Mathematical Analysis of the Two Species Lotka‑Volterra Predator‑Prey Inter-specific Game Theoretic Competition Model

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Abstract

Interspecies or Intraspecies competition is a natural phenomena in the real world situation. Generally two or more species compete for resources, space, territory etc. living in the same environment. For two species only the strongest prevails, driving the other competitor to extinction. It leads one species to wins as its members are more suitable for finding or exploiting resources and an opposite relation happens to the other species. All these situations can be modeled and described in terms of nonlinear differential equations in the form of game theoretic competition model. The purpose of this paper is to analyze Lotka-Volterra inter-specific competition model based on the Logistic equation. Graphical representation of steady states of the model is used to describe the completion between two species. In this study, we investigate that this model is stable at three different steady states. It is shown that the stable phenomena can be useful in studying real-world behavior.

Keywords: Mathematical model, Logistic equation, steady states, intra-specific competition, inter-specific competition.

Mathematics Subject Classifications (MSC): 34D05, 34D20, 92D25.

1 INTRODUCTION

In recent years, predator-prey models are arguably the most fundamental building blocks of the any bio-and ecosystems as all biomasses are grown out of their resource masses. Species compete, evolve and disperse often simply for the purpose of seeking resources to sustain their struggle for their very existence. Their extinctions are often the results of their failure in obtaining the minimum level of resources needed for their subsistence. Depending on their specific settings of applications, predator-prey models can take the forms of resource-consumer, plant-herbivore, parasite-host, tumor cells (virus)-immune system, etc. Mathematical models in terms of ordinary differential equation (ODE) have been widely used to model physical phenomena, engineering systems, economic behavior, biological and biomedical processes. In particular, ODE models have recently played a prominent role in describing the dynamic behavior of predator-prey systems. Interspecies or Intraspecies competition models have been the subjects central discussions in ecological and biological systems. Among the competition models, Lotka-Volterra inter-specific competition model occupies the top role to discuss the competitive behavior of the biological species which determines the present state in terms of past state and changes with the period of time. The competition models are used in forecasting of species growth rate, maximum and minimum consumption of resource, food preserving, environment capacities, and many others applications. The study of population phenomena or growth phenomena or competition between two species is really dominated problem in the biological system. Volterra (1926) first developed a competition model between a predator and a prey. In this paper, we have

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studied a game theoretic Lotka-Volterra prey-predator competition model and its solution with phase portraits and stability analysis in the equilibrium points. Then we consider two species competing with each other in a state of prey and predator. These two species compete for same resource or food or habitation etc. We have tried to find out the conditions of situations where one species dominates over the other and where they coexist. We use the steady states of the model to describe stability or instability. Finally we have discussed the two species competition model by the investigation of the steady states of the model and the stability of the model at those steady states. Further this paper gives an insight on how one species wins and another species dies.

2 METHODOLOGY
Methodology is the systematic, theoretical analysis of the methods applied to a field of study. It comprises the theoretical analysis of the body of methods and principles associated with a branch of knowledge. Typically, it encompasses concepts such as paradigm, theoretical model, phases and quantitative or qualitative techniques.

2.1 Logistic Model
The logistic model is a modification of the Malthusian model. It is also known as Verhulst model following according to the author P.F. Verhulst (1809-1849). Verhulst was a Belgian mathematician who introduced the model for human population growth in 1838. He referred to it as logistic growth; the equation given by him is called the logistic equation. We have exponential growth function as

$$\frac{dy}{dt} = ry \tag{1}$$

where, the proportional constant r is called the rate of growth depending on whether it is positive or negative. Now using the initial condition $y(0) = y_0$, we obtain the following solution

$$y = y_0 e^{rt}. \tag{2}$$

From (2), we get three important decisions.

  i.   When $r < 0$, then $y(t) = 0$.
        i.e., in the long run, the population will be extinct.
  ii.   When $r = 0$, then $y(t) = y_0$.
        i.e. constant population at the zero growth rate.
  iii. When $r > 0$, then $y(t) = \infty$.
        i.e., in the long run, the population will be a great quantity.

The last case makes the Malthusian model unrealistic for any long term prediction. Also from a biological point of view Malthusian model takes a parameter which represents the carrying capacity of the system. Carrying capacity k is the population level at which the birth and death rates of a species precisely match, resulting in a stable population over time. The general logistic equation is

$$\frac{dy}{dt} = (a - by)y \tag{3}$$

Where a is called the rate of growth or decline, b is a positive constant, y is the population at time t. It can be written as

$$\frac{dy}{dt} = a\left(1 - \frac{y}{\frac{a}{b}}\right)y$$

$$\Rightarrow \frac{dy}{dt} = a\left(1 - \frac{y}{k}\right)y \tag{4}$$

where, the constant $k = \dfrac{a}{b}$ is called the carrying capacity of that biological environment.

From (4), we get

$$\frac{dy}{dt} = ay\left(1 - \frac{y}{k}\right)$$

$$\Rightarrow dt = \frac{dy}{ay\left(1 - \frac{y}{k}\right)}.$$

Taking Partial Fraction in the R.H.S, we get

$$\Rightarrow dt = \frac{dy}{ay} + \frac{\left(\frac{1}{k}\right)dy}{a\left(1 - \frac{y}{k}\right)}$$

[Integrating both sides]

$$\Rightarrow t + c = \frac{1}{a}\ln\left(\frac{y}{1 - \frac{y}{k}}\right)$$

$$\therefore \ln\left(\frac{y}{1 - \frac{y}{k}}\right) = at + ac. \tag{5}$$

Putting the initial condition $y(t_0) = y_0$, we get

$$\ln\left(\frac{y_0}{1 - \frac{y_0}{k}}\right) = a(t_0 + c)$$

$$\Rightarrow ac = \ln\left(\frac{y_0}{1 - \frac{y_0}{k}}\right) - at_0.$$

Putting the value of ac in the equation (5), we get

$$\Rightarrow \ln\left\{\frac{y\left(1 - \frac{y_0}{k}\right)}{y_0\left(1 - \frac{y}{k}\right)}\right\} = a(t - t_0)$$

$$\Rightarrow y = \frac{y_0 k e^{a(t-t_0)}}{y_0 e^{a(t-t_0)}\left(1 + \dfrac{k - y_0}{y_0}.e^{-a(t-t_0)}\right)}$$

$$\therefore y(t) = \frac{k}{1 + e^{-a(t-t_0)}\left(\dfrac{k - y_0}{y_0}\right)}. \tag{6}$$

This is the required solution of the logistic model.
We can conclude the followings.

   (a) When the initial population is less than the carrying capacity i.e. $y_0 < k$, the population increases until it becomes the number of carrying capacity.

   (b) When the initial population and carrying capacity are the same, then there is no increase or decrease in population.

   (c) When the initial population is more than the carrying capacity, then the population decreases with time and finally it will be the same population to the carrying capacity.
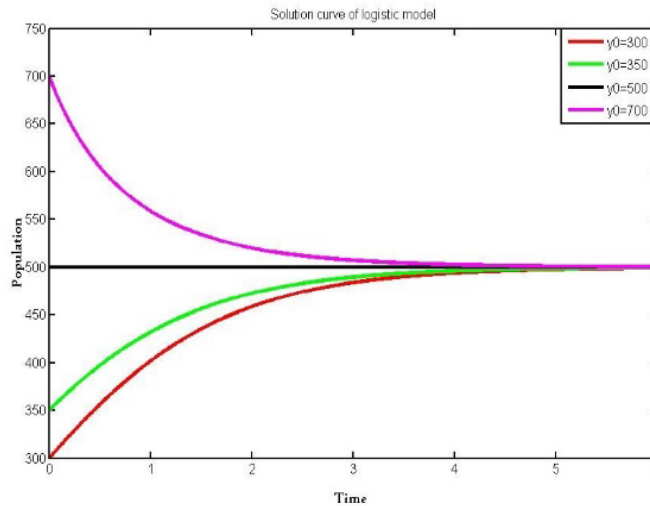

Fig 1: The solution curve of (3.11) for different initial populations y_0 with $a = 1, t_0 = 0$ and $k = 500$.

2.2 Lotka-Volterra Model

The system of predator-prey is one of the well-known models which have been studied a lot. The Lotka-Volterra predator-prey system has been modeled by Lotka and Volterra to describe the chemical interactions and predator-prey interactions respectively independently around 1926. See ([3], [6], [7], [14], [15], [18], [19], [21] and [23]) for further studies. We take the model as

$$\frac{dx}{dt} = x(a - by), \tag{7}$$

$$\frac{dy}{dt} = y(-c + dx), \tag{8}$$

where a, b, c and d are positive constants and x and y represent the abundances of prey and predator respectively.

The assumptions of the model are:

Mathematical Analysis of Two Species Inter-specific Game Theoretic Competition Model

   i.   The prey in the absence of any predation grows unboundedly in a Malthusian way; this is the ax term in (7).

  ii.   The effect of the predation is to reduce the prey's per capita growth rate by a term proportional to the prey and predator populations, this is the $-bxy$ term.

 iii.   In the absence of any prey for sustenance, the predator's death rate results in an exponential decay, that is the $-cy$ term in (8).

The prey's contribution to the predators growth rate is $dxy.$ It is proportional to the available prey as well as to the size of the predator population. The xy terms can be thought of as representing the conversion of energy from one source to another; bxy is taken from the prey and cxy accrues to the predators.

Let us first discuss the analytical solution of the model.

Dividing (7) by (8), we get

$$\frac{dx}{dy} = \frac{x(a-by)}{y(-c+dx)}$$

$$\Rightarrow \left(-\frac{c}{x}+d\right)dx = \left(\frac{a}{y}-b\right)dy. \tag{9}$$

Integrating both sides of (9), we get

$-c\ln x + d.x = a\ln y - by + \ln \lambda$, where $\ln \lambda$ is an integrating constant. This is equivalent to

$c\ln x - d.x = -a\ln y + by + \ln \lambda$

$$\Rightarrow x^c e^{-d.x} = y^{-a}e^{by}\lambda. \tag{10}$$

Now using the initial condition $x(0) = x_0$, $y(0) = y_0$ in (10), we get

$$\lambda = \frac{x_0^c e^{-d.x_0}}{y_0^{-a}e^{by_0}}$$

$$\Rightarrow \lambda = \frac{x_0^c \cdot y_0^a}{e^{(d.x_0+by_0)}}. \tag{11}$$

$\therefore$ Putting the value of λ in (10), we obtain

$$x^c e^{-d.x} = y^{-a}e^{by}\left[\frac{x_0^c y_0^a}{e^{(d.x_0+by_0)}}\right]. \tag{12}$$

This is the analytical solution of the system (7)-(8). The nonlinear behavior of prey and predator dynamics of (7) and (8) is shown in **Fig.** 2.
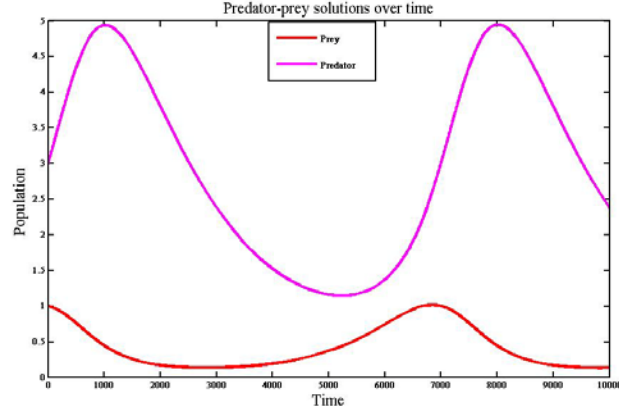
Fig. 2 Prey and predator dynamics of (7) and (8) for $a = 1.3, b = .5, c = .7$ and $d = 1.6$.

A complete phase-plane diagram of the predator prey system is shown **Fig**. 3.

Here, two isoclines $\dfrac{dx}{dt} = 0$ and $\dfrac{dy}{dt} = 0$ are drawn (the isoclines coinciding with the x- axis and y-axis have been omitted). The isoclines intersect in the neutrally stable state. Each curve completely determined by the initial state (x_0, y_0) i.e. $(1, 3)$. The integral curve is closed and we see that the populations are cyclic.
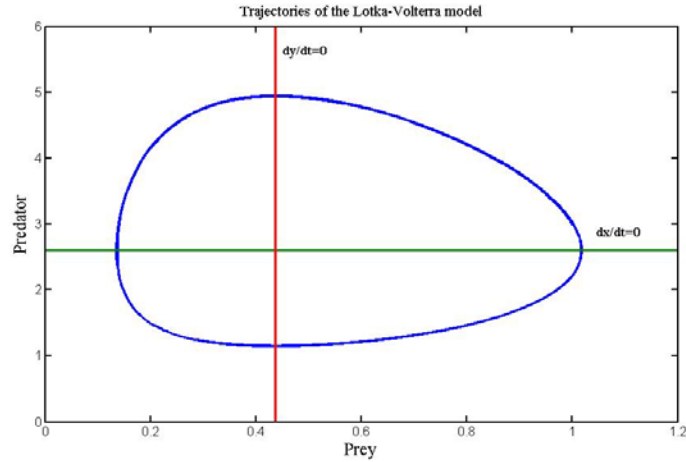

Fig. 3: The solution curves in the phase plane of the system (7) and (8) for $x_0 = 1,\ y_0 = 3,\ a = 1.3, b = .5, c = .7$ and $d = 1.6$.

Now in order to gain better understanding of the neutral stability of the original prey-predator system in which prey population have the property of self-regulation [9], we generalize the model (7) and (8) given by

$$\frac{dx}{dt} = ax\left(1 - \frac{x}{k}\right) - by\frac{x}{a_1 + x}, \tag{7a}$$

$$\frac{dy}{dt} = -cy + dy\frac{x}{a_1 + x}, \tag{8a}$$

236

Mathematical Analysis of Two Species Inter-specific Game Theoretic Competition Model

where $\dfrac{x}{a_1 + x}$ reflects the number of prey consumed per predator and a_1 is a new parameter.

Now for two pair of initial populations $(x_0 = .7, y_0 = 3)$ and $(x_0 = .2, y_0 = 6)$, the isoclines and phase portraits of two trajectories are shown in **Fig.** 4.
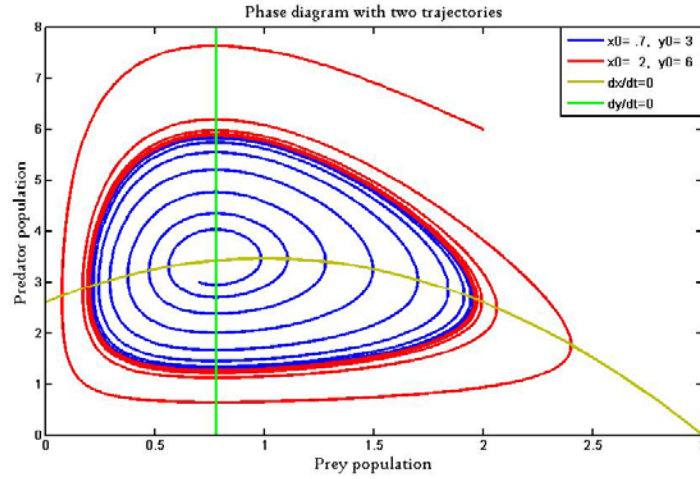

Fig. 4: Solution curves in the phase plane of (7a) and (8a) for two pair of initial populations with $a = 1.3, b = .5, c = .7, d = 1.6, a_1 = 1$ and $k = 3$.

From **Fig**. 4, we observe that when $\dfrac{dx}{dt} = 0$, the function of predator (y) is quadratic and for $\dfrac{dy}{dt} = 0$, the function of prey population (x) represents a vertical line. The interior equilibrium is given by the intersection of these functions. It is clear that for the initial populations $(x_0 = .7, y_0 = 3)$ the orbit spirals outward toward the interior equilibrium point. The orbit spirals inward toward the interior equilibrium point for the initial populations $(x_0 = .2, y_0 = 6)$.

2.3 Lotka-Volterra Inter-specific Competition Model

We recall that interspecies is the competition for food, space and shelter between different species. Intraspecies is the competition for food, space and shelter between different animals in the same species. The logistic equation in (13) defines a rate of population increase that is limited by intra-specific competition (i.e. members of the same species competing with one another).

$$\frac{dN}{dt} = rN\left(\frac{k - N}{k}\right), \tag{13}$$

where N is the population of the given species, k is the carrying capacity and r is the intrinsic rate of increase of the population. The term (rN) on the right side of (13) describes growth in the absence of competition. The second term $\left(\dfrac{k - N}{k}\right)$ incorporates intra-specific competition or density-dependence into the model and takes a value between 0 and 1. As population size (N) approaches carrying capacity (k), the numerator $(k - N)$

becomes smaller but the denominator (k) stays the same. So the second term $\left(\dfrac{k-N}{k}\right)$ decreases. The logistic equation (13) can be modified to include the effects of intra-specific competition as well as inter-specific competition. See [12], [17], [20] and [23] for details. The Lotka-Volterra model of inter-specific competition can be written by the following equations for population 1 and population 2 respectively.

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{k_1 - N_1 - a_{12} N_2}{k_1} \right), \tag{14}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{k_2 - N_2 - a_{21} N_1}{k_2} \right), \tag{15}$$

where

- $N_1 =$ Population of Species 1
- $N_2 =$ Population of Species 2
- $k_1 =$ Carrying Capacity of Species 1
- $k_2 =$ Carrying Capacity of Species 2
- $a_{12} =$ Effect of Species 2 on Species 1
- $a_{21} =$ Effect of Species 1 on Species 2
- $r_1 =$ The intrinsic rate of increase of species 1
- $r_2 =$ The intrinsic rate of increase of species 2.

The population of prey species increases in absence of predator species as the following logistic growth model

$$\frac{dN_1}{dt} = \frac{r_1 N_1 (k_1 - N_1)}{k_1}. \tag{16}$$

Similarly, the population of predator species increases in absence of prey species as the following logistic growth model

$$\frac{dN_2}{dt} = \frac{r_2 N_2 (k_2 - N_2)}{k_2}. \tag{17}$$

2.3.1 Steady States and Isoclines

The system (14) and (15) has four equilibrium points or the steady states. They are as follows

$$(\bar{N}_1, \bar{N}_2) = (0,0), \left(\frac{k_1 - k_2 a_{12}}{1 - a_{12} a_{21}}, \frac{k_2 - k_1 a_{21}}{1 - a_{12} a_{21}} \right), (0, k_2) \text{ and } (k_1, 0). \tag{18}$$

The isoclines of the system (14) and (15) are just the points that satisfy the following equations

$\dfrac{dN_1}{dt} = 0$ and $\dfrac{dN_2}{dt} = 0.$

From (14), we arrive at the N_1 isoclines as

$$N_1 = 0, \tag{19}$$

$$k_1 - N_1 - a_{12} N_2 = 0. \tag{20}$$

From (15), we arrive at the N_2 isoclines as

$$N_2 = 0, \tag{21}$$

$$k_2 - N_2 - a_{21}N_1 = 0. \tag{22}$$

To simplify the notation slightly we take (19), (20), (21) and (22) as the lines L_{1a}, L_{1b}, L_{2a} and L_{2b} respectively. Here $N_1 = 0$ and $N_2 = 0$ are just the N_2 and N_1 axes respectively whereas L_{1a} and L_{2a} intersect the axes as follows:

L_{1b} meets the axes (N_1 N_2) at $(k_1, 0)$ and $\left(0, \dfrac{k_1}{a_{12}}\right)$ respectively.

L_{2b} meets the axes (N_1 N_2) at $\left(\dfrac{k_2}{a_{21}}, 0\right)$ and $(0, k_2)$ respectively.

Now for the proper representation of isoclines, we consider the following situations.

Case i: $k_1 > \dfrac{k_2}{a_{21}}$ and $\dfrac{k_1}{a_{12}} > k_2$,

Case ii: $\dfrac{k_2}{a_{21}} > k_1$ and $k_2 > \dfrac{k_1}{a_{12}}$,

Case iii: $k_1 > \dfrac{k_2}{a_{21}}$ and $k_2 > \dfrac{k_1}{a_{12}}$,

Case iv: $\dfrac{k_2}{a_{21}} < k_1$ and $\dfrac{k_1}{a_{12}} > k_2$.

3   RESULTS AND DISCUSSIONS

We will proceed to the stability analysis of the model at steady states using the cases described in Section 4. We start with different combinations of species abundances. The abundance of species 1 is plotted on the N_1-axis and the abundance of species 2 is plotted on the N_2-axis in the N_1N_2 plane. Each state space represents a combination of abundances of the two species. For each species, there is a straight line on the graph called a zero isoclines. Now depending on the four cases, the following four graphs i.e. **Figs.** 2, 3, 4 and 5, include isoclines of both species and interpret the possible outcomes of inter-specific competition. In each graph, the solid yellow line represents the isoclines of species 1 and the dashed blue line represents the isoclines of species 2. The black arrows represent the joint trajectories of the two populations.
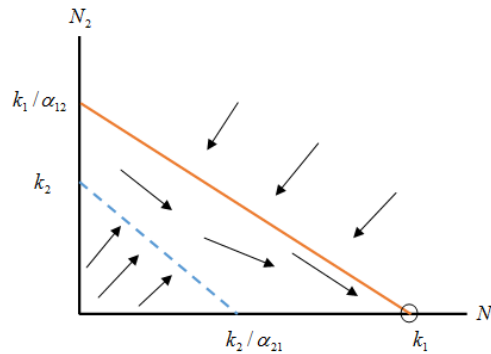
Case i:

Fig. 5: First species wins and second species dies.

From **Fig.** 5, we can see that for any point in the lower left corner of the graph (i.e. any combination of species abundances) both populations are below their respective isoclines and both increase. For any point in the upper corner of the graph, both species are above their isoclines respectively and decrease. For any point in between the two isoclines we see that species 1 is still below its isoclines and increases while species 2 is above its isoclines and decreases. The joint trajectories of the two species (black arrows) are down and to the right. So species 2 is driven to extinction and species 1 increases until it reaches its carrying capacity (k_1). The open circle at the point $(k_1, 0)$ represents a stable equilibrium. In this case, species 1 wins and species 2 dies at last.
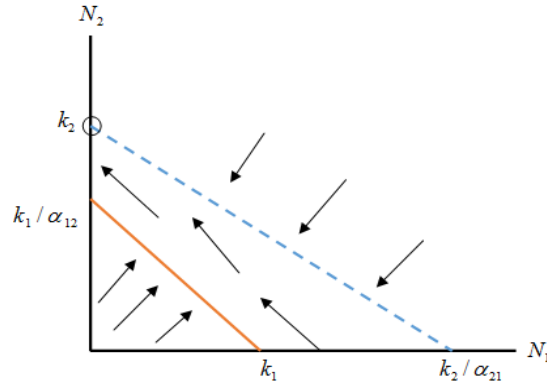
Case ii:

Fig. 6: Second species wins and first species dies.

From **Fig**. 6, we see that the **Case ii** is the opposite of the Case i. The isoclines of species 2 is above and to the right of the isoclines for species 1. Here, the joint trajectory of two populations is up and to the left in between the isoclines. The point $(0, k_2)$ represents a stable equilibrium. In this case, species 2 always wins and species 1 dies eventually.
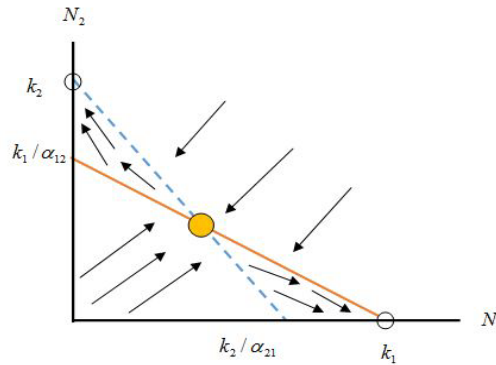
Case iii:

Fig. 7: Either species survives depending on the initial conditions.

From the **Fig**. 7, we see that the isoclines of the two species cross one another and below both isoclines and above both isoclines the populations increase and decrease respectively. There is an unstable equilibrium point (closed circle) where the isoclines intersect each other. From **Fig.** 4, it is also clear that there are two stable equilibrium points (open circles). In this case, the outcome depends on the initial abundances of the two species. For points above the isoclines of species 1 and below the isoclines of species 2, the outcome represents the stable equilibrium

point $(k_1, 0)$. On the other hand, for points above the isoclines of species 2 and below the isoclines of species 1, the outcome represents the stable equilibrium point $(0, k_2)$.
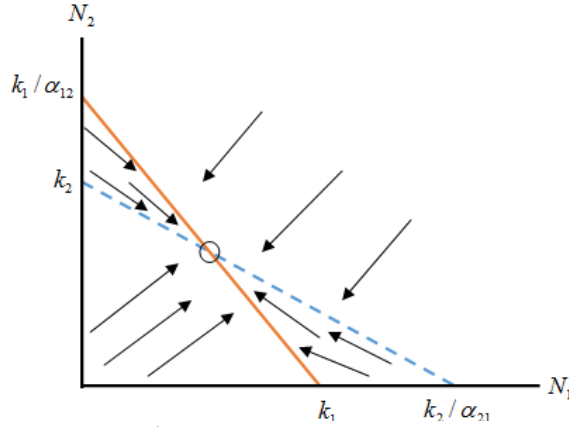
Case iv:

Fig. 5: two species coexist.

From **Fig.** 5, we see that the isoclines also cross one another like Case iii. In this case, both species carrying capacities are lower than the other's capacity divided by the competition coefficient (i.e. $k_1 < \dfrac{k_2}{a_{21}}$ and $k_2 < \dfrac{k_1}{a_{12}}$).

Again below both isoclines the populations increase and above both isoclines the populations decrease. When populations of the two species are between the isoclines their joint trajectories always head toward the intersection of the isoclines. The two species are able to coexist at this stable equilibrium point (open circle).

From above analysis, it can be shown that outcome of competition is as follows:

    a.   in Case i: only $(k_1, 0)$ is stable,

    b.   in Case ii: only $(0, k_2)$ is stable,

    c.   in Case iii: both $(k_1, 0)$ and $(0, k_2)$ are stable,

    d.   in Case iv: only the steady state $\left(\dfrac{k_1 - k_2\, a_{12}}{1 - a_{12}a_{21}}, \dfrac{k_2 - k_1\, a_{21}}{1 - a_{12}a_{21}} \right)$ is stable.

The assumptions of the model (such as there can be no migration and the carrying capacities and competition coefficients for both species are constants) may not be very realistic but are necessary for simplifications. A variety of factors not included in the model can affect the outcome of competitive interactions by affecting the dynamics of one or both populations. Environmental change, disease, and chance are just a few of these factors.

4   CONCLUSIONS

Lotka-Volterra inter-specific competition model through this paper predict that in a steady state when the two species co-exist, the first abundance is completely determined by the parameters associated with the second species. Similarly, the second species in this steady state is determined by the parameters i.e. life-history characteristic of the first species. Among the different competition models in a biological system, Lotka-Volterra inter specific model is standard model where Logistic equation gives proper situation. This study investigates the steady states which are used in describing competition. We claim that this study will play an important role in the multi-species model in the field of competition. Multi-species models would seem to be the most important topics for future research. Although, the small amount of work of this present subject has produced results that are not always initiatively obvious, further work may open the way for the general framework of competition models. We believe that

extensive and continuous involvement in mathematical biology research may result into answer many questions for the development of this topics.

5 ACKNOWLEDGEMENTS

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