# Nonlinear Lotka-Volterra Competition Models 




#### Abstract

The classical Lotka-Volterra equations that model the interactions between two species competing for a limited resource have many potential modifications to improve biological accuracy; this paper explores modifications to the exponent of the competition term. After an introduction to the behavior of the classical Lotka-Volterra model is given, a nonlinear modification to this model by Taylor and Crizer is discussed. In section 2, an extension of this modification is proposed, in which the population variable of the competition term is raised first to the power of positive real numbers and, next, small integers. A proof is offered that at most 3 coexistent equilibrium points exist for any positive exponent values, and additional proofs further limit the number of equilibria for certain exponent and parameter values. In section 3, we prove that, in such models, the stability of the equilibria alternates between stable and unstable when considered in a northwest to southeast configuration. Combining these results allows us to describe the equilibrium behavior of a broad class of competition models.


## 1 Introduction

Competition models consider scenarios involving two species that compete for the same limited prey or other vital resources. In 1925, American biophysicist Alfred Lotka and Italian mathematician Vito Volterra proposed one of the first valid competition models to describe cases of coexistence or competitive exclusion [4].
A competition model implies a reciprocal, negative interaction between the two species. Further, the Lotka-Volterra model treats the competition as density-dependent, and the

[^0]equations include terms for both intraspecific and interspecific competition:
\[

\left\{$$
\begin{array}{l}
\frac{d x}{d t}=\beta_{1} x\left(K_{1}-x-\mu_{1} y\right)  \tag{1}\\
\frac{d y}{d t}=\beta_{2} y\left(K_{2}-y-\mu_{2} x\right)
\end{array}
$$\right.
\]



Figure 1: The isocurves of the classical Lotka-Volterra equations.
where $\beta_{i}, K_{i}$, and $\mu_{i}$ are positive constants for $i=1,2$ [3]. Next, $\frac{d x}{d t}$ and $\frac{d y}{d t}$ denote the growth rates of populations $x$ and $y$ at time $t$. The $\beta_{i}$ constants are the respective intrinsic growth rates, the $K_{i}$ constants are the carrying capacities, and the $\mu_{i}$ constants are the competition coefficients, which represent the negative effect of one species on the other. The isocurves are linear and fall into one of four cases, depending upon parameter relationships, as depicted in Figure 1. As shown, the relative values of parameters $K_{1}$ versus $K_{2} / \mu_{2}$ and $K_{2}$ versus $K_{1} / \mu_{1}$ determine the relative positions of the $x$ - and $y$-intercepts of the isocurves, consequently impacting the number of possible intersection points.
These classical Lotka-Volterra equations have been modified in various studies [1][4][5]. Taylor and Crizer introduce a nonlinear relationship to model the effects of each species on the other,

$$
\left\{\begin{array}{l}
\frac{d x}{d t}=\beta_{1} x\left(K_{1}-x-\mu_{1} y^{2}\right)  \tag{2}\\
\frac{d y}{d t}=\beta_{2} y\left(K_{2}-y-\mu_{2} x^{2}\right)
\end{array}\right.
$$

where $\beta_{i}, K_{i}$, and $\mu_{i}$ again are positive constants for $i=1,2$ [5]. Because the isocurves
are nonlinear, they are not limited to a maximum of one intersection point, as addressed in [4].
In this paper, we examine the more general nonlinear relationship

$$
\left\{\begin{array}{l}
\frac{d x}{d t}=\beta_{1} x\left(K_{1}-x-\mu_{1} y^{w_{1}}\right)  \tag{3}\\
\frac{d y}{d t}=\beta_{2} y\left(K_{2}-y-\mu_{2} x^{w_{2}}\right)
\end{array}\right.
$$

where $\beta_{i}, K_{i}$, and $\mu_{i}$ are positive constants and $w_{i}$ is any positive real number for $i=1,2$. We first determine that the four cases of parameter relationships contain several subcases, which will be investigated in Section 2. We establish the number of possible intersection points for any positive real exponents on the competition terms. Next, we prove that isocurves for any exponents are limited to a maximum of three intersection points, with an even smaller number allowed for small positive integer exponents. Finally, we detail the stability patterns of these equilibria and their biological implications.

## 2 Number of Intersection Points

### 2.1 Exponents as Positive Real Numbers

Given the modified Lotka-Volterra equations in equation (3), the equilibrium points are given by $(0,0),\left(K_{1}, 0\right),\left(0, K_{2}\right)$ and positive solutions to the following system:

$$
\left\{\begin{array}{l}
x+\mu_{1} y^{w_{1}}=K_{1}  \tag{4}\\
y+\mu_{2} x^{w_{2}}=K_{2}
\end{array}\right.
$$

Defining $v_{1}=\sqrt[w_{1}]{K_{1} / \mu_{1}}$ and $v_{2}=\sqrt[w_{2}]{K_{2} / \mu_{2}}$, we have the following case divisions:
Case 1: $K_{1}>v_{2}$ and $K_{2}<v_{1}$
Case 2: $K_{1}<v_{2}$ and $K_{2}>v_{1}$
Case 3: $K_{1}<v_{2}$ and $K_{2}<v_{1}$
Case 4: $K_{1}>v_{2}$ and $K_{2}>v_{1}$.
We consider these cases as they mirror the four cases seen in the original LotkaVolterra equations, defining the relative intercept positions of the isocurves. We also define

$$
\begin{aligned}
& F(x, y)=\beta_{1}\left(K_{1}-x-\mu_{1} y^{w_{1}}\right) \\
& G(x, y)=\beta_{2}\left(K_{2}-y-\mu_{2} x^{w_{2}}\right)
\end{aligned}
$$

and let $f$ and $g$ denote the curves $F(x, y)=0$ and $G(x, y)=0$, respectively.
Lemma 1. Isocurves $f$ and $g$ are monotonically decreasing.
Proof. Using equation (4), we see that the two terms on the left hand side of each equation add to $K_{i}$, a fixed constant. Hence, in both equations, as $x$ increases, $y$ decreases, causing both curves to decrease monotonically.

We then solve the second equation from the set in (4) for $y$ and substitute the result into $x+\mu_{1} y^{w_{1}}=K_{1}$. Defining this result as a function of $x$, we obtain $h(x)=0$ where

$$
h(x)=K_{1}-x-\mu_{1}\left(K_{2}-\mu_{2} x^{w_{2}}\right)^{w_{1}} .
$$

The roots of this equation give the $x$-coordinate of any intersection points of the isocurves $f$ and $g$. Taking the first derivative with respect to $x$, we have

$$
h^{\prime}(x)=-1+\mu_{1} \mu_{2} w_{1} w_{2} x^{w_{2}-1}\left(K_{2}-\mu_{2} x^{w_{2}}\right)^{w_{1}-1}
$$

Again taking the derivative, we have

$$
h^{\prime \prime}(x)=\mu_{1} \mu_{2} w_{1} w_{2} x^{w_{2}-2}\left(K_{2}-\mu_{2} x^{w_{2}}\right)^{w_{1}-2}\left[K_{2}\left(w_{2}-1\right)-\mu_{2} x^{w_{2}}\left(w_{1} w_{2}-1\right)\right]
$$

The roots and undefined points of $h^{\prime \prime}(x)$ give the $x$-coordinate of any inflection points of $h(x)$, allowing us to determine the maximum number of critical points and therefore zeros of $h(x)$.

Theorem 1. For any $w_{1}$ and $w_{2}, f$ and $g$ have a maximum of 3 intersection points in the interior of the first quadrant.



Figure 2: The 4 possible cases, each with one subcase, where $f$ is dashed and $g$ is solid. As shown in Section 3, solid points are stable equilibria, and open points are unstable equilibria. The cases marked with ' $A$ ' indicate the subcase of each numbered case with 0 or 1 intersection points, and the cases marked with ' B ' indicate the subcase with 2 or 3 intersection points.

Proof. As a consequence of Rolle's Theorem, to show $f$ and $g$ can have at most 3 intersection points, we need only to show that $h(x)$ has at most one inflection point. We see that $h^{\prime \prime}(x)=0$ or $h^{\prime \prime}(x)$ is undefined when $x=0, \sqrt[w_{2}]{K_{2} / \mu_{2}}$, or $\sqrt[w_{2}]{\frac{K_{2}\left(w_{2}-1\right)}{\mu_{2}\left(w_{1} w_{2}-1\right)}}$, depending on the values of $w_{1}$ and $w_{2}$. Because $x=0$ and $\sqrt[w_{2}]{K_{2} / \mu_{2}}$ mark points where $f$ or $g$ would intersect a coordinate axis, the only inflection point that could produce a coexistent equilibria is at $x=\sqrt[w_{2}]{\frac{K_{2}\left(w_{2}-1\right)}{\mu_{2}\left(w_{1} w_{2}-1\right)}}$. Hence, there is a maximum of one inflection point for $h(x)$.

Theorem 2. There are 8 possible configurations of the graphs of $f$ and $g$, shown in Figure 2.

Proof. Because the isocurves are continuous and can intersect a maximum of 3 times in the first quadrant, the geometric positions of the intercepts $K_{i}$ and $v_{i}$ determine which of the 8 configurations are possible, and their limited intersections limit the number of configurations.

### 2.2 Cases of Small Integer Exponents

Theorem 3. If $w_{1}=2$ and if $w_{2}$, written from here on as $w$ for simplicity, is any integer greater than or equal to 2 ,
(1) In case 1, equation (4) has in the first quadrant either 0 or 2 solutions.
(2) In case 2, equation (4) has in the first quadrant either 0 or 2 solutions.
(3) In case 3, equation (4) has in the first quadrant either 1 or 3 solutions.
(4) In case 4, equation (4) has in the first quadrant exactly 1 solution.

Proof. Following the work of [4], to find the number of intersection points of the isocurves, we begin by obtaining the polynomials, derived from equation (4), which are satisfied by the equilibrium solutions. Starting with $y+\mu_{2} x^{w}=K_{2}$, we solve for $y$ and substitute into $x+\mu_{1} y^{2}=K_{1}$ to obtain $x+\mu_{1}\left(K_{2}-\mu_{2} x^{w}\right)^{2}=K_{1}$, which expands to:

$$
\begin{equation*}
\mu_{1} \mu_{2}^{2} x^{2 w}-2 \mu_{1} \mu_{2} K_{2} x^{w}+x+\mu_{1} K_{2}^{2}-K_{1}=0 \tag{5}
\end{equation*}
$$

Similarly, we next start with $x+\mu_{1} y^{2}=K_{1}$, solve for $x$, and substitute the result into $y+\mu_{2} x^{w}=K_{2}$ to obtain $y+\mu_{2}\left(K_{1}-\mu_{1} y^{2}\right)^{w}-K_{2}=0$, which, using the Binomial Theorem, expands to:

$$
\begin{gather*}
y+\mu_{2}\left(K_{1}-\mu_{1} y^{2}\right)^{w}-K_{2}=y-K_{2}+\sum_{k=0}^{w}\binom{w}{k} \mu_{2} K_{1}^{w-k}\left(-\mu_{1} y^{2}\right)^{k} \\
=\sum_{k=1}^{w}\binom{w}{k} \mu_{2} K_{1}^{w-k}\left(-\mu_{1} y^{2}\right)^{k}+y+\mu_{2} K_{1}^{w}-K_{2}=0, \tag{6}
\end{gather*}
$$

where $k \in \mathbb{Z}$. Because the term $\mu_{1} y^{2}$ is preceded by a negative sign, the sign of each term from the summation will alternate. As we will be using Descartes' Rule of Signs later in this proof, it is notable that the polynomial in equation (5) has either 1 or 2 sign changes depending on the sign of $\mu_{1} K_{2}^{2}-K_{1}$, and the polynomial in equation (6) has either $w$ or $w+1$ sign changes, dependent upon the sign of $\mu_{2} K_{1}^{w}-K_{2}$. It is also notable that the only coefficients whose sign is dependent upon the parameter values are $\mu_{2} K_{1}^{w}-K_{2}$ for any $w$. Hence, the only information required to determine the number of sign changes in the polynomial defined by equation (6) are the signs of $\mu_{1} K_{2}^{2}-K_{1}$ and $\mu_{2} K_{1}^{w}-K_{2}$.

From Theorem 2, we see that, for cases 1, 2, and 3, all 6 possible ways of intersection could occur, as Descartes' Rule of Signs eliminates no possibilities.

In case $4, \mu_{2} K_{1}^{w}-K_{2}>0$ and $\mu_{1} K_{2}^{2}-K_{1}>0$. Then equation (5) has 2 sign changes and equation (6) has $w$ sign changes. Hence, by Descartes' Rule of Signs, equation (4) has at most $\min (2, w)$ solutions in the interior of the first quadrant. The positions of the intercepts indicate that the curves must intersect an odd number of times, so equation (4) has exactly one solution, eliminating case 4B.

As seen, the smaller of $w_{1}$ and $w_{2}$ serves as a limiting factor in determining the number of intersection points of the isocurves. Thus, when $w_{1}=2$, any integer value of $w_{2} \geq 2$ will yield the same results as would $w_{1}=w_{2}=2$. Further, the case in which $w_{2}=2$ and $w_{1} \geq 2$ is symmetric and yields the same number of intersection points in the symmetric cases.




Figure 3: Examples of the subcases for $w_{1}=2, w_{2}=3$, and $\beta_{1}=\beta_{2}=1$ resulting in 0 , 1,2 , and 3 intersection points.

Theorem 4. If $w_{1}=1$ and if $w_{2}$, written from here on as $w$ for simplicity, is any integer greater than or equal to 1 ,
(1) In case 1, equation (4) has in the first quadrant either 0 or 2 solutions.
(2) In case 2, equation (4) has in the first quadrant 0 solutions.
(3) In case 3, equation (4) has in the first quadrant exactly 1 solution.
(4) In case 4, equation (4) has in the first quadrant exactly 1 solution.

Proof. Following the arguments in the proof for Theorem 3, solutions to equation (4) under the above conditions will satisfy the following equations:

$$
\begin{equation*}
-\mu_{1} \mu_{2} x^{w}+x+\mu_{1} K_{2}-K_{1}=0 \tag{7}
\end{equation*}
$$

and

$$
\begin{equation*}
y+\mu_{2}\left(K_{1}-\mu_{1} y\right)^{w}-K_{2}=0 . \tag{8}
\end{equation*}
$$

(1) In case 1 , we see from Theorem 2 that either case 1 A or 1 B could occur.
(2) In case $2, \mu_{2} K_{1}^{w}-K_{2}<0$ and $\mu_{1} K_{2}-K_{1}>0$. This yields 1 sign change from equation (7) and either $w$ or $w+1$ sign changes from equation (8). Thus, equation (4) has at most $\min (1, w)$ or $\min (1, w+1)$ solutions, or at most 1 . From the intercepts, there must be an even number of intersection points, so there are 0 positive solutions, eliminating case 2B.
(3) In case $3, \mu_{2} K_{1}^{w}-K_{2}<0$ and $\mu_{1} K_{2}-K_{1}<0$. This yields 2 sign changes from equation (7) and either $w$ or $w+1$ sign changes from equation (8). Thus, equation (4) has at most $\min (2, w)$ or $\min (2, w+1)$ solutions, or at most 2 . From the intercepts, there must be an odd number of intersection points, so there is exactly 1 positive solution, eliminating case 3B.
(4) In case $4, \mu_{2} K_{1}^{w}-K_{2}>0$ and $\mu_{1} K_{2}-K_{1}>0$. This yields 1 sign change from equation (7) and either $n$ or $w+1$ sign changes from equation (8). Thus, equation (4) has at most $\min (1, w)$ or $\min (1, w+1)$ solutions, or at most 1 . From the intercepts, there must be an odd number of intersection points, so there is exactly 1 positive solution, eliminating case 4B.

The case where one of the exponents is zero is well-known and will not be discussed here.

While Theorem 1 indicates that any parameter combination results in a maximum of 3 intersections and Theorems 3 and 4 show how possible cases may be eliminated, we can perform further analysis to determine further restrictions on the number of intersection points by case divisions.

Theorem 5. The table below indicates when $h(x)$ has one inflection point inside the interval of interest, which indicates when $f$ and $g$ can have 3 intersection points. Letting $m=\sqrt[w_{2}]{\frac{K_{2}\left(w_{2}-1\right)}{\mu_{2}\left(w_{1} w_{2}-1\right)}}$ :

|  | Cases 1 and 4 | Cases 2 and 3 |
| :--- | :--- | :--- |
| A: $w_{1}<1, w_{2}<1$ | always | $m<K_{1}$ |
| B: $w_{1}>1, w_{2}>1$ | always | $m<K_{1}$ |
| C: $w_{1}<1, w_{2}>1$ | never | never |
| D: $w_{1}>1, w_{2}<1$ | never | never |

Table 1: The conditions under which $h(x)$ has one inflection point.
Proof. Recall that when $h(x)$ has one inflection point, it can have at most 3 zeros and, accordingly, $f$ and $g$ can intersect at most 3 times. When $h(x)$ has no inflection points, $f$ and $g$ are limited to a maximum of 2 intersection points. Also note that we are only interested in intersection points with the $x$-coordinate in the interval $0<x<\min \left(K_{1}, v_{2}\right)$.
(A) We see that $\sqrt[w_{2}]{\frac{K_{2}\left(w_{2}-1\right)}{\mu_{2}\left(w_{1} w_{2}-1\right)}}$ will under the radical have a negative numerator and negative denominator, resulting in a positive radicand and a real $x$ value. Then since $\frac{w_{2}-1}{w_{1} w_{2}-1}<1, m<\sqrt[w_{2}]{\frac{K_{2}}{\mu_{2}}}$ and is therefore inside the interval of interest for cases 1 and 4 of the divisions of parameter relationships. Hence, there is one positive inflection point in cases 1 and 4 . In cases 2 and 3, only the values of $m<K_{1}$ are inside the interval of interest. Hence, there is one inflection point in cases 2 and 3 when $m<K_{1}$ and zero inflection points when $m>K_{1}$.
(B) We see that the radicand is positive, resulting in a real $x$ value. Since $\frac{w_{2}-1}{w_{1} w_{2}-1}<1$, $m<\sqrt[w_{2}]{\frac{K_{2}}{\mu_{2}}}$ and is therefore inside the interval of interest for all cases. Hence, there is one inflection point. Following the same reasoning as above, there is one inflection point in cases 1 and 4. In cases 2 and 3, there is one inflection point when $m<K_{1}$ and zero inflection points when $m>K_{1}$.
(C) The radicand may be either positive or negative. If $w_{1} w_{2}<1$, the radicand is negative and the solution has no real parts, resulting in zero inflection points. If $w_{1} w_{2}>1$, the radicand is positive and $\frac{w_{2}-1}{w_{1} w_{2}-1}>1$, meaning that $m>\sqrt[w_{2}]{\frac{K_{2}}{\mu_{2}}}$ and is always outside our interval of interest. Hence, both possibilities yield zero inflection points.
(D) The radicand may be either positive or negative. If $w_{1} w_{2}<1$, the radicand is negative and there are zero inflection points. If $w_{1} w_{2}>1$, the radicand is positive
and $\frac{w_{2}-1}{w_{1} w_{2}-1}>1$, meaning that $m>\sqrt[w_{2}]{\frac{K_{2}}{\mu_{2}}}$ and is always inside our interval of interest. Hence, there are again zero inflection points.

This exploration of the numbers of inflection points places restrictions on the number of possible intersection points of the two isocurves. We have shown above that for any combination of positive exponent values, there is a maximum of one inflection point for the polynomial whose zeros give the $x$-coordinate of intersection points of $f$ and $g$; hence, this polynomial has a maximum of three roots, indicating that $f$ and $g$ are limited to a maximum of 3 intersection points in the interior of the first quadrant. From above, we now know that the appearance of 3 equilibria depends on the relative values of $\sqrt[w_{2}]{\frac{K_{2}\left(w_{2}-1\right)}{\mu_{2}\left(w_{1} w_{2}-1\right)}}$ and $K_{1}$ in cases 2 and 3 . Further, there will never be 3 equilibria in cases when both $w_{1}<1$ and $w_{2}>1$ or $w_{1}>1$ and $w_{2}<1$. In the cases that result in zero inflection points, the isocurves have a maximum of 2 intersection points. While the complicated parameter relationships make it difficult to offer distinct value ranges for $w_{1}$ and $w_{2}$ that yield specific numbers of intersection points, we have found restrictions for the maximum numbers of equilibria and the cases in which they may occur.

## 3 Stability of Equilibria

The dynamic stability of equilibria is significant as only stable equilibria are realistic points where the populations can be maintained in equilibrium. The sample population trajectories in Figure 4 illustrate that coexistent equilibria can either be stable or unstable. Following the work of Hirsch, Smale, and Devaney in [2], we offer a proof regarding the stability of equilibrium points in the interior of the first quadrant.


Figure 4: Left: Sample trajectories for case 1. Right: Sample trajectories for case 2.
We note the following facts regarding $F$ and $G$ :
$F 1$. The populations of the two species $x$ and $y$ are inversely related; if the population of one increases, then the growth rate of the other decreases. Thus, $F_{y}<0$ and $G_{x}<0$.
$F 2$. If either population reaches a large value, then both populations decrease. In particular, letting $K=\max \left\{K_{1}, K_{2},\left(K_{1} / \mu_{1}\right)^{1 / w_{1}},\left(K_{2} / \mu_{2}\right)^{1 / w_{2}}\right\}$, we have that $F(x, y)<$

0 and $G(x, y)<0$ if $x \geq K$ or $y \geq K$.
$F 3$. If the population of one species is zero, then the other species has a positive growth rate to a certain population value and a negative growth rate beyond it. In particular, $F(x, 0)$ is positive when $x<K_{1}$ and negative when $x>K_{1}$, and $G(0, y)$ is positive when $y<K_{2}$ and negative when $y>K_{2}$.

Theorem 6. Each intersection point of isocurves $f$ and $g$ in the interior of the first quadrant yields a locally stable equilibrium if and only if $f$ is above $g$ to the left of the intersection and $f$ is below $g$ to the right.

Proof. Any coexistent equilibria of this system modeled by equation (3) are given by the intersection(s) of the isocurves in the interior of the first quadrant. At an intersection point, the slope of $f=-\frac{F_{x}}{F_{y}}$ and the slope of $g=-\frac{G_{x}}{G_{y}}$ by the Implicit Function Theorem. We know that any intersection points occur under one of three cases:

Case A. $f$ is above $g$ to the left of the intersection, and $f$ is below $g$ to the right.
Case B. $g$ is above $f$ to the left of the intersection, and $g$ is below $f$ to the right.
Case C. $g$ and $f$ are tangent to each other and touch at a point without crossing at that point.


Figure 5: Case 1, where the slope of $f$ is steeper than that of $g$.
(A) As shown in Figure 5, the slope of $f$ is steeper than that of $g$, meaning $-\frac{F_{x}}{F_{y}}<$ $-\frac{G_{x}}{G_{y}}<0$, as both curves are monotonically decreasing. From fact $F 1, F_{y}<0$ and $G_{x}<0$, and we conclude that $F_{x}<0$ and $G_{y}<0$, as we have $-\frac{F_{x}}{F_{y}}<0$ and $-\frac{G_{x}}{G_{y}}<0$.

To determine the local stability at this critical point, we next seek the eigenvalues of the Jacobian matrix,

$$
\left[\begin{array}{cc}
F_{x} & F_{y} \\
G_{x} & G_{y}
\end{array}\right]=\left[\begin{array}{cc}
\beta_{1} K_{1}-2 \beta_{1} x-\beta_{1} \mu_{1} y^{w_{1}} & -w_{1} \beta_{1} \mu_{1} x y^{w_{1}-1} \\
-w_{2} \beta_{2} \mu_{2} y x^{w_{2}-1} & \beta_{2} K_{2}-2 \beta_{2} y-\beta_{2} \mu_{2} x^{w_{2}}
\end{array}\right] .
$$

Along the isocurves, $F(x, y)=0$ and $G(x, y)=0$, so we substitute these values into the matrix, yielding

$$
\left[\begin{array}{cc}
-\beta_{1} x & -w_{1} \beta_{1} \mu_{1} x y^{w_{1}-1} \\
-w_{2} \beta_{2} \mu_{2} y x^{w_{2}-1} & -\beta_{2} y
\end{array}\right] .
$$

The trace of the Jacobian matrix is $-\beta_{1} x-\beta_{2} y<0$. The determinant is $\beta_{1} \beta_{2}(x y-$ $w_{1} w_{2} \mu_{1} \mu_{2} x^{w_{2}} y^{w_{1}}$, which we see, generally, is $x y\left(F_{x} G_{y}-F_{y} G_{x}\right)$. In case $\mathrm{A},-\frac{F_{x}}{F_{y}}<-\frac{G_{x}}{G_{y}}$, meaning $\frac{F_{x}}{F_{y}}>\frac{G_{x}}{G_{y}}$ and consequently $F_{x} G_{y}>F_{y} G_{x}$, so the determinant is positive. The eigenvalues are the roots of the characteristic polynomial $p(\lambda)$ of the matrix, which, for a standard $2 \times 2$ matrix, is given by

$$
p(\lambda)=\operatorname{det}(A-\lambda I)=\lambda^{2}-\operatorname{tr}(A) \lambda+\operatorname{det}(A)
$$

Using the quadratic formula, the eigenvalues of the general matrix are

$$
\lambda=\frac{\operatorname{tr}(A) \pm \sqrt{\operatorname{tr}(A)^{2}-4 \operatorname{det}(A)}}{2}
$$

Returning to our Jacobian matrix, we see that, since the determinant is positive, $|\operatorname{tr}(A)|>\sqrt{\operatorname{tr}(A)^{2}-4 \operatorname{det}(A)}$, meaning that the real part of both eigenvalues must always be negative as the trace is negative. Hence, both eigenvalues have negative real parts, indicating a locally stable equilibrium point.
(B) We begin with $-\frac{G_{x}}{G_{y}}<-\frac{F_{x}}{F_{y}}<0$. Again, the trace of the matrix is $-\beta_{1} x-\beta_{2} y<0$. The determinant is $x y\left(F_{x} G_{y}-F_{y} G_{x}\right)$, which in this case is negative.

From our Jacobian matrix, we see that both the trace and determinant are negative. Hence, both eigenvalues will be real. Further, since $\sqrt{\operatorname{tr}(A)^{2}-4 \operatorname{det}(A)}>\operatorname{tr}(A)$, one eigenvalue must be negative and the other must be positive, indicating an unstable equilibrium point.
(C) In this case, the two isocurves are tangent and touch without crossing. While this case is highly biologically improbable, we show that this tangent point yields an unstable equilibrium.

For the two curves to touch without crossing, their slopes must be equal at the point we consider; thus, we begin with $-\frac{G_{x}}{G_{y}}=-\frac{F_{x}}{F_{y}}<0$. Since $F_{x} G_{y}=F_{y} G_{x}$, the determinant is zero. We then have

$$
\lambda=\frac{\operatorname{tr}(A) \pm \sqrt{\operatorname{tr}(A)^{2}}}{2}
$$

The eigenvalue $\lambda=0$ implies an unstable equilibrium at this intersection point, as at least one of the eigenvalues of this matrix has a nonnegative real part.

Since both isocurves are monotonically decreasing, the equilibria have a well-defined order moving from a northwest to southeast direction. In this order, any one of the two possible cases of intersection with crossing isocurves cannot occur twice in a row. In other words, if more than one intersection point exists on the interior of the first quadrant, the stability of adjacent equilibria will alternate between stable and unstable when the equilibria are being considered in a northwest to southeast configuration. Therefore, knowing the stability of just one equilibrium point in these models is sufficient to determine the local stability of the rest.

Though we do not do so here, facts $F 2$ and $F 3$ can be used to show that the locally stable equilibria are actually globally stable, as done in [2]. To demonstrate the degree of information we can now readily obtain from modified Lotka-Volterra systems in the form of equation (3), we now discuss a numerical example. Letting $\mu_{1}=0.59, \mu_{2}=$ $0.74, K_{1}=1.21, K_{2}=1.36, w_{1}=2$, and $w_{2}=3$, we see that $v_{1} \approx 1.43$ and $v_{2} \approx 1.22$.

Because $K_{1}<v_{2}$ and $K_{2}<v_{1}$, these parameters place us in case 3 . Using the table from Theorem 5, we have that $m \approx 0.74<K_{1}$ and hence these parameters yield isocurves with 3 intersection points in the first quadrant, which is case 3B. Using Theorem 6 and the aid of Figure 2, we see that the relative positions of the intercepts indicate that the first equilibrium point when considered in a northwest to southeast configuration, which is $\left(0, K_{2}\right)$, must be unstable. Continuing down the isocurves in this direction, the first intersection is stable, the second is unstable, the third is stable, and $\left(K_{1}, 0\right)$ is unstable. Hence, we have determined the number of equilibria and their stability with minimal calculations.

## 4 Areas of Further Research

While these explorations of the models have added insight into Lotka-Volterra modifications, there is much more to be explored. Placing additional restrictions on the parameters of Table (1), for example, would enable more efficient and clear determination of the possible number of intersection points, as the parameter relationships are clearly complicated. Additionally, the number of intersection points in Theorems 1, 3 , and 4 is dependent upon parameter relationships. Further exploration of the cases in these theorems could reveal which number of intersection points actually occurs for more specific parameter values. Moreover, investigating relationships between $w_{1}$ and $w_{2}$ could offer additional restrictions on when certain numbers of equilibria occur.

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[^0]:    *Corresponding author: mara.smith@myemail.indwes.edu

