation

$$\frac{dx}{dt} = a_5 \sqrt{x} - b_5 x = F_1(x). \quad (5.3)$$

Note that if

$$0 < x_0 < \left(\frac{a_5}{b_5}\right)^2 = x_\infty, \quad (5.4)$$

then the prey population monotonically increases to the value x_∞ i.e., the prey population is bounded by x_∞ and this is its carrying capacity. The following P-P model is now possible

$$\frac{dx}{dt} = a_5 \sqrt{x} - b_5 x - c_5 \sqrt{x} \sqrt{y}, \quad \frac{dy}{dt} = -d_5 \sqrt{y} + e_5 \sqrt{x} \sqrt{y}, \quad (5.5)$$

and using the variable changes, $u = \sqrt{x}$ and $v = \sqrt{y}$, a pair of coupled, linear, constant coefficient ODE's will be obtained, and they can be solved exactly.

It is important to note that while the relationship in Eq. (5.3) is not the standard logistic equation, i.e., [2],

$$\frac{dx}{dt} = a_6 x - a_7 x^2, \quad (5.6)$$

the solutions of Eq. (5.3) have exactly the same qualitative properties as the solutions to Eq. (5.6) [5]. Consequently, Eq. (5.3) may be considered a modified or generalized logistic equation providing population growth for the prey population. This prey population dynamics is given in Eq. (5.5).

At this time, we have not investigated the effects of a predation term which includes saturation effects. The inclusion of such a term

may not allow the corresponding coupled differential equations to be exactly solvable in terms of elementary functions and it is this task that is the subject of the current paper.

It should be clear that the above methodology can also be applied to SIR diseases spread models [5]. Our next research task is to extend these techniques to three level systems where z preys on y , y preys on x , but x does not interact with z and can survive on its own in the absence of y .

REMARK

This paper is dedicated to the memory of our dear friend and colleague Professor Anthony Uyi Afuwape. In addition to being a great mathematician, he was a great mentor, researcher, and family man. We will miss him.

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