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Abstract. Lotka-Volterra competition model has been applied in many areas, including in biological systems and market-share competition in economics. In this paper, we study a modified version of the two-species competition model where the growth of the first population follows the exponential growth model. The modified model has three equilibria namely the extinction equilibrium, the coexistence equilibrium, and the extinction of first population equilibrium. We found that the extinction equilibrium and the coexistence equilibrium are unstable. We also found that the extinction of the first population is conditionally asymptotically stable. Furthermore, we estimated parameters of the modified model from competition data of two Paramecium species, where the data cited from literature.

Keywords: competition model, equilibrium stability, Paramecium competition.

INTRODUCTION

Organisms live in an ecological community, a collection of populations of at least two different species that directly and indirectly interact in a particular geographical area [1]. There are several classes of interactions between organisms found in many habitats and ecosystems. Ecological interactions can be divided into two types of interactions, namely intraspecific interactions and interspecific interactions. Intraspecific interactions are interactions between individuals of the same species, whereas interactions that occur between two or more species are called interspecific interactions. Interspecific interactions include competition, predation, herbivory, and symbiosis [2].

In ecology, interspecific competition is a form of competition in which individuals from different species compete to obtain the same resources in an ecosystem. Competition is an interaction of individuals who compete to obtain shared resources where the availability of these resources is limited. Competition can also be defined as a direct or indirect interaction of organisms that leads to changes in fitness when organisms share the same resources. The impact of competition usually produces negative effects on weaker species [2]. One example of competition is the competition of leopards and lions in hunting for prey. Interspecific competition also occurs when several plant species absorb nutrients from the soil. If natural resources cannot support both populations, this can reduce the growth and survival of a population. The result is the extinction of the population in an ecosystem. The interspecific competition in populations has been formulated into a mathematical model, called the Lotka-Volterra competition model. The Lotka-Volterra competition model which describes competition of two different species is given by [3, 4]:

$$\frac{dz_1}{dt} = r_1 z_1 \left(1 - \frac{z_1}{K_1}\right) - b_1 z_1 z_2 \tag{1}$$

$$\frac{dz_2}{dt} = r_2 z_2 \left(1 - \frac{z_2}{K_2}\right) - b_2 z_1 z_2 \tag{2}$$

Here $z_1(t), z_2(t)$ are number of first species and second species respectively. Parameters r1, r2 are the growth rate, while K_1, K_2 are carrying capacity parameters of first and second species respectively. Hence the reduction rate of first species and second species due to interspecific competition are represented by b_1, b_2 parameters respectively.

Many researchers applied the Lotka-Volterra competition model to describe competition in social sciences. Lee et al. used the model to describe competition of the Korean stock market [5]. Hung et al. described retail industry competition in Taiwan by using the Lotka-Volterra model [6]. Hung et al. also employed the model to explain retailing formats competition [7]. Recently Fatmawati et al. apllied the competition model to describe competition between commercial banks and rural banks in Indonesia [8]. However in some real cases, either parameter K_1 or K_2 in the model indicate to has infinite value. Here we propose a modification of the competition mathematical model as presented in eqs. (1)-(2).

A MODIFICATION OF LOTKA-VOLTERRA COMPETITION MODEL

The modification of competition mathematical model uses the following assumptions:
(1) There are only two different species compete some natural resources in an ecosystem.
(2) There is no species migration in the system.
(3) Growth of the first species follows the exponential growth, while second species growth follows the logistic growth.
(4) Reduction rates of both species due to interspecific competition are assumed to be constant.

From the assumptions, we proposed the following modification model of interspecific competition between two different species:

$$\frac{dz_1}{dt} = r_1 z_1 - b_1 z_1 z_2 \qquad (3)$$

$$\frac{dz_2}{dt} = r_2 z_2 \left(1 - \frac{z_2}{K_2}\right) - b_2 z_1 z_2 \qquad (4)$$

The proposed model in eqs. (3)-(4) has three equilibria, namely the extinction equilibrium (P1), the coexistence equilibrium (P2) and the extinction of first population equilibrium (P3). Equilibria of the proposed model are given by:

$$P_1(z_1, z_2) = (0,0),$$
$$P_2(z_1, z_2) = \left(\frac{r_2}{b_2 b_1 K_2}(b_1 K_2 - r_1), \frac{r_1}{b_1}\right),$$
$$P_3(z_1, z_2) = (0, K_2),$$

respectively. The extinction equilibrium and the extinction of first population equilibrium are always exist, while the coexistence equilibrium P_2 exists if $r_1 < b_1 K_2$ (the growth rate of first population is lower than its removal rate due to competition). Jacobian matrix of the proposed model in eqs. (3)-(4) is given by

$$J = \begin{bmatrix} r_1 - b_1 z_2 & -b_1 z_1 \\ -b_2 z_2 & r_2 - 2r_2 \frac{z_2}{K_2} - b_2 z_1 \end{bmatrix}. \qquad (5)$$

Theorem 1 gives instability of the extinction equilibrium.

Theorem 1. *The extinction equilibrium P_1 is unconditionally unstable.*

Proof. The Jacobian matrix of the proposed model evaluated at the extinction equilibrium is given by

$$J(P_1) = \begin{bmatrix} r_1 & 0 \\ 0 & r_2 \end{bmatrix}.$$

Eigenvalues of $J(P_1)$ are $\lambda_1 = r_1, \lambda_2 = r_2$. Hence $\lambda_1, \lambda_2 > 0$. Therefore, the extinction equilibrium P_1 is unconditionally unstable. ∎

Theorem 2 gives instability of the coexistence equilibrium.

Theorem 2. *The coexistence equilibrium P_2 is unconditionally unstable.*

Proof. The coexistence equilibrium P_2 exists if $r_1 < b_1 K_2$. Hence we may assume $r_1 < b_1 K_2$. The Jacobian matrix of the proposed model evaluated at the coexistence equilibrium is given by

$$J(P_2) = \begin{bmatrix} 0 & -\frac{r_2}{b_2 K_2}(b_1 K_2 - r_1) \\ -\frac{r_1 b_2}{b_1} & -\frac{r_1 r_2}{b_1 K_2} \end{bmatrix}.$$

Eigenvalues of $J(P_2)$ are satisfy the following characteristic equation

$$\lambda^2 + \frac{r_1 r_2}{b_1 K_2} \lambda - \frac{r_2}{K_2} \frac{r_1}{b_1} (b_1 K_2 - r_1) = 0.$$

Since $-\frac{r_2}{K_2} \frac{r_1}{b_1} (b_1 K_2 - r_1) < 0$ then one of the eigenvalue of $J(P_2)$ is positive. Hence the coexistence equilibrium is unconditionally unstable. ■

Theorem 3 gives stability of the extinction of first species equilibrium.

Theorem 3. *The extinction of first species equilibrium P_3 is asymptotically stable if* $r_1 < b_1 K_2$.

Proof. Let $r_1 < b_1 K_2$. The Jacobian matrix of the proposed model evaluated at the extinction of first species equilibrium is given by

$$J(P_3) = \begin{bmatrix} r_1 - b_1 K_2 & 0 \\ -b_2 K_2 & -r_2 \end{bmatrix}.$$

Eigenvalues of $J(P_3)$ are $\lambda_1 = r_1 - b_1 K_2, \lambda_2 = -r_2$. Since $\lambda_1, \lambda_2 < 0$ then the extinction of first species is asymptotically stable. ■

APPLICATION OF THE MODIFIED COMPETITION MODEL

In this section, we apply the proposed model to describe interspecific competition between *Paramecium caudatum* and *Paramecium aurelia* species, two kind of Protozoa species. In 1934, Gause conducted some experiments to describe competition between two Protozoa species. The experimental data from Gause is shown in the Table 1. Data in the Table 1 is cited from literature [4].

TABLE 1. *Paramecium caudatum* and *Paramecium aurelia* data (number of individual/cc) [4]

Time (days)	Paramecium caudatum (z_1)	Paramecium aurelia (z_2)	Time (days)	Paramecium caudatum (z_1)	Paramecium aurelia (z_2)
0	2	2	9	15	150
1	8	4	10	12	175
2	20	29	11	9	260
3	25	66	12	12	276
4	24	141	13	6	285
5	-	162	14	9	225
6	-	219	15	3	222
7	-	153	16	0	220
8	21	162			

Here we estimate parameters of the proposed model by using Firefly algorithm. We estimate the parameters such that the mean square error (MSE)

$$MSE = \frac{1}{n_1 + n_2} \left(\sum_{i=1}^{n_1} (z_{1i} - \widehat{z_{1i}})^2 + \sum_{i=1}^{n_2} (z_{2i} - \widehat{z_{2i}})^2 \right)$$

is minimum. Here n_1, n_2 are number of observation data of Paramecium caudatum and Paramecium aurelia respectively. We estimate the parameter values by using Firefly algorithm from 20 trials. The algorithm is stopped after 100 iterations. Statistics of the MSE and the best results from the firefly algorithm are presented in the Table 2 and Table 3 respectively.

TABLE 2. Statistics of the MSE

Statistics of MSE	MSE
Minimum (The best result)	488.0929
Maximum	488.1176
Mean	488.1003
Standard deviation	0.0061

TABLE 3. Best parameters from Firefly algorithm

r_1	b_1	r_2	b_2	K_2	MSE
1.0346	0.00697	1.58997	0.01583	250.96	488.0929

By using parameters from the Table 3, we perform numerical simulation of the proposed model. In the Figure 1 and Figure 2, we present the simulation results.
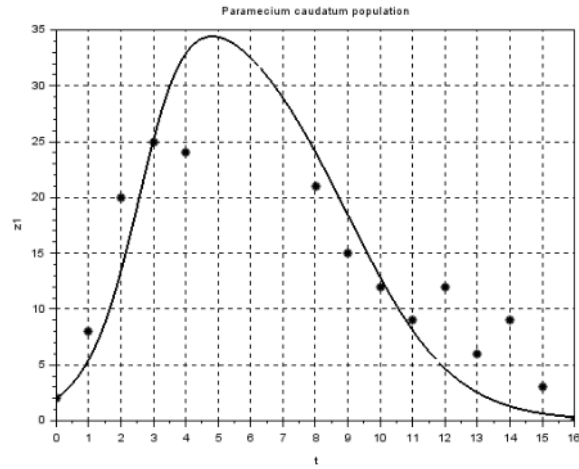

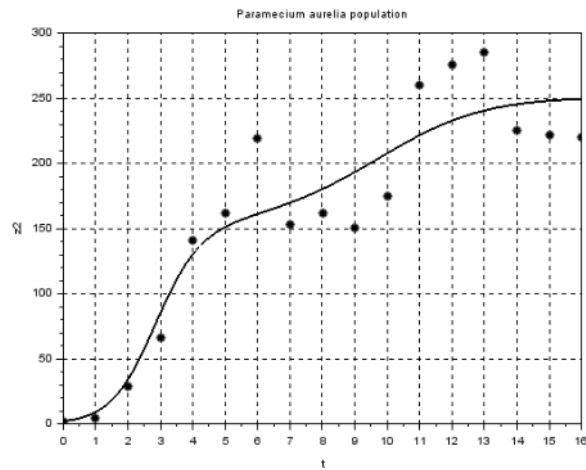**FIGURE 1.** Dynamics of *Paramecium caudatum*

FIGURE 2. Dynamics of *Paramecium aurelia*

From numerical simulation results, we found that *Paramecium caudatum* species dies, while *Paramecium aurelia* exist. This predicted results are in agreement with the data. We also found that the results from the model do not significantly differ with the data. This indicates the proposed model could be used to describe interspecific competition between *Paramecium caudatum* species and *Paramecium aurelia* species.

CONCLUSIONS

We have proposed a modification of the Lotka-Volterra competition model. We also apply the proposed model to describe *Paramecium caudatum* and *Paramecium aurelia* competition, where the data is cited from literature. Simulation results from the model are in agreement with the data. This results indicates that the proposed model can be used as an alternative model to describe interspecific competition between two different species.

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