A Modified Lotka-Volterra Competition Model with a Non-Linear Relationship Between Species

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Abstract

In this article, we consider a modified Lotka-Volterra competition model, which incorporates a non-linear relationship representing the interaction between species. We study the qualitative properties of this new system and compare them to the qualitative properties of the classical Lotka-Volterra equations, obtaining results suggesting that the modified model is a better representation of some biological situations.

1 Introduction

Population dynamics is a widely studied field in the area of mathematical biology. Many models have been developed in order to predict or describe the long-term growth or decline of species. Improving these models in order to make better predictions is often a topic of research. The Lotka-Volterra competition model describes two populations that affect each other in a negative fashion; for instance, they may compete for a limited shared resource. The model uses the equation,

$$\begin{cases} x'(t) = \beta_1 x(K_1 - x - \mu_1 y), \\ y'(t) = \beta_2 y(K_2 - y - \mu_2 x), \\ x(0) > 0 \; and \; y(0) > 0, \end{cases} \tag{1}$$

where β_i, K_i, μ_i, $i = 1, 2$, are positive constants [2].

Research has been conducted on many modifications of this model. For instance, one modification of the model incorporates a time-delay between birth and maturity and assumes that only adult members of each species compete [1].

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Research has also been done on a spatial stochastic version of the Lotka-Volterra equations [3].

Our research has to do with the assumption of the linear relationship between the interaction of two species in the classical model, that is, between x' and the linear function -$\mu_1 y$, and between y' and the linear function -$\mu_2 x$. What if this relationship is in fact non-linear? Can the model be modified to incorporate such a biological situation?

2 The Classical Model

The classical Lotka-Volterra competition model describes two populations, x and y, that compete for a limited shared resource using the equation (1).

According to the qualitative theory of differential equations we need to find and analyze the critical points, or points where $x'(t) = y'(t) = 0$, because these points can be used to determine the stabilities of equation (1). The critical points of equation (1) are $(0, 0)$, $(K_1, 0)$, $(0, K_2)$ and the solution to the following equation,

$$\begin{cases} x + \mu_1 y = K_1, \\ y + \mu_2 x = K_2. \end{cases} \tag{2}$$

Since x and y represent populations, negative values for x and y do not make since. Therefore we are only concerned with the solutions to equation (2) that are confined to the first quadrant. Four possible cases, shown in **Figure 1**, arise based on the straight lines defined by $x + \mu_1 y = K_1$ and $y + \mu_2 x = K_2$.

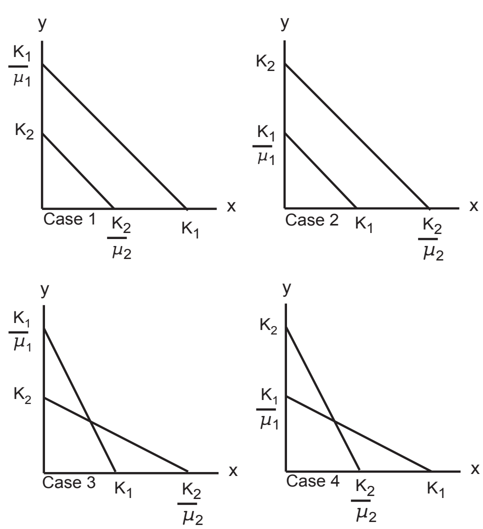

Figure 1: Four cases based on the lines defined by $x + \mu_1 y = K_1$ and $y + \mu_2 x = K_2$.

In case 1, $(K_1, 0)$ is the stable equilibrium which biologically implies population x will survive and population y will become extinct. In case 2, $(0, K_2)$ is the stable equilibrium which means population y will survive and population x will become extinct. In case 3, the stable equilibrium is the solution to equation (2). Biologically this implies that both populations will coexist. In case 4, both $(K_1, 0)$ and $(0, K_2)$ are stable equilibria and the solution to equation (2) is a saddle point, meaning the initial population values determine which population survives. The phase portraits for each case are shown in **Figure 2**.

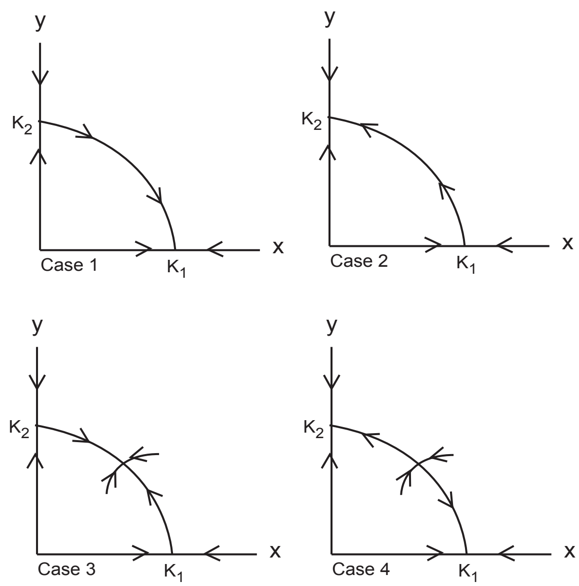

Figure 2: Phase portraits for classical Lotka-Volterra competition model.

3 Modification of the Classical Model

The classical model assumes that x' is negatively affected by the linear function -$\mu_1 y$, and y' is negatively affected by the linear function -$\mu_2 x$, that is, population y interferes with population x in a linear fashion and vice versa. Biologically it makes sense that this relationship could be non-linear, and we suppose that as the population size of x grows the population is more efficient at gathering the resource that is shared with population y thus resulting in population x having a larger effect on population y. On the other hand, if population x is very small it may be very inefficient at gathering the shared resource and hence population x has a smaller effect on population y.

Consider the graphs of x and x^2. When $0 < x < 1$, $x^2 < x$ and when $x > 1$, $x^2 > x$. The equation below is a modification of the classical Lotka-Volterra model which suggests a non-linear effect of population y on population x and vice versa,

$$\begin{cases} x'(t) = \beta_1 x(K_1 - x - \mu_1 y^2), \\ y'(t) = \beta_2 y(K_2 - y - \mu_2 x^2), \\ x(0) > 0 \; and \; y(0) > 0, \end{cases} \tag{3}$$

where again β_i, K_i, μ_i, $i = 1, 2$, are positive constants. The modified model is more realistic than the classic model because in the modified model, if population x is very small (less than 1) then it has a smaller effect on population y and if population x is greater than 1 then it has a larger effect on population y and vice versa, where 1 is regarded as some "threshold" in a certain biology application.

We will see that making a change from the linear relationship to the non-linear relationship creates a lot of difficulties, as is typical when moving from the study of linear problems to the study of non-linear problems. However, by using some advanced results in the qualitative theory of differential equations along with a geometric argument, we can still provide a complete analysis for the modified model and derive phase portraits.

4 Analysis of the Modified Model

Lemma 1. *If a solution to equation (3) starts in the first quadrant it must stay in the first quadrant.*

Proof. On the $y = 0$ line $y'(t) = 0$, therefore a solution of equation (3) cannot cross the $y = 0$ line. Similarly on the $x = 0$ line $x'(t) = 0$, therefore a solution of equation (3) cannot cross the $x = 0$ line. □

Now $(K_1, 0)$, $(0, K_2)$, and $(0, 0)$ are critical points of equation (3) along with the non-negative solutions of the equation,

$$\begin{cases} x + \mu_1 y^2 = K_1, \\ y + \mu_2 x^2 = K_2. \end{cases} \tag{4}$$

Comparatively to the original model there are four cases that follow based on the curves defined by $x + \mu_1 y^2 = K_1$ and $y + \mu_2 x^2 = K_2$. See **figure 3**.

In cases 3 and 4, the fourth critical point, denoted (x_c, y_c), occurs in the first quadrant. Finding this critical point requires solving a fourth degree polynomial that can be derived by using equation (4),

$$\mu_1^2 \mu_2 y_c^4 - 2K_1 \mu_1 \mu_2 y_c^2 + y_c + \mu_2 K_1^2 - K_2 = 0. \tag{5}$$

Equation (5) cannot be solved for y_c using coefficients. Thus we use the relationships given in equation (4) for the fourth critical point. This is different from the classical Lotka-Volterra model where the fourth critical point can be solved from linear equation (2).

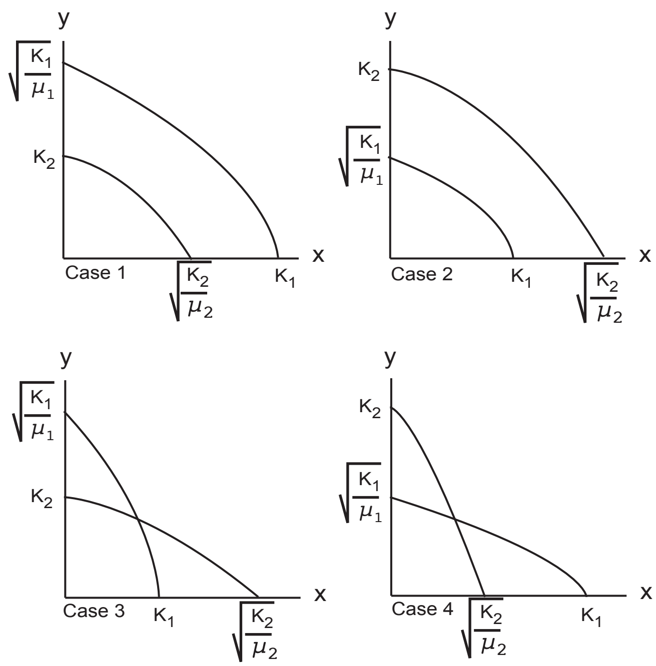

Figure 3: Four cases based on the curves defined by $x + \mu_1 y^2 = K_1$ and $y + \mu_2 x^2 = K_2$.

We now shift the critical points to the origin $(0, 0)$ in order to apply the available results in the qualitative theory of differential equations concerning the stability of the origin. This is done by denoting one of the four critical points as (x_c, y_c) and changing the variables $\overline{x} = x - x_c$ and $\overline{y} = y - y_c$ to derive the equation

$$\begin{cases} \overline{x}'(t) = \beta_1(\overline{x} + x_c)(K_1 - (\overline{x} + x_c) - \mu_1(\overline{y} + y_c)^2), \\ \overline{y}'(t) = \beta_2(\overline{y} + y_c)(K_2 - (\overline{y} + y_c) - \mu_2(\overline{x} + x_c)^2). \end{cases} \tag{6}$$

After expanding equation (6) the following equation is derived,

$$\begin{cases} \overline{x}'(t) = \beta_1(K_1 - 2x_c - \mu_1 y_c^2)\overline{x} - 2\beta_1\mu_1 x_c y_c \overline{y} - \beta_1(\overline{x}^2 + \mu_1 \overline{x}\overline{y}^2 + 2\mu_1 y_c \overline{x}\overline{y} + \mu_1 x_c \overline{y}^2), \\ \overline{y}'(t) = \beta_2(K_2 - 2y_c - \mu_2 x_c^2)\overline{y} - 2\beta_2\mu_2 x_c y_c \overline{x} - \beta_2(\overline{y}^2 + \mu_2 \overline{y}\overline{x}^2 + 2\mu_2 x_c \overline{x}\overline{y} + \mu_2 y_c \overline{x}^2), \end{cases} \tag{7}$$

where (0,0) is a critical point for equation (7) which corresponds to the critical point (x_c, y_c) for equation (3).

To show that equation (7) is an almost linear system, let

$$\begin{cases} f(\overline{x}, \overline{y}) = -\beta_1(\overline{x}^2 + \mu_1 \overline{x}\overline{y}^2 + 2\mu_1 y_c \overline{x}\overline{y} + \mu_1 x_c \overline{y}^2), \\ g(\overline{x}, \overline{y}) = -\beta_2(\overline{y}^2 + \mu_2 \overline{y}\overline{x}^2 + 2\mu_2 x_c \overline{x}\overline{y} + \mu_2 y_c \overline{x}^2), \end{cases}$$

and show that $\frac{\mathrm{f}(\overline{\mathrm{x}},\overline{\mathrm{y}})}{\sqrt{(\overline{\mathrm{x}}^2+\overline{\mathrm{y}}^2)}} \to 0$ and $\frac{\mathrm{g}(\overline{\mathrm{x}},\overline{\mathrm{y}})}{\sqrt{(\overline{\mathrm{x}}^2+\overline{\mathrm{y}}^2)}} \to 0$ as $\sqrt{(\overline{x}^2+\overline{y}^2)} \to 0$.

To do this we will show that each term in $\frac{\mathrm{f}(\overline{\mathrm{x}},\overline{\mathrm{y}})}{\sqrt{(\overline{\mathrm{x}}^2+\overline{\mathrm{y}}^2)}}$ goes to zero. The first term, $\frac{\overline{\mathrm{x}}^2}{\sqrt{(\overline{\mathrm{x}}^2+\overline{\mathrm{y}}^2)}}$, goes to zero because as $\sqrt{(\overline{x}^2+\overline{y}^2)} \to 0, \overline{x} \to 0$ and $0 \leq \frac{\overline{\mathrm{x}}^2}{\sqrt{\overline{\mathrm{x}}^2+\overline{\mathrm{y}}^2}} \leq \frac{\overline{\mathrm{x}}^2}{\sqrt{\overline{\mathrm{x}}^2}} = \overline{x}$, so $\frac{\overline{\mathrm{x}}^2}{\sqrt{\overline{\mathrm{x}}^2+\overline{\mathrm{y}}^2}} \to 0$. The second term, $\frac{\overline{\mathrm{xy}}^2}{\sqrt{\overline{\mathrm{x}}^2+\overline{\mathrm{y}}^2}}$, goes to zero because as $\sqrt{(\overline{x}^2+\overline{y}^2)} \to 0$, $\overline{xy} \to 0$, and $0 \leq \frac{\overline{\mathrm{xy}}^2}{\sqrt{\overline{\mathrm{x}}^2+\overline{\mathrm{y}}^2}} \leq \frac{\overline{\mathrm{xy}}^2}{\sqrt{\overline{\mathrm{y}}^2}} = \overline{xy}$, which implies that $\frac{\overline{\mathrm{xy}}^2}{\sqrt{\overline{\mathrm{x}}^2+\overline{\mathrm{y}}^2}} \to 0$. Analyzing the third term, $\frac{\overline{\mathrm{xy}}}{\sqrt{\overline{\mathrm{x}}^2+\overline{\mathrm{y}}^2}}$, goes to zero because as $\sqrt{(\overline{x}^2+\overline{y}^2)} \to 0$, $\frac{\sqrt{\overline{\mathrm{xy}}}}{\sqrt{2}} \to 0$, and $0 \leq \frac{\overline{\mathrm{xy}}}{\sqrt{\overline{\mathrm{x}}^2+\overline{\mathrm{y}}^2}} \leq \frac{\overline{\mathrm{xy}}}{\sqrt{2\overline{\mathrm{xy}}}} = \frac{\sqrt{\overline{\mathrm{xy}}}}{\sqrt{2}}$, which implies that $\frac{\overline{\mathrm{xy}}}{\sqrt{\overline{\mathrm{x}}^2+\overline{\mathrm{y}}^2}} \to 0$. Similarly it can be shown that the last term of $\frac{\mathrm{f}(\overline{\mathrm{x}},\overline{\mathrm{y}})}{\sqrt{(\overline{\mathrm{x}}^2+\overline{\mathrm{y}}^2)}}$ and all of the terms of $\frac{\mathrm{g}(\overline{\mathrm{x}},\overline{\mathrm{y}})}{\sqrt{(\overline{\mathrm{x}}^2+\overline{\mathrm{y}}^2)}}$ go to 0 as $\sqrt{(\overline{x}^2+\overline{y}^2)} \to 0$. Therefore the system is almost linear and so, for our purposes, stability properties of the linear system can be extended to the non-linear system.

We obtain the matrix of linearization for equation (7) by finding the Jacobian matrix of the system, which is

$$\begin{pmatrix} \beta_1(K_1 - 2x_c - \mu_1 y_c^2) & -2\beta_1\mu_1 x_c y_c \\ -2\beta_2\mu_2 x_c y_c & \beta_2(K_2 - 2y_c - \mu_2 x_c^2) \end{pmatrix}.$$

The local qualitative properties at each critical point can be found by evaluating the matrix of linearization at each critical point and finding the eigenvalues of the resulting matrix.

Evaluating the matrix of linearization at the critical point $(x_c, y_c) = (0, 0)$ gives the following matrix,

$$\begin{pmatrix} \beta_1 K_1 & 0 \\ 0 & \beta_2 K_2 \end{pmatrix}.$$

This matrix is a diagonal matrix whose eigenvalues are on the diagonal. Since each parameter is always positive this results in two positive eigenvalues. Thus, the critical point occuring at $(0, 0)$ is always unstable.

At the critical point $(x_c, y_c) = (K_1, 0)$ the matrix of linearlization becomes

$$\begin{pmatrix} -\beta_1 K_1 & 0 \\ 0 & \beta_2(K_2 - \mu_2 K_1^2) \end{pmatrix},$$

which is a diagonal matrix with one eigenvalue, namely $-\beta_1 K_1$, always being negative. When $K_2 - \mu_2 K_1^2 < 0$ the second eigenvalue is negative and therefore $(K_1, 0)$ is a stable equilibrium. When $K_2 - \mu_2 K_1^2 > 0$ the second eigenvalue is positive and therefore $(K_1, 0)$ is a saddle point. In the case that $K_2 - \mu_2 K_1^2 = 0$, $\overline{x} \to 0$ and $\overline{y}$ is constant which implies that $x \to x_c = K_1$ and y is constant. This case is not intersesting biologically since y is constant.

When the critical point $(x_c, y_c) = (0, K_2)$ is used the matrix of linearization becomes

$$\begin{pmatrix} \beta_1(K_1 - \mu_1 K_2^2) & 0 \\ 0 & -\beta_2 K_2 \end{pmatrix}.$$

This matrix is also diagonal with one eigenvalue, namely $-\beta_2 K_2$, always being negative. When $K_1 - \mu_1 K_2^2 < 0$ the second eigenvalue is negative and therefore $(0, K_2)$ is a stable equilibrium. When $K_1 - \mu_1 K_2^2 > 0$ the second eigenvalue is positive and therefore $(0, K_2)$ is a saddle point. In the case that $K_1 - \mu_1 K_2^2 = 0$, $\overline{x}$ is constant and $\overline{y} \to 0$ which implies that x is constant and $y \to y_c = K_2$. This case is not intersesting biologically since x is constant.

The analysis of the fourth critical point will be given later.

4.1 Case by Case Analysis

In the analysis of the modified model the following theorems will be useful:

Theorem 1 [2] *Every periodic orbit in $\Re^2$ has a critical point inside its interior.*

Theorem 2 (Poincaré-Bendixson Theorem) [2] *If a trajectory $x(t,p)$ of the equation,*

$$x'(t) = kx(t), \;\; x(t_0) = x_0,$$

is bounded in $\Re^2$ for $t \geq 0$ (the corresponding results for $t \leq 0$ are also true), then one of the following three things must happen.

1. *there exists a sequence of points on the trajectory as $t \to \infty$ that approaches a critical point,*
2. *$x(t,p)$ is a periodic orbit,*
3. *$\omega(t)$ is a periodic orbit, and $x(t,p)$ approaches $\omega(p)$ spirally as $t \to \infty$, where $\omega(t)$ is the set such that each point of $\omega(t)$ is a limit of some sequence of points on the trajectory as $t \to \infty$.*

Theorem 3 (Bendixson-Dulac's Criterion) [2] *Let $P(x,y)$, $Q(x,y)$, and $B(x,y)$ have continuous first partial derivatives in a simply connected domain $D \subset \Re^2$ and assume that $\frac{\partial(\mathrm{PB})}{\partial \mathrm{x}} + \frac{\partial(\mathrm{QB})}{\partial \mathrm{y}}$ is not identically zero and does not change sign in any open set of D. Then the equation,*

$$\begin{cases} x'(t) = P(x(t), y(t)), \\ y'(t) = Q(x(t), y(t)), \; x, \; y, \; t \in \Re. \end{cases}$$

has no periodic orbit in D.

Case 1. (see figure (3)) $\sqrt{\frac{\mathrm{K}_2}{\mu_2}} < K_1$ and $\sqrt{\frac{\mathrm{K}_1}{\mu_1}} > K_2$. Now, $(K_1, 0)$ is a stable equilibrium and $(0, K_2)$ is a saddle point. In this case, the critical point that is the solution to equation (4) is not in the first quadrant. Using theorem 1, since there is no critical point in the interior of the first quadrant then a periodic orbit cannot exist in the first quadrant. Furthermore, if a point (x, y) is in the first quadrant and above the curves defined by $x + \mu_1 y^2 = K_1$ and $y + \mu_2 x^2 = K_2$ then one has $x + \mu_1 y^2 > K_1$ and $y + \mu_2 x^2 > K_2$. From these inequalities we obtain $x' < 0$ and $y' < 0$ at the point (x, y) above the curves. Therefore, the solutions in the first quadrant must be bounded. Furthermore, since solutions started in the first quadrant must remain in the first quadrant by Lemma 1, every trajectory started in the first quadrant, except those starting with $x = 0$, will tend toward the stable node $(K_1, 0)$ by using the Poincaré-Bendixson theorem (Theorem 2). Thus population x survives and population y becomes extinct: $\lim_{t\to\infty} x(t) = K_1$ and $\lim_{t\to\infty} y(t) = 0$.

Case 2. (see figure (3)) $\sqrt{\frac{\mathrm{K_2}}{\mu_2}} > K_1$ and $\sqrt{\frac{\mathrm{K_1}}{\mu_1}} < K_2$. For this case, $(K_1, 0)$ is a saddle point and $(0, K_2)$ is a stable equilibrium. Similarly to case 1, there is no periodic orbit in the first quadrant and the solutions in the first quadrant are bounded. Therefore, every trajectory started in the first quadrant, except those that initially have $y = 0$, will tend to the stable equilibrium $(0, K_2)$. Thus population y survives and population x becomes extinct: $\lim_{t\to\infty} y(t) = K_2$ and $\lim_{t\to\infty} x(t) = 0$.

Case 3. (see figure (3)) $\sqrt{\frac{\mathrm{K_2}}{\mu_2}} > K_1$ and $\sqrt{\frac{\mathrm{K_1}}{\mu_1}} > K_2$. Now $(K_1, 0)$ and $(0, K_2)$ are both saddle points. The fourth critical point, (x_c, y_c), that is the solution to equation (4) is now in the first quadrant. To show that there is no periodic orbit in the first quadrant we use the Bendixson-Dulac's criterion (Theorem 3).

Choose the domain to be the interior of the first quadrant and let $B(x, y) = \frac{1}{\mathrm{xy}}$. Then with $P(x, y) = \beta_1 x(K_1 - x - \mu_1 y^2)$ and $Q(x, y) = \beta_2 y(K_2 - y - \mu_2 x^2)$:

$$\frac{\partial(\mathrm{PB})}{\partial \mathrm{x}} = \frac{-\beta_1}{\mathrm{y}},$$
$$\frac{\partial(\mathrm{QB})}{\partial \mathrm{y}} = \frac{-\beta_2}{\mathrm{x}},$$
$$\frac{\partial(\mathrm{PB})}{\partial \mathrm{x}} + \frac{\partial(\mathrm{QB})}{\partial \mathrm{y}} = -\left(\frac{\beta_1}{\mathrm{y}} + \frac{\beta_2}{\mathrm{x}}\right) < 0 \ \forall \ (x, y) \ \epsilon \ D,$$

therefore by the Bendixson-Dulac's criterion (Theorem 3), there are no periodic orbits in the first quadrant. As in case 1, every trajectory started within the first quadrant must stay in the first quadrant and is bounded.

The critical point located in the interior of the first quadrant satisfies the conditions in equation (4) and the matrix of linearization evaluated at this critical point simplifies to

$$\begin{pmatrix} -\beta_1 x_c & -2\beta_1\mu_1 x_c y_c \\ -2\beta_2\mu_2 x_c y_c & -\beta_2 y_c \end{pmatrix}.$$

This matrix has the characteristic polynomial

$$\lambda^2 + (\beta_1 x_c + \beta_2 y_c)\lambda + \beta_1\beta_2 x_c y_c (1 - 4\mu_1\mu_2 x_c y_c), \tag{8}$$

whose roots are the eigenvalues

$$
\begin{aligned}
\lambda &= \frac{-(\beta_1 \mathrm{x_c} + \beta_2 \mathrm{y_c}) \pm \sqrt{(\beta_1 \mathrm{x_c} + \beta_2 \mathrm{y_c})^2 - 4\beta_1\beta_2 \mathrm{x_c}\mathrm{y_c}(1 - 4\mu_1\mu_2 \mathrm{x_c}\mathrm{y_c})}}{2} \\
&= \frac{-(\beta_1 \mathrm{x_c} + \beta_2 \mathrm{y_c}) \pm \sqrt{(\beta_1 \mathrm{x_c} - \beta_2 \mathrm{y_c})^2 + 16\beta_1\beta_2\mu_1\mu_2 \mathrm{x_c^2}\mathrm{y_c^2}}}{2}. \qquad (9)
\end{aligned}
$$

Since $(\beta_1 x_c - \beta_2 y_c)^2 + 16\mu_1\mu_2 x_c^2 y_c^2 > 0$ there are two distinct, real eigenvalues.

Using the quadratic form (9) or Descarteś Rule of Signs for the roots of (8), we see that the sign of $1 - 4\mu_1\mu_2 x_c y_c$ determines the signs of the eigenvalues. However, it seems that the sign of $1 - 4\mu_1\mu_2 x_c y_c$ cannot be determined directly using $\sqrt{\frac{\mathrm{K_2}}{\mu_2}} > K_1$ and $\sqrt{\frac{\mathrm{K_1}}{\mu_1}} > K_2$ in case 3. This is a significant difference from the classical model, where the signs of the eigenvalues are immediate consequences of the corresponding cases. Therefore, in the following analysis we will use some advanced results in the qualitative theory of differential equations to determine the sign of $1 - 4\mu_1\mu_2 x_c y_c$ indirectly.

If $1 - 4\mu_1\mu_2 x_c y_c = 0$ then the characteristic equation becomes

$$
\lambda^2 + (\beta_1 x_c + \beta_2 y_c)\lambda = 0. \qquad (10)
$$

Equation (10) gives eigenvalues of $\lambda_1 = 0$ and $\lambda_2 = -(\beta_1 x_c + \beta_2 y_c)$. To find the solutions to $\overline{x}(t)$ and $\overline{y}(t)$ we use the theory of differential equations and transform the linearization of equation (7) to

$$
\begin{pmatrix} v \\ w \end{pmatrix}' = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix} \begin{pmatrix} v \\ w \end{pmatrix} = \begin{pmatrix} 0 & 0 \\ 0 & -\beta_1 x_c - \beta_2 y_c \end{pmatrix} \begin{pmatrix} v \\ w \end{pmatrix}, \qquad (11)
$$

which gives the solution

$$
\begin{cases} v = v_0, \\ w = w_0 e^{-(\beta_1 x_c + \beta_2 y_c)t}. \end{cases} \qquad (12)
$$

The solution of the simpler system (11), which is given in (12), along with the transformation matrix P can be used to give the solution through the relationship $[\overline{x}(t), \overline{y}(t)]^T = P[v(t), w(t)]$. The tranformation matrix P is made up of eigenvectors that correspond to λ_1 and λ_2. An eigenvector for λ_1 is $[1, -2\mu_2 x_c]^T$ and an eigenvector for λ_2 is $[1, \frac{2\mu_2\beta_2 \mathrm{y_c}}{\beta_1}]^T$. These eigenvectors give the matrix

$$
P = \begin{pmatrix} 1 & 1 \\ -2\mu_2 x_c & \frac{2\mu_2\beta_2 \mathrm{y_c}}{\beta_1} \end{pmatrix}.
$$

$P[v(t), w(t)]$ gives the solution

$$
\begin{cases} \overline{x}(t) = v_0 + w_0 e^{-(\beta_1 x_c + \beta_2 y_c)t}, \\ \overline{y}(t) = -2\mu_2 x_c v_0 + (\frac{2\mu_2\beta_2 \mathrm{y_c}}{\beta_1}) w_0 e^{-(\beta_1 x_c + \beta_2 y_c)t}. \end{cases} \qquad (13)
$$

As $t \to \infty$, $\overline{x}(t)$ will go to v_0 and $\overline{y}(t)$ will go to $-2\mu_2 x_c v_0$. Thus since $x = \overline{x} + x_c$ and $y = \overline{y} + y_c$, $x(t) \to v_0 + x_c$ and $y(t) \to -2\mu_2 x_c v_0 + y_c$. By the

Poincaré-Bendixson theorem, there exists a sequence of points on the trajectory $(x(t), y(t))$ that approaches a critical point, since scenarios 2 and 3 are ruled out because there is no periodic orbit. Since all other critical points are unstable this particular critical point must be (x_c, y_c). So there exists t_m such that as $t_m \to \infty$, $x(t_m) \to x_c$ and $y(t_m) \to y_c$. Therefore as $t_m \to \infty$, $x(t_m) \to v_0 + x_c = x_c$ and $y(t_m) \to -2\mu_2 x_c v_0 + y_c = y_c$, which implies $v_0 = 0$. The initial value of v, v_0, does not have to be 0, so we have reached a contradiction and therefore $1 - 4\mu_1\mu_2 x_c y_c \neq 0$.

Suppose $1 - 4\mu_1\mu_2 x_c y_c < 0$, which by Descarteś Rule of Sign's gives one positive and one negative root of polynomial (8), and thus there is one positive and one negative eigenvalue. Using similar analysis as the case $1 - 4\mu_1\mu_2 x_c y_c = 0$, the origin of the transformed system behaves as a saddle point, so there exists a trajectory $(x(t), y(t))$ that goes away from (x_c, y_c) for large t values. As before, by the Poincaré-Bendixson theorem there exists a sequence of points on the trajectory $(x(t), y(t))$ that approach a critical point. But the other two critical points, $(K_1, 0)$ and $(0, K_2)$, are saddle points that attract only the trajectories on the x-axis and y-axis respectively, so this critical point must be (x_c, y_c). This is a contradiction to the critical point (x_c, y_c) behaving as a saddle point and therefore $1 - 4\mu_1\mu_2 x_c y_c \not< 0$.

Since $1 - 4\mu_1\mu_2 x_c y_c \neq 0$ and $1 - 4\mu_1\mu_2 x_c y_c \not< 0$, $1 - 4\mu_1\mu_2 x_c y_c$ must be greater than 0. Using Descarteś Rule of Signs again this gives two negative roots of polynomial (8), or two negative eigenvalues and thus the fourth critical point is stable.

This result can also be seen geometrically in **Figure 4**.

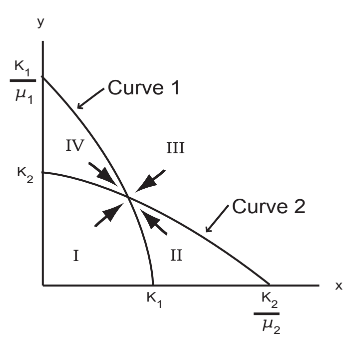

Figure 4: Case 3.

For a point (x,y) in region I of figure (4) we have the relationships $x + \mu_1 y^2 < K_1$ and $y + \mu_2 x^2 < K_2$. These inequalities imply that for any point in this region $x'(t) > 0$ and $y'(t) > 0$. For a point (x,y) in region II we have the relationships $x + \mu_1 y^2 > K_1$ and $y + \mu_2 x^2 < K_2$, which imply that $x'(t) < 0$ and $y'(t) > 0$ for any point in this region. For a point (x,y) in region III we have the relationships $x + \mu_1 y^2 > K_1$ and $y + \mu_2 x^2 > K_2$, consequently for any point in this region, $x'(t) < 0$ and $y'(t) < 0$. For a point (x,y) in region IV we have the relationships

$x + \mu_1 y^2 < K_1$ and $y + \mu_2 x^2 > K_2$, and thus for any point in this region, $x'(t) > 0$ and $y'(t) < 0$.

Note that in figure (4) curve 1 is a null cline where $x'(t) = 0$ and curve 2 is a null cline where $y'(t) = 0$. The equilibrium point (x_c, y_c) is the intersection of curve 1 and curve 2. If a trajectory crosses curve 1 it must cross it vertically. For any trajectory that crosses curve 1 where $y > y_c$, the trajectory must cross curve 1 vertically in the downward direction and for any trajectory that crosses curve 1 where $y < y_c$, the trajectory must cross curve 1 vertically in the upward direction. Similarly curve 2 must be crossed horizontally. For any trajectory that crosses curve 2 where $x < x_c$, curve 2 must be crossed horizontally going toward the positive x direction and for any trajectory that crosses curve 2 where $x > x_c$, curve 2 must be crossed horizontally going toward the negative x direction.

This implies that solutions that start in regions II or IV are bounded in the region they originated and flow to (x_c, y_c). Depending on initial conditions, a solution that starts in region I can either remain in region I or go into regions II or IV. If it remains in region I it must tend toward (x_c, y_c). If it crosses into region II or IV, then once in those regions they can be regarded as started from those regions so the trajectories flow to (x_c, y_c). Similar analysis leads to trajectories beginning in region III flowing to (x_c, y_c) as well, suggesting that the critical point (x_c, y_c) is a stable equilibrium. Therefore any trajectory started in the first quadrant, except those in which $x = 0$ or $y = 0$, will go to (x_c, y_c). This gives rise to the coexistence of both populations.

Case 4. (see figure (3)) $\sqrt{\frac{K_2}{\mu_2}} < K_1$ and $\sqrt{\frac{K_1}{\mu_1}} < K_2$. Now $(K_1, 0)$ and $(0, K_2)$ are both stable equilibria. Similarly to case 3 it can be shown by Bendixson-Dulac's criterion that there are no periodic orbits inside of the first quadrant. If $1 - 4\mu_1\mu_2 x_c y_c > 0$ the critical point inside of the first quadrant is a stable equilibrium and if $1 - 4\mu_1\mu_2 x_c y_c < 0$ the critical point inside of the first quadrant is a saddle point. We could not use the conditions on the parameters for this case to determine which of these scenarios would occur so we will resort to looking at it geometrically, as we did in the supporting geometric argument for case 3. See **Figure 5**.

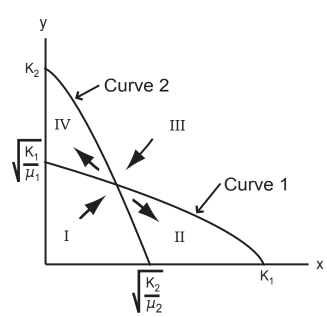

Figure 5: Case 4.

Similarly to case 3, it can be shown that in region I of figure (5), $x'(t) > 0$ and $y'(t) > 0$; in region II $x'(t) > 0$ and $y'(t) < 0$; in region III $x'(t) < 0$ and $y'(t) < 0$; and in region IV $x'(t) < 0$ and $y'(t) > 0$. Note that solutions that start in regions II and IV flow away from the equlibrium point (x_c, y_c). This implies that the critical point (x_c, y_c) is an unstable point. Biologically since $(K_1, 0)$ and $(0, K_2)$ are both stable equilibria, this means that depending on initial population values either population x will survive and population y will become extinct or vice versa.

The phase portraits for the four cases are similar to those in **Figure 2**. Trajectories are given in **Figure 6** using Maple, which match our analysis.

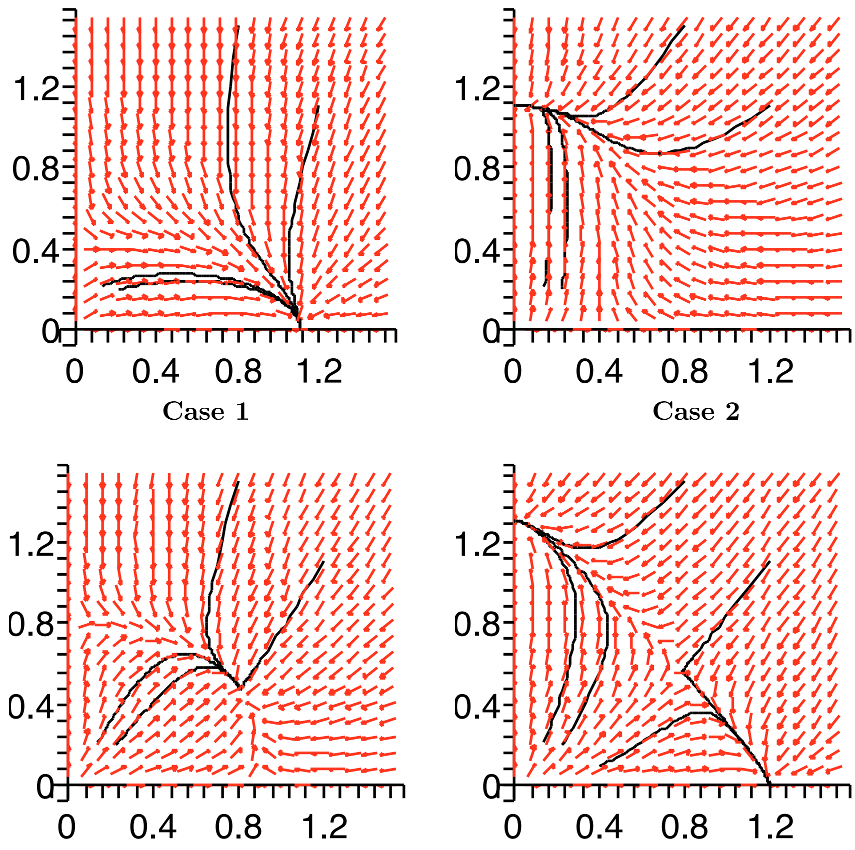

Figure 6: Phase Portraits and sample trajectories for each case created by the Maple 9.5 software package using paramters $\beta_1 = 0.2$, $\beta_2 = 0.3$ and:
Case 1: $K_1 = 1.1$, $K_2 = 0.4$, $\mu_1 = 0.4$, $\mu_2 = 0.5$
Case 2: $K_1 = 0.4$, $K_2 = 1.1$, $\mu_1 = 0.4$, $\mu_2 = 0.5$
Case 3: $K_1 = 0.9$, $K_2 = 0.8$, $\mu_1 = 0.4$, $\mu_2 = 0.5$
Case 4: $K_1 = 1.2$, $K_2 = 1.3$, $\mu_1 = 1.3$, $\mu_2 = 1.2$

5 Conclusions

The analysis of the modified Lotka-Volterra model reveals similar qualitative properties to the classic Lotka-Volterra model. Both models share $(0,0)$, $(K_1,0)$, and $(0,K_2)$ as critical points and the stability of these points is also the same in all cases.

The major difference between the classical model and the modified model is how the stability of the fourth critical point was determined. In the classic model, the stability of the fourth critical point depends on whether the expression $1-\mu_1\mu_2$ is positive or negative which is easy to determine using linear equation (2) for cases 3 and 4 of the classical model. In the modified model, the stability of the fourth critical point depends on whether the expression $1-4\mu_1\mu_2x_cy_c$ is positive or negative which we were not able to determine using non-linear equation (4). For case 3 we used a transformed differential equation and corresponding transformation matrix together with the Poincarè-Bendixson theorem to rule out $1-4\mu_1\mu_2x_cy_c$ being equal to zero or negative so the expression must be positive which implies the fourth critical point is a stable equilibrium in case 3. In case 4 we turned to geometry to show the fourth critical point is a saddle point.

One qualitative difference in the models is the conditions for each case. The original model uses the relationships between $\frac{K_2}{\mu_2}$ and K_1 and between $\frac{K_1}{\mu_1}$ and K_2 whereas the modified model uses the relationships between $\sqrt{\frac{K_2}{\mu_2}}$ and K_1 and between $\sqrt{\frac{K_1}{\mu_1}}$ and K_2. Therefore it is possible for the models to predict different outcomes. For example if $K_1=0.9$, $K_2=1.1$, $\mu_1=0.4$, and $\mu_2=1.3$, the classic model predicts case 1 (population x survives and population y becomes extinct) but the modified model predicts case 3 (coexistence).

If in a biological situation the population had a non-linear effect on each other (i.e. as the population grows it becomes more efficient at gathering the shared resource) then the prediction of the modified model would be better than that of the classical model.

References

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