TMJM
THE MINDANAWAN
Journal of Mathematics

The Mindanawan Journal of Mathematics
Official Journal of the Department of Mathematics and Statistics
Mindanao State University-Iligan Institute of Technology
ISSN: 2094-7380 (Print) | 2783-0136 (Online)

Vol. 4 (2022), no. 2, pp. 81–90

A Qualitative Analysis on the Effects of Toxicant of the Lotka-Volterra Competition Model

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Received: 22nd December 2022 Revised: 21st January 2023

Abstract

The Lotka-Volterra competition model is a system that consists of the pair of differential equations given in (1), where the variables x and y are the competing species, and ax and by are their respective growth rates. But what happens if one of the competing species, say x, is subjected to a toxicant stress? In this paper, we study the qualitative analysis on the effects of the decrease in the birth rates and an increase in the mortality rates due to exposing one of the species in the competition under a toxicant stress. Results show that the effect of the toxicant changes only the outcome of the competition but not the stability of the equilibrium solutions. A persistence and extinction analysis can lead to indicators that can be used to assess risk in this type of a competition model.

1 Introduction

A fundamental problem faced by ecologists is that the spatial and temporal scales of which measurements are practical, are typically smaller than those at which the most important phenomena occur [4]. For example in plant ecology, the growth, survivorship, fecundity and seed dispersal of individual plants can be measured by using simple differential equations. Hence, ecological modeling is concerned with the use of mathematical model and systems analysis for description of each system [3], [2]. The Lotka–Volterra competition dynamical system is one model to consider. This model is frequently used to describe the dynamics of ecological systems in which two species interact [6]. It is a model system that consists of the pair of differential equations

$$\begin{aligned} \frac{dx}{dt} &= [a - Ax - \alpha y]x \\ \frac{dy}{dt} &= [b - By - \beta x]y \end{aligned} \tag{1}$$

with initial conditions $x(0) = x_0 > 0$ and $y(0) = y_0 > 0$. The variables x and y are the competing species and ax and by are their respective growth rates. Many studies about the

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2020 Mathematics Subject Classification: 34C60, 34D20
Keywords and Phrases: Differential equation, LV-competition model, Bernoulli equation, intraspecific competition, interspecific competition, stable solution

Lotka-Volterra model have been made since then. In particular, a persistence and extinction analysis have been established for the said model in [1], [3], and [8]. Interspecific competition of this model was studied in [7]. This type of competition refers to the competition between two or more species for some limiting resources like food, nutrients, space, mates and resting sites. It can theoretically predict the outcomes of two species. Depending on the initial size, carrying capacity and competition coefficient, either species is always the sole survivor or the two species will co-exist [7].

But what happens if one of the competing species, say x, is subjected to a toxicant stress? In this case, the growth rate of the affected species becomes a function of the toxicant concentration denoted by c_o and is called the *body burden.* Thus, the per capita growth rate x of the affected species can be written as $\frac{1}{x}\frac{dx}{dt} = a - H(c_o) - Ax - \alpha y$, where $H(c_o) = r_1 c_o$ is called a *linear dose-response function* with $r_1 > 0$, so that the new model having a toxicant stress has the following pair of equations

$$\begin{aligned} \frac{dx}{dt} &= [a - H(c_o) - Ax - \alpha y]x \\ \frac{dy}{dt} &= [b - By - \beta x]y \end{aligned} \tag{2}$$

with initial conditions $x(0) = x_0 > 0$ and $y(0) = y_0 > 0$.

This paper focuses on the qualitative analysis on the effects of the decrease in the birth rates and an increase in the mortality rates due to exposing one of the species in the competition under a toxicant stress. A persistence and extinction analysis can lead to indicators that can be used to assess risk in this type of a competition model.

2 Fundamental Concepts

Definition 2.1. [2] The *Lotka-Volteraa competition model* is a system consisting of the pair of differential equations

$$\begin{aligned} \frac{dx}{dt} &= [a - Ax - \alpha y]x \\ \frac{dy}{dt} &= [b - By - \beta x]y \end{aligned}$$

with initial conditions $x(0) = x_0 > 0$ and $y(0) = y_0 > 0$. The variables x and y are the competing species, and the ax and by are their respective growth rates.

Definition 2.2. [5] The *Bernoulli equation* is a differential equation which has the form $y' + P(x)y = Q(x)y^n$, where $n \neq 0, 1$.

Definition 2.3. [5] An *equilibrium solution* of a system of ordinary differential equation is a point (x, y) where $x' = 0$ and $y' = 0$. An equilibrium solution is a constant solution of the system and is sometimes called a *critical point.*

Definition 2.4. [5] The *stability* of an equilibrium solution is classified according to the behavior of the integral curves near it. The integral curves represent the graphs of the particular solution satisfying the initial conditions. If the nearby integral curves all converge to an equilibrium solution as t increases, then the equilibrium solution is *stable*, and if the nearby integral curves all diverge away from an equilibrium solution as t increases, then the equilibrium solution is *unstable.*

3 Main Results

3.1 The Lotka-Volterra competition model with a toxicant stress

When the LV-competition model is subjected to a toxicant stress, we may have many possible outcomes. In this study, we will focus only on the effects to a decrease in the birth rate and an increase in the mortality rate. Let x be the affected species and y be the unaffected species, so that this time, the growth rate of the affected species becomes a function of a toxicant concentration, denoted by c_o, which is also called the *body burden*. Hence, the per capita growth rate of the x species may now be written as $\frac{1}{x}\frac{dx}{dt} = a - H(c_o) - Ax - \alpha y$, where $H(c_o) = r_1 c_o$, a commonly used linear dose-response with $r_1 > 0$. There are other forms of dose-response function such as the Sigmoid dose -response function curve but here, we assume $H(c_o) = r_1 c_o$.

The first toxicant system (2) we will consider is having a constant accumulation of toxic chemical in the body of the exposed species. That is, a non-dynamic body burden c_o. Thus, we will have the pair of differential equations

$$\begin{aligned} \frac{dx}{dt} &= [a - H(c_o) - Ax - \alpha y]x \\ \frac{dy}{dt} &= [b - By - \beta x]y \end{aligned}$$

with initial conditions $x(0) = x_0 > 0$ and $y(0) = y_0 > 0$. Table 1 shows the parameters used in this section.

Table 1: Description and Definitions of Parameters

Parameter	**Dimension**	**Definition**
a	time^{-1}	ax – growth rate of x
b	time^{-1}	by – growth rate of y
A	biomass^{-1}time^{-1}	Ax – intra-specific competition rate of x
B	biomass^{-1}time^{-1}	By – intra-specific competition rate of y
α	biomass^{-1}time^{-1}	αx – inter-specific competition rate of x
β	biomass^{-1}time^{-1}	βy – inter-specific competition rate of y
c_o	$\frac{\mu\text{g}}{g \text{ tissue}}$	body burden
c_E	$\frac{\mu\text{g}}{g \text{ tissue}}$	concentration of toxicant in the environment
θ	$\frac{\mu\text{g}}{g \text{ tissue}}$	concentration of toxicant in the food
γ	time^{-1}	$\gamma\theta$ – rate of food intake

3.2 The integral representations of the competing species

Since the differential equations in the system (2) are Bernoulli type equations, then we have the following integral representations of the two competing species given by

$$x(t) = \frac{x_0 e^{\int_0^t [a - r_1 c_o - \alpha y(s)] ds}}{1 + A x_0 \int_0^t e^{\int_0^s [a - r1 c_o - \alpha y(u)] du} ds} \tag{3}$$

and

$$y(t) = \frac{y_0 e^{\int_0^t [B - \beta x(s)]ds}}{1 + By_0 \int_0^t e^{\int_0^s [B - \beta x(u)]du} ds} \tag{4}$$

The positivity and boundedness of the components follow immediately from these integral representations. The following results simply say that under what condition one species wins over the other species.

Theorem 3.1. (Extinction Theorem 1)
Assume that $\lim_{t\to+\infty} y(t) = y^*$ *exists. If* $y^* > \frac{a - r_1 c_o}{\alpha}$*, then all components have limits and*

(*i*) $\lim_{t\to+\infty} x(t) = 0$

(*ii*) $\lim_{t\to+\infty} y(t) = y^* = \frac{b}{B}$.

Proof. Using the integral representation of $x(t)$ given in (3) and taking the limit as $t \to +\infty$, then we have

$$\begin{aligned} \lim_{t\to+\infty} x(t) &= \lim_{t\to+\infty} \frac{x_0 e^{\int_0^t [a - r_1 c_o - \alpha y(s)]ds}}{1 + Ax_0 \int_0^t e^{\int_0^s [a - r1c_o - \alpha y(u)]du} ds} \\ &\leq \lim_{t\to+\infty} x_0 e^{\int_0^t [a - r_1 c_o - \alpha y(s)]ds}. \end{aligned}$$

By assumption that $y^* > \frac{a - r_1 c_o}{\alpha}$, then $\lim_{t\to+\infty} x(t) = 0$.

To establish (*ii*), consider the integral representation of $y(t)$ given in (4) and taking the limit as $t \to +\infty$, then we have

$$\begin{aligned} \lim_{t\to+\infty} y(t) &= \lim_{t\to+\infty} \frac{y_0 e^{\int_0^t [B - \beta x(s)]ds}}{1 + By_0 \int_0^t e^{\int_0^s [B - \beta x(u)]du} ds} \\ &= \lim_{t\to+\infty} \frac{y_0 e^{\int_0^t [B - \beta x(s)]ds} \frac{d}{dt}\left[\int_0^t [b - \beta x(s)]ds\right]}{By_0 \frac{d}{dt}\left[\int_0^t e^{\int_0^s [B - \beta x(u)]du} ds\right]} \end{aligned}$$

by applying L'Hôpital's Rule

$$
\begin{aligned}
&= \lim_{t\to+\infty} \frac{e^{\int_0^t [b-\beta x(s)]ds}[b-\beta x(t)]}{Be^{\int_0^t [b-\beta x(s)]ds}} \\
&= \lim_{t\to+\infty} \frac{b-\beta x(t)}{B} \\
&= \frac{b}{B}
\end{aligned}
$$

since $\lim_{t\to+\infty} x(t) = 0$. Thus, the feasible equilibrium solution $\left(0, \frac{b}{B}\right)$ is stable. □

Theorem 3.2. (Extinction Theorem 2)

Assume that $\lim_{t\to+\infty} x(t) = x^*$ *exists. If* $x^* > \frac{b}{B}$, *then all components have limits and*

(*i*) $\lim_{t\to+\infty} y(t) = 0$

(*ii*) $\lim_{t\to+\infty} x(t) = x^* = \frac{a - r_1 c_o}{A}$.

Proof. Using the integral representation of $y(t)$ given in (4) and taking the limit as $t \to +\infty$, then we have

$$
\begin{aligned}
\lim y(t) &= \lim_{t\to+\infty} \frac{y_0 e^{\int_0^t [B-\beta x(s)]ds}}{1 + By_0 \int_0^t e^{\int_0^s [B-\beta x(u)]du} ds} \\
&\leq \lim_{t\to+\infty} y_0 e^{\int_0^t [B-\beta x(s)]ds}.
\end{aligned}
$$

By assumption that $x^* > \frac{b}{B}$, then $\lim_{t\to+\infty} y(t) = 0$.

To establish (*ii*), consider the integral representation of $x(t)$ given in (3) and taking the limit as $t \to +\infty$, then we have

$$
\begin{aligned}
\lim_{t\to+\infty} x(t) &= \lim_{t\to+\infty} \frac{x_0 e^{\int_0^t [a - r_1 c_o - \alpha y(s)]ds}}{1 + Ax_0 \int_0^t e^{\int_0^s [a - r1 c_o - \alpha y(u)]du} ds} \\
&= \lim_{t\to+\infty} \frac{x_0 e^{\int_0^t [a - r_1 c_o - \alpha y(s)]ds} \frac{d}{dt}\left[\int_0^t [a - r_1 c_o - \alpha y(s)]ds\right]}{Ax_0 e^{\int_0^t [a - r_1 c_o - \alpha y(s)]ds}}
\end{aligned}
$$

by applying L'Hôpital's Rule

$$\begin{aligned} &= \lim_{t\to+\infty} \frac{a - r_1 c_o - \alpha y(t)}{A} \\ &= \frac{a - r_1 c_o - \alpha(0)}{A} \\ &= \frac{a - r_1 c_o}{A} \end{aligned}$$

since $\lim_{t\to+\infty} y(t) = 0$. Thus, the feasible equilibrium solution $\left(\frac{a - r_1 c_o}{A}, 0\right)$ is stable. □

Remark 3.3. The following are immediate.

1. The extinction condition in Theorem 3.1 simply says that y wins over x ($y >> x$) if the intraspecific competition is less. This means that the intraspecific competition among the y species is very less compared to the intraspecific competition among the x species. This is so because of the assumption that $y^* > \frac{a - r_1 c_o}{a}$.

2. Similarly, the extinction condition in Theorem 3.2 with the assumption that $x^* > \frac{b}{\beta}$ shows that the effect of the toxicant lessens much the intraspecific competition among the x species compared to the intraspecific competition among the y species. Thus, the x species wins over the y species.

3. One can verify that the equilibrium solutions $(x^*, 0)$ and $(0, y^*)$ are stable solutions.

4 Dynamics of the Body Burden

In this section, we discuss the inclusion of the body burden c_o in the system. That is, the new system contains the third component, the dynamics of the body burden c_o given in (5)

$$\begin{aligned} \frac{dx}{dt} &= [a - H(c_o) - Ax - \alpha y]x \\ \frac{dy}{dt} &= [b - By - \beta x]y \\ \frac{dc_o}{dt} &= \gamma\theta x + a_1 c_E - (L_1 + L_2)c_o \end{aligned} \tag{5}$$

with initial conditions $x(0) = x_0 > 0$, $y(0) = y_0 > 0$ and $c_o(0) > 0$. Table 2 shows the additional parameters used in this section

Table 2: Description and Definitions of Parameters

Parameter	**Dimension**	**Definition**
m_E	$***$	unit of mass of the environment
m_O	$***$	unit of mass of the organism
a_1	$m_E m_O^{-1} t^{-1}$	$a_1 c_E$ – rate of intake from environment
L_1	t^{-1}	$L_1 c_o$ – rate of egestion
L_2	t^{-1}	$L_2 c_o$ – rate of depuration

Theorem 4.1. (Persistence Theorem)
Assume that $\lim_{t\to+\infty} c_0(t) < \infty$. *If* $\dfrac{a}{r_1} > \dfrac{a_1c_E + \gamma\theta x^*}{L_1 + L_2}$ *and* $\dfrac{b}{B} > \dfrac{a - r_1c_o}{\beta}$, *then a feasible equilibrium exist with components*

(i) $\lim_{t\to+\infty} c_o(t) = c_o^* = \dfrac{a_1c_E + \gamma\theta x^*}{L_1 + L_2}$

(ii) $\lim_{t\to+\infty} x(t) = x^* = \dfrac{a - r_1c_o^* - \alpha y^*}{A}$

(iii) $\lim_{t\to+\infty} y(t) = y^* = \dfrac{b - \beta x^*}{B}$

The feasible equilibrium solution is stable.

Proof. Since the first two equations in system (5) are Bernoulli type and the last equation is linear, then the integral representations of the components are as follows:

$$x(t) = \frac{x_0 e^{\int_o^t [a - r_1c_0 - \alpha y(s)]ds}}{1 + Ax_0 \int_0^t e^{\int_0^s [a - r_1c_o - \alpha y(u)]du} ds} \tag{6}$$

$$y(t) = \frac{y_0 e^{\int_o^t [b - \beta x(s)]ds}}{1 + By_0 \int_0^t e^{\int_0^s [b - \beta x(u)]du} ds} \tag{7}$$

$$c_o(t) = e^{-(L_1+L_2)t} \int_0^t [a_1c_E + \gamma\theta x(s)] e^{(L_1+L_2)s} ds. \tag{8}$$

To establish (i), consider the integral representation of $c_o(t)$ given in (8) and taking the limit as $t \to +\infty$, then we have

$$\begin{aligned}
\lim_{t\to+\infty} c_o(t) &= \lim_{t\to+\infty} e^{-(L_1+L_2)t} \int_0^t [a_1c_E + \gamma\theta x(s)] e^{(L_1+L_2)s} ds \\
&= \lim_{t\to+\infty} \frac{\int_0^t [a_1c_E + \gamma\theta x(s)] e^{(L_1+L_2)s} ds}{e^{(L_1+L_2)t}} \\
&= \lim_{t\to+\infty} \frac{\dfrac{d}{dt}\left[\int_0^t [a_1c_E + \gamma\theta x(s)] e^{(L_1+L_2)s} ds\right]}{\dfrac{d}{dt}\left[e^{(L_1+L_2)t}\right]}
\end{aligned}$$

by applying the L'Hôpital's Rule. Now, suppose that $f'(s) = [a_1c_E + \gamma\theta x(s)]e^{(L_1+L_2)s}$. Then $\int_0^t f'(s)ds = f(s)|_0^t = f(t) - f(0)$. Moreover,

$$\frac{d}{dt}\left[\int_0^t f'(s)ds\right] = \frac{d}{dt}\left[f(s)|_0^t\right] = \frac{d}{dt}[f(t) - f(0)] = \frac{d}{dt}[f(t) - 0] = f'(t).$$

Hence,

$$\frac{d}{dt}\left[\int_0^t [a_1c_E+\gamma\theta x(s)]e^{(L_1+L_2)s}ds\right]=[a_1c_E+\gamma\theta x(s)]e^{(L_1+L_2)t}.$$

Thus,

$$\begin{aligned}
\lim_{t\to+\infty}\frac{\dfrac{d}{dt}\left[\displaystyle\int_0^t [a_1c_E+\gamma\theta x(s)]e^{(L_1+L_2)s}ds\right]}{\dfrac{d}{dt}\left[e^{(L_1+L_2)t}\right]} &= \lim_{t\to+\infty}\frac{[a_1c_E+\gamma\theta x(s)]e^{(L_1+L_2)t}}{(L_1+L_2)e^{(L_1+L_2)t}}\\
&= \lim_{t\to+\infty}\frac{[a_1c_E+\gamma\theta x(s)]}{(L_1+L_2)}\\
&= \frac{[a_1c_E+\gamma\theta \lim\limits_{t\to+\infty} x(s)]}{(L_1+L_2)}\\
&= \frac{[a_1c_E+\gamma\theta x^*]}{(L_1+L_2)}.
\end{aligned}$$

Now, let us show that $\lim\limits_{t\to+\infty} x(t)$ is finite. Since $\lim\limits_{t\to+\infty} c_o(t)=\dfrac{[a_1c_E+\gamma\theta x^*]}{(L_1+L_2)}$, we have that $\lim\limits_{t\to+\infty} x(t)=x^*=\dfrac{(L_1+L_2)c_o^*-a_1c_E}{\gamma\theta}$ is finite since c_o^* is finite.

To establish (ii), consider the integral representation of $x(t)$ given in (6). Taking the limit on both sides as $t\to+\infty$, then we have

$$\begin{aligned}
\lim_{t\to+\infty} x(t) &= \lim_{t\to+\infty}\frac{x_0e^{\int_o^t [a-r_1c_0-\alpha y(s)]ds}}{1+Ax_0\displaystyle\int_0^t e^{\int_0^s [a-r_1c_o-\alpha y(u)]du}ds}\\
&= \lim_{t\to+\infty}\frac{x_0e^{\int_o^t [a-r_1c_0-\alpha y(s)]ds}\dfrac{d}{dt}\left[\displaystyle\int_0^t [a-r_1c_o-\alpha y(s)]ds\right]}{Ax_0\dfrac{d}{dt}\left[\displaystyle\int_0^t e^{\int_0^s [a-r_1c_o-\alpha y(u)]du}ds\right]}\\
&= \lim_{t\to+\infty}\frac{x_0e^{\int_o^t [a-r_1c_0-\alpha y(s)]ds}[a-r_1c_o-\alpha y(t)]}{Ax_0e^{\int_0^s [a-r_1c_o-\alpha y(s)]ds}}\\
&= \lim_{t\to+\infty}\frac{[a-r_1c_o-\alpha y(t)]}{A}\\
&= \frac{\left[a-r_1\lim\limits_{t\to+\infty} c_o(t)-\alpha\lim\limits_{t\to+\infty} y(t)\right]}{A}\\
&= \frac{[a-r_1c_o^*-\alpha y^*]}{A}.
\end{aligned}$$

Lastly, to establish (iii), consider the integral representation of $y(t)$ given in (7). Then taking the limit as $t\to+\infty$, we have

$$
\begin{aligned}
\lim_{t\to+\infty} y(t) &= \lim_{t\to+\infty} \frac{y_0 e^{\int_o^t [b-\beta x(s)]ds}}{1 + By_0 \int_0^t e^{\int_0^s [b-\beta x(u)]du} ds} \\
&= \lim_{t\to+\infty} \frac{y_0 e^{\int_o^t [b-\beta x(s)]ds} \frac{d}{dt}\left[\int_0^t [b-\beta x(s)]ds\right]}{By_0 \frac{d}{dt}\left[\int_0^t e^{\int_0^s [b-\beta x(u)]du} ds\right]} \\
&\quad \text{by applying L'Hôpital's Rule} \\
&= \lim_{t\to+\infty} \frac{e^{\int_0^t [b-\beta x(s)]ds} [b-\beta x(t)]}{Be^{\int_0^t [b-\beta x(s)]ds}} \\
&= \lim_{t\to+\infty} \frac{b-\beta x(t)}{B} \\
&= \frac{b-\beta \lim_{t\to+\infty} x(t)}{B} \\
&= \frac{b-\beta x^*}{B}.
\end{aligned}
$$

Thus, the feasible equilibrium solution (x^*, y^*, c_o^*) is stable. □

Population dynamics, being the branch of science that studies the size of population as dynamic system has been continues to be a dominant branch of mathematical biology. One such model is the Lotka-Volterra competition model in (1). The most common application of the Lotka-Volterra model in economics is the description of concurrence in fund markets, technological competition, marketing and trade relationships [9]. Some other applications of the model are in sociology and other social sciences.

Acknowledgements

The authors are grateful to the anonymous referee for the helpful comments and suggestions.

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