

MODELING SYMBIOSIS BY A LOTKA-VOLTERRA-TYPE SYSTEM  
OF DIFFERENTIAL EQUATIONS

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BY

LANEY WILLIAMS

DENTON, TEXAS

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TEXAS WOMAN'S UNIVERSITY  
DENTON, TEXAS

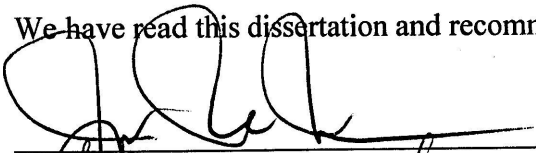
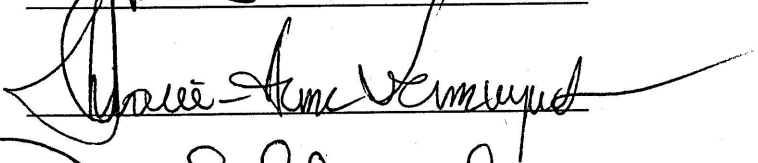

April 9, 2013

To the Dean of the Graduate School:

I am submitting herewith a thesis written by Laney Williams entitled "Modeling Symbiosis by a Lotka-Volterra-Type System of Differential Equations." I have examined this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science with a major in Mathematics.

  
\_\_\_\_\_  
Ellina Grigorieva, Ph.D., Major Professor

We have read this dissertation and recommend its acceptance:

  
\_\_\_\_\_  
  
\_\_\_\_\_  
  
\_\_\_\_\_  
Department Chair

Accepted:

  
\_\_\_\_\_  
Interim Dean of the Graduate School



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## **DEDICATION**

**To my mother, Tracy, my late father, Mike, and to my sister, Weatherly,  
for your love and support**

## ACKNOWLEDGMENTS

I would like to gratefully acknowledge the many individuals who have contributed to this thesis. I would like to thank my thesis advisor Dr. Ellina Grigorieva. Your guidance was indispensable to writing this thesis. I would also like to thank the members of my thesis committee: Dr. Junalyn Navarra-Madsen (for being my advisor the first semester), Dr. Marie-Anne Demuynck (for a discussion on genetic algorithms), and Dr. Don Edwards (for accepting me to the mathematics program in the first place). And last but most importantly, I would like to thank my family for putting up with my quirkiness until it turned into something good. None of this would have been possible without you.

## ABSTRACT

LANEY WILLIAMS

### MODELING SYMBIOSIS BY A LOTKA-VOLTERRA-TYPE SYSTEM OF DIFFERENTIAL EQUATIONS

MAY 2013

Biological symbiosis is necessary for life on earth. However, population based models of symbiosis are rare in literature. One problem is defining symbiosis, and whether it includes mutualism, commensalism and parasitism, or only mutualism. Additionally, there are obligate and facultative types. Another problem is that basic models of symbiosis have relied on a variation of the Lotka-Volterra competition equation, which can lead to unrealistic results, such as unlimited population growth. Several stable models have limited the growth by using equations for carrying capacity which are functions of the symbiont species. In this work a new model is proposed which uses a modified Holling Type II functional response for the carrying capacities. The broadest definition of symbiosis for thoroughness is used. This new model has stable equilibria for many different types of symbiosis.

## TABLE OF CONTENTS

	Page
COPYRIGHT .....	iii
DEDICATION .....	iv
ACKNOWLEDGMENTS .....	v
ABSTRACT .....	vi
LIST OF TABLES .....	ix
LIST OF FIGURES .....	x
Chapter	
I. INTRODUCTION .....	1
Technological Symbiosis .....	4
II. REVIEW OF OTHER MODELS .....	6
Interaction functions.....	6
Carrying capacity functions.....	18
Predator prey similarities.....	25
III. NEW SYMBIOSIS MODEL.....	28
Derivation.....	29
Nondimensionalization .....	32
Phase plane analysis .....	34
Limits for obligate mutualism .....	46

IV. CONCLUSION.....	50
---------------------	----

REFERENCES .....	52
------------------	----

## LIST OF TABLES

Table	Page
1. Symbiotic Relationships.....	3

## LIST OF FIGURES

Figure	Page
1. LVC Case 1.....	10
2. LVC Case 2.....	10
3. LVC Case 3.....	11
4. LVC Case 4.....	11
5. LVS Case 1.....	15
6. LVS Case 2.....	15
7. Wright Model.....	17
8. Dean Model Case 1.....	20
9. Dean Model Case 2.....	20
10. Dean Model Case 3.....	21
11. Dean Model Case 4.....	21
12. Yukalov Model Case 1.....	24
13. Yukalov Model Case 2.....	24
14. Leslie-Gower Predator-Prey Model.....	26
15. Obligate-Obligate Case 1 Phase Plane Analysis.....	35
16. Obligate-Obligate Phase Case 1 Phase Portrait.....	36
17. Obligate-Obligate Case 2 Phase Plane Analysis.....	36
18. Obligate-Obligate Phase Case 2 Phase Portrait.....	37



19. Facultative-Facultative Phase Plane Analysis .....	38
20. Facultative-Facultative Phase Portrait.....	39
21. Obligate-Facultative Phase Plane Analysis .....	40
22. Obligate-Facultative Phase Portrait.....	41
23. Commensal-Obligate Phase Plane Analysis.....	42
24. Commensal-Obligate Phase Portrait .....	42
25. Commensal-Facultative Phase Plane Analysis.....	43
26. Commensal-Facultative Phase Portrait .....	44
27. Parasitic Phase Plane Analysis .....	45
28. Parasitic Phase Portrait.....	46
29. Numerical Solution to Obligate-Obligate .....	49

## CHAPTER I

### INTRODUCTION

Symbiosis is an important and critical feature of biological life. However, in literature, symbiosis has been either ignored or not discussed in depth. One of the reasons is that the definition of symbiosis has not been agreed upon. Symbiosis is complex and has different types. Another reason is that mathematical models of symbiosis are often unrealistic or difficult to analyze. These issues often arise because symbiosis is seen as the opposite of competition; however, it is much more complicated than this.

According to Daida et al. [1] symbiosis is “relationships that are constant and intimate between dissimilar species”. This is a very broad definition. Symbiosis can be divided into several different types. These are mutualism, commensalism, and parasitism. In addition to these relationships, species in mutualism and commensalism can be called either obligate or facultative. This definition is generally agreed upon; however, some disagree whether commensalism and parasitism should be included in symbiosis. Darwin believed that symbiosis was a synonym for mutualism [1]. This paper will use the broadest definition in defining symbiosis, including all the different types. The relationships are agreed to have the following definitions. In mutualism, both species benefit from the relationship. In commensalism, one species benefits while the

other is neither benefited nor harmed. In parasitism, one species benefits while the other is harmed. In the obligate form of symbiosis, a species must have the other species to survive, while in facultative symbiosis a species can survive without the other. While the terms mutualism, commensalism, and parasitism apply to the relationship between the species, the terms obligate and facultative only apply to one species in the relationship. Therefore, in a relationship between two species, both can be obligate, both can be facultative, or one species can be obligate and the other facultative.

There are many species which exhibit the different kinds of symbiosis. The following list gives some examples:

- An example of obligate-obligate mutualism is lichens. Fungus and alga must come together to form a lichen, each gaining essential nutrients from the other.
- An example of facultative-facultative mutualism is clownfish and sea anemone. Clownfish gain protection from sea anemone and sea anemone gains nutrients from clownfish activity, but either could live without the other.
- An example of obligate-facultative mutualism is flowering plants and butterflies. Most flowering plants require external modes of pollination. Butterflies can pollinate and consume the nectar, but have other food sources.
- An example of obligate commensalism is hermit crabs and gastropods. Hermit crabs require gastropod shells for homes. Gastropods, which discard their shells, are unaffected.

- An example of facultative commensalism is egrets and cattle. Grazing cattle disturb insects which egrets feed on. The cattle are unaffected, and the egrets gain easy access to food but can obtain food in other ways.
- An example of parasitism is fleas and mammals. Fleas feed exclusively on the blood of mammals or birds and lay their eggs on the skin. The fleas require the animals for nutrition, but the animals are harmed by blood loss and irritation from the bites.

These relationships are listed in Table 1. A species that is harmed is denoted with a “-”, a species that benefits in a facultative way from the relationship is denoted with a “+”, and a species that benefits in an obligate way is denoted by “++”.

**Table 1 Symbiotic Relationships**

Relationship	Species		Example
	A	B	
Mutualism (obligate-obligate)	++	++	Lichen Fungus (A) Lichen Alga (B)
Mutualism (facultative-facultative)	+	+	Clownfish (A) Anemone (B)
Mutualism (obligate-facultative)	++	+	Flowering Plant (A) Butterfly (B)
Commensalism (obligate)	++	0	Hermit crabs (A) Gastropods (B)
Commensalism (facultative)	+	0	Egrets (A) Cattle (B)
Parasitism	++	-	Fleas (A) Mammals (B)

Mathematical modeling of symbiosis is also difficult. This is because some models can give unrealistic results, such as unbounded growth. These models are often based on the Lotka-Volterra competition equation. More realistic models are often

complex, and involve many coefficients. These models will be discussed in the next chapter.

In mathematical models of population growth, including symbiosis, there are some common coefficients which have real-world meaning. One of these is the growth rate. This is commonly denoted with the letter ' $r$ '. This is simply the rate at which the population increases in a given time period, usually expressed as a percent. The carrying capacity, denoted with the letter ' $K$ ', is the maximum number of individuals which the environment can sustain. Finally there is the symbiotic coefficient; usually the letter ' $a$ ' but it could be any other letter. This is the quantification of how much one species is affected by the other species. If it is greater than one, then the species is affected more by the other species than by members of its own species.

### **Technological Symbiosis**

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In industrial applications, symbiosis can be used to describe two technological innovations that have a relationship [2, 3]. This would be a situation where the technologies function together as complementary goods. This is contrasted with competition where one technology is a substitute for the other. Modis [3] gives a similar to the table in the above to describe the relationships between two technologies. Symbiosis can be used to model the growth of these technologies in the economy.

Both Pistorius and Utterback [2] and Modis [3] use Lotka-Volterra sets of differential equations to model the economic situation. In the models the coefficients have different meanings than in biological models. The growth rate is the measure of attractiveness of the technology. The carrying capacity would be the niche capacity or the number of technologies that the economy can sustain. The symbiotic coefficient represents how well one technology can substitute for another. Using these models, companies can help make economic decisions.

## CHAPTER II

### REVIEW OF OTHER MODELS

There are two main types of symbiotic functions. Each is based on the logistic growth equation. The first type describes the interaction of the two species with a function, and the second type describes the species carrying capacity as a function. There have been several different models within each type. A few will be discussed in this section.

#### Interaction functions

---

The Lotka-Volterra competition equation was formulated separately by Lotka and Volterra. It is based on the logistic differential equation for population growth, with an extra term added. The Lotka-Volterra Competition (LVC) equations take the form:

$$\frac{dx}{dt} = \frac{r_1}{K_1} x (K_1 - x - a_{12}y)$$

$$\frac{dy}{dt} = \frac{r_2}{K_2} y (K_2 - y - a_{21}x)$$

These are identical to the logistic equation, except that an extra term is subtracted to represent the effect that  $y$  has on the growth of  $x$  (with coefficient  $a_{12}$ ) and the effect  $x$  has on the growth of  $y$  (with coefficient  $a_{21}$ ). In other words, the “ $a$ ”-coefficients represent the success of the competitor in substituting for or replacing the other

species. The “ $r$ ”-coefficients represent the growth rate, the “ $K$ ”-coefficients represent the carrying capacity.

The LVC equations have very well-known behavior, dependent on the values of the coefficients. The nullclines for the LVC are:

$$x = 0, \quad y = -1/a_{12}x + K_1/a_{12}$$

$$y = 0, \quad y = -a_{21}x + K_2$$

The equilibria for LVC occur at  $(0,0)$ ,  $(K_1,0)$ ,  $(0,K_2)$ , and the intersection point

$\left(\frac{K_1 - a_{12}K_2}{1 - a_{12}a_{21}}, \frac{K_2 - a_{21}K_1}{1 - a_{12}a_{21}}\right)$  if it exists. The solutions for  $x$  will converge to 0,  $\frac{K_1 - a_{12}K_2}{1 - a_{12}a_{21}}$ , or  $K_1$ .

The solutions for  $y$  will converge to 0,  $\frac{K_2 - a_{21}K_1}{1 - a_{12}a_{21}}$ , or  $K_2$ . At the intersection point

$(x^*, y^*) = \left(\frac{K_1 - a_{12}K_2}{1 - a_{12}a_{21}}, \frac{K_2 - a_{21}K_1}{1 - a_{12}a_{21}}\right)$ , in the first quadrant, the following inequalities hold:

$0 \leq x^* \leq K_1$  and  $0 \leq y^* \leq K_2$ . From this information, we can see that the solutions for  $x$  will be bounded from below by 0 and bounded from above by  $K_1$ , and solutions for  $y$  will be bounded from below by 0 and bounded from above by  $K_2$ , as long as initial values are  $0 \leq x(0) \leq K_1$  and  $0 \leq y(0) \leq K_2$ .

In order to show the behavior at the equilibria, the Jacobian matrix for LVC is analyzed:

$$J_c = \begin{bmatrix} r_1 - \frac{2r_1}{K_1}x - \frac{r_1a_{12}}{K_1}y & -\frac{r_1a_{12}}{K_1}x \\ -\frac{r_2a_{21}}{K_2}y & r_2 - \frac{2r_2}{K_2}y - \frac{r_2a_{21}}{K_2}x \end{bmatrix}$$

At point  $(0,0)$ :



$$\begin{bmatrix} r_1 & 0 \\ 0 & r_2 \end{bmatrix}$$

Here, the eigenvalues will always be positive, because the growth rates will always be positive. Therefore, (0,0) is always a source.

At  $(K_1, 0)$ :

$$\begin{bmatrix} -r_1 & -r_1 a_{12} \\ 0 & r_2 \left(1 - a_{21} \frac{K_1}{K_2}\right) \end{bmatrix}$$

As this is an upper triangular matrix, the eigenvalues are the diagonal values. The first eigenvalue will always be negative. Either the point will either be a saddle, if  $\frac{K_2}{a_{21}} > K_1$ , as in Figure 1 and Figure 4, or the point will be a sink if  $\frac{K_2}{a_{21}} < K_1$ , as in Figure 2 and Figure 3.

At  $(0, K_2)$ :

$$\begin{bmatrix} r_1 \left(1 - a_{12} \frac{K_2}{K_1}\right) & 0 \\ -r_2 a_{21} & -r_2 \end{bmatrix}$$

As this is a lower triangular matrix, the eigenvalues are the diagonal values. The second eigenvalue will always be negative. The point will be a saddle if  $\frac{K_1}{a_{12}} > K_2$ , as in Figure 2 and Figure 4. It will be a sink if  $\frac{K_1}{a_{12}} < K_2$ , as in Figure 1 and Figure 3.

At point  $\left(\frac{K_1 - a_{12}K_2}{1 - a_{12}a_{21}}, \frac{K_2 - a_{21}K_1}{1 - a_{12}a_{21}}\right)$ , calculating eigenvalues of the Jacobian becomes

complicated. However, there is a well-known relationship between the sign of the trace, the sign of the determinant, and the signs of the eigenvalues.

- If  $\det(J)$  is negative, eigenvalues will have opposite signs. The point is a saddle point.
- If  $\det(J)$  is positive and  $\text{trace}(J)$  is positive, eigenvalues will both be positive. The point is a source.
- If  $\det(J)$  is positive and  $\text{trace}(J)$  is negative, eigenvalues will both be negative.

The point is a sink.

The trace and determinant at  $\left(\frac{K_1 - a_{12}K_2}{1 - a_{12}a_{21}}, \frac{K_2 - a_{21}K_1}{1 - a_{12}a_{21}}\right)$  are:

$$\det(J_c) = \frac{r_1 r_2 (K_1 K_2 - a_{21} K_1^2 - a_{12} K_2^2 + K_1 K_2 a_{12} a_{21})}{K_1 K_2 (1 - a_{12} a_{21})}$$

$$\text{trace}(J_c) = \frac{r_1 a_{12} K_2^2 + r_2 a_{21} K_1^2 - r_1 K_1 K_2 - r_2 K_1 K_2}{K_1 K_2 (1 - a_{12} a_{21})}$$

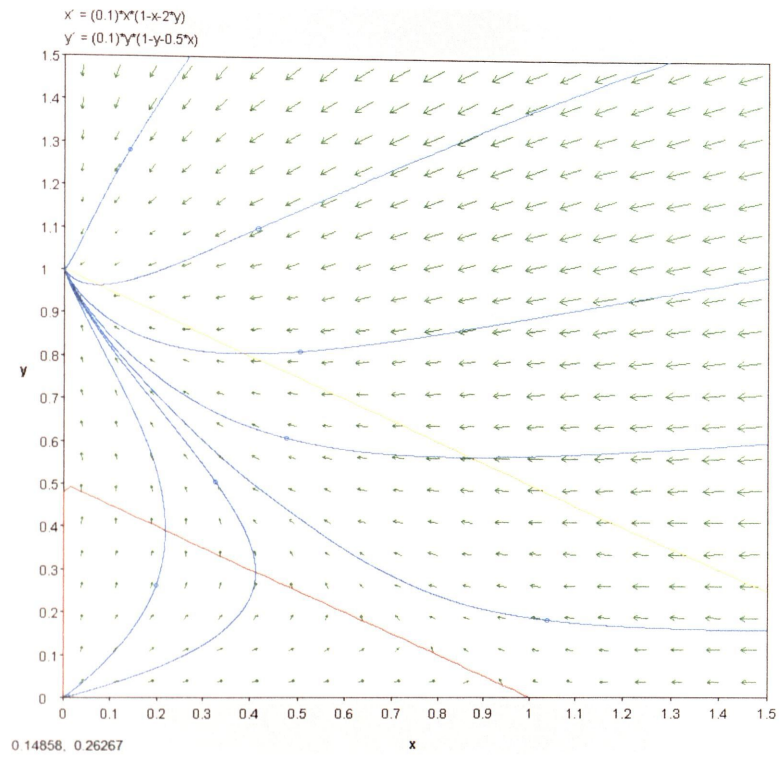
When  $\det(J_c) < 0$ ,  $K_1 K_2 - a_{21} K_1^2 - a_{12} K_2^2 + K_1 K_2 a_{12} a_{21} > 0$ , this factors to  $(a_{12} K_2 - K_1)(a_{21} K_1 - K_2) > 0$ ,

or when  $K_2 > K_1/a_{12}$  and  $K_1 > K_2/a_{21}$ , the point will be a saddle point, as in Figure 3.

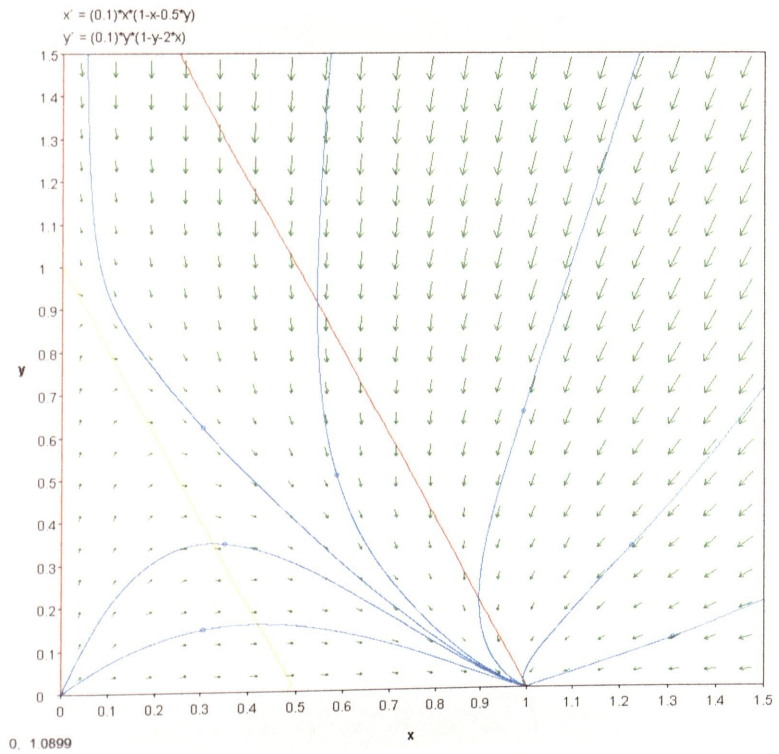
When  $\text{trace}(J_c) < 0$ ,  $r_1 a_{12} K_2^2 + r_2 a_{21} K_1^2 - r_1 K_1 K_2 - r_2 K_1 K_2 > 0$ , this factors to  $r_1 K_2 (K_1 - K_2 a_{12}) +$

$r_2 K_1 (K_2 - K_1 a_{21}) > 0$ , or when  $K_1/a_{12} > K_2$  and  $K_2/a_{21} > K_1$ . This is exactly when  $\det(J_c) > 0$ ,

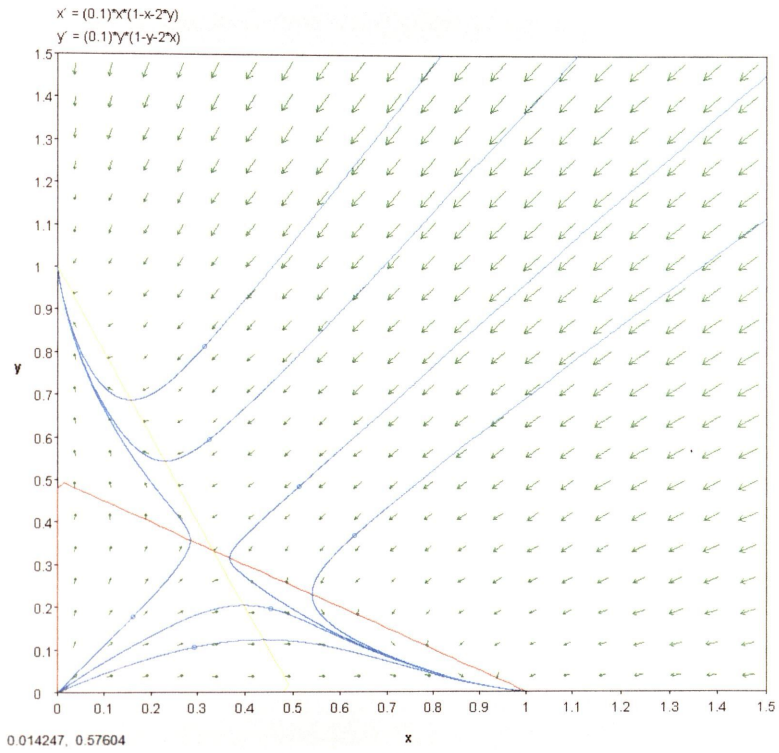
meaning the point is a sink, as in Figure 4.



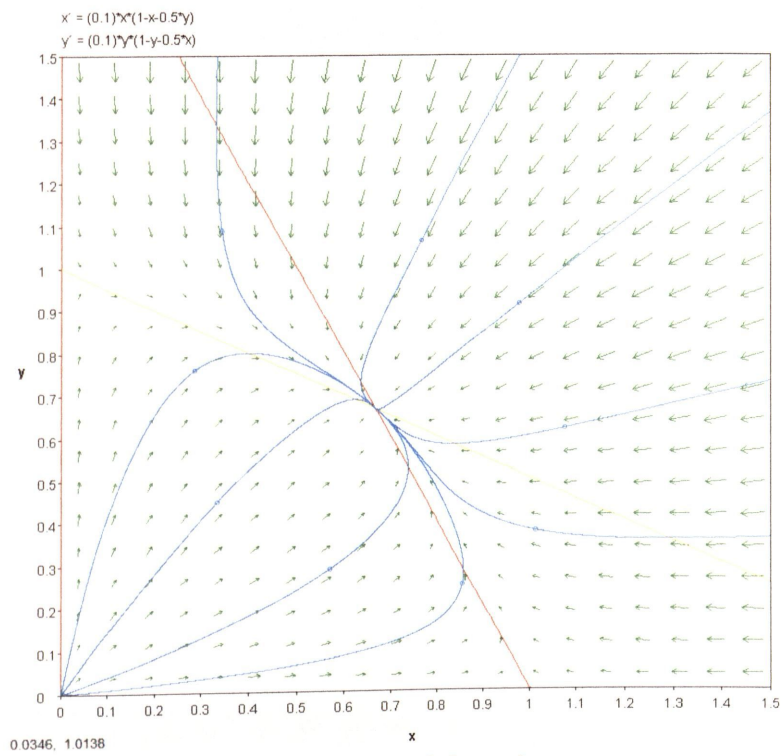
**Figure 1. LVC Case 1**



**Figure 2. LVC Case 2**



**Figure 3. LVC Case 3**



**Figure 4. LVC Case 4**

The LVC equations assume that  $x$  and  $y$  have a negative interaction with each other. However, according to Pistorius and Utterback [2] and Modis [3], this equation can be modified to model symbiosis. The model of the Lotka-Volterra symbiosis (LVS) equations takes the form:

$$\frac{dx}{dt} = \frac{r_1}{K_1} x(K_1 - x + a_{12}y)$$

$$\frac{dy}{dt} = \frac{r_2}{K_2} y(K_2 - y + a_{21}x)$$

All that has been done is to change the signs of the coefficients  $a_{12}$  and  $a_{21}$  in LVC to account for the positive effect each species has on the other. However this model can lead to a population with uncontrolled growth toward infinity, which is not realistic. The nullclines for LVS are:

$$x = 0, \quad y = 1/a_{12}x - K_1/a_{12}$$

$$y = 0, \quad y = a_{21}x + K_2$$

The equilibria for LVS occur at  $(0,0)$ ,  $(K_1,0)$ ,  $(0,K_2)$ , and the intersection point

$\left(\frac{K_1+a_{12}K_2}{1-a_{12}a_{21}}, \frac{K_2+a_{21}K_1}{1-a_{12}a_{21}}\right)$  if it exists. Unlike the LVC, in the LVS the intersection coordinates

$(x^*, y^*) = \left(\frac{K_1+a_{12}K_2}{1-a_{12}a_{21}}, \frac{K_2+a_{21}K_1}{1-a_{12}a_{21}}\right)$ , in the first quadrant, the following inequalities hold:

$x^* \geq K_1$  and  $y^* \geq K_2$ . The LVS solutions for  $x$  and  $y$  are bounded from below by 0 (when initial values are greater than 0), but are not bounded from above, and could increase infinitely.

To show the behavior at the equilibria, the Jacobian matrix for LVC is analyzed:

$$J_s = \begin{bmatrix} r_1 - \frac{2r_1}{K_1}x + \frac{r_1 a_{12}}{K_1}y & \frac{r_1 a_{12}}{K_1}x \\ \frac{r_2 a_{21}}{K_2}y & r_2 - \frac{2r_2}{K_2}y + \frac{r_2 a_{21}}{K_2}x \end{bmatrix}$$

At point (0,0):

$$\begin{bmatrix} r_1 & 0 \\ 0 & r_2 \end{bmatrix}$$

Here, the eigenvalues will always be positive, because the growth rates will always be positive. Therefore (0,0) is always a source.

At (K<sub>1</sub>,0):

$$\begin{bmatrix} -r_1 & r_1 a_{12} \\ 0 & r_2 \left(1 + a_{21} \frac{K_1}{K_2}\right) \end{bmatrix}$$

As this is an upper triangular matrix, the eigenvalues are the diagonal values. The first eigenvalue will always be negative, and the second eigenvalue will always be positive. Therefore, (K<sub>1</sub>,0) is always a saddle point, as shown in Figure 5 and Figure 6.

At (0,K<sub>2</sub>):

$$\begin{bmatrix} r_1 \left(1 + a_{12} \frac{K_2}{K_1}\right) & 0 \\ r_2 a_{21} & -r_2 \end{bmatrix}$$

As this is a lower triangular matrix, the eigenvalues are the diagonal values. The first eigenvalue will always be positive, and the second eigenvalue will always be negative. Therefore (0,K<sub>2</sub>) is always a saddle point, as shown in Figure 5 and Figure 6.

At point  $\left(\frac{K_1 + a_{12}K_2}{1 - a_{12}a_{21}}, \frac{K_2 + a_{21}K_1}{1 - a_{12}a_{21}}\right)$ , calculating eigenvalues of the Jacobian becomes complicated. However, I will use the same relationship between the sign of the trace,

the sign of the determinant, and the signs of the eigenvalues, as stated above. The

trace and determinant at  $\left(\frac{K_1+a_{12}K_2}{1-a_{12}a_{21}}, \frac{K_2+a_{21}K_1}{1-a_{12}a_{21}}\right)$  are:

$$\det(J_s) = \frac{-r_1r_2(K_1K_2 + a_{21}K_1^2 + a_{12}K_2^2 + K_1K_2a_{12}a_{21})}{K_1K_2(a_{12}a_{21} - 1)}$$

$$\text{trace}(J_s) = \frac{r_1a_{12}K_2^2 + r_2a_{21}K_1^2 + r_1K_1K_2 + r_2K_1K_2}{K_1K_2(a_{12}a_{21} - 1)}$$

The numerator of  $\det(J_s)$  will be negative, and the numerator of  $\text{trace}(J_s)$  will be positive.

The denominators of  $\det(J_s)$  and  $\text{trace}(J_s)$  are the same and equal to  $K_1K_2(a_{12}a_{21}-1)$ . For

the nullclines to intersect in the first quadrant, the slope of the y-nullcline must be less

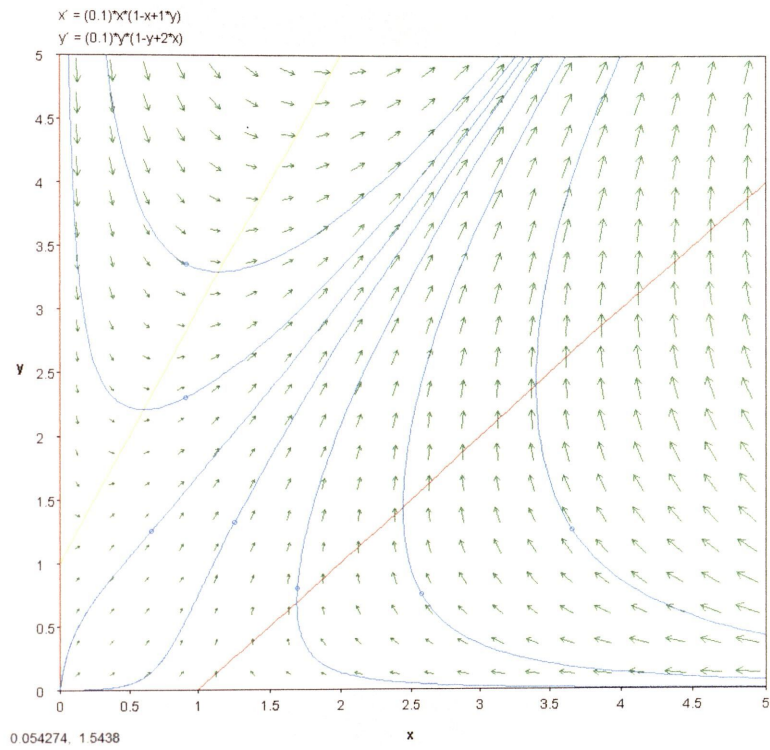
than the slope of the x-nullcline,  $a_{21} < 1/a_{12}$ , or  $a_{12}a_{21}-1 < 0$ . Therefore, the

denominators of  $\det(J_s)$  and  $\text{trace}(J_s)$  are negative. This makes  $\det(J_s)$  positive and

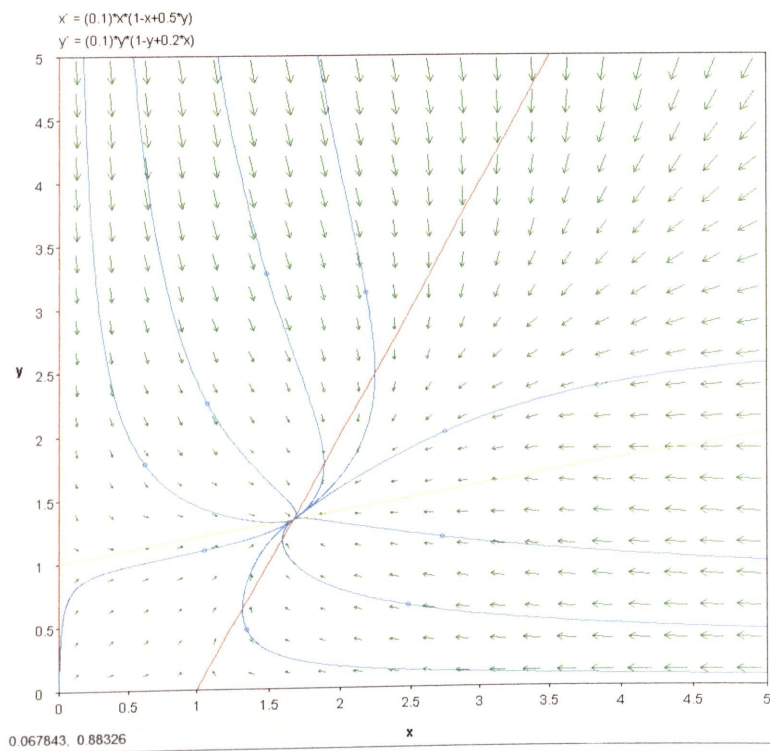
$\text{trace}(J_s)$  negative. Therefore, this point is a sink when it exists in the first quadrant, as in

Figure 6. If this point does not exist in the first quadrant, then (0,0) will still be a source,

and there will be unbounded growth, as in Figure 5.



**Figure 5. LVS Case 1**



**Figure 6. LVS Case 2**



Wright [4] created a model of mutualism that uses handling time. He used the Holling Type II functional response to model the benefits of interaction with the other species.

$$\frac{dx}{dt} = r_1x(1 - c_1x) + x\left(\frac{b_1Ay}{1 + Ahy}\right)$$

$$\frac{dy}{dt} = r_2y(1 - c_2y) + y\left(\frac{b_2Ax}{1 + Ahx}\right)$$

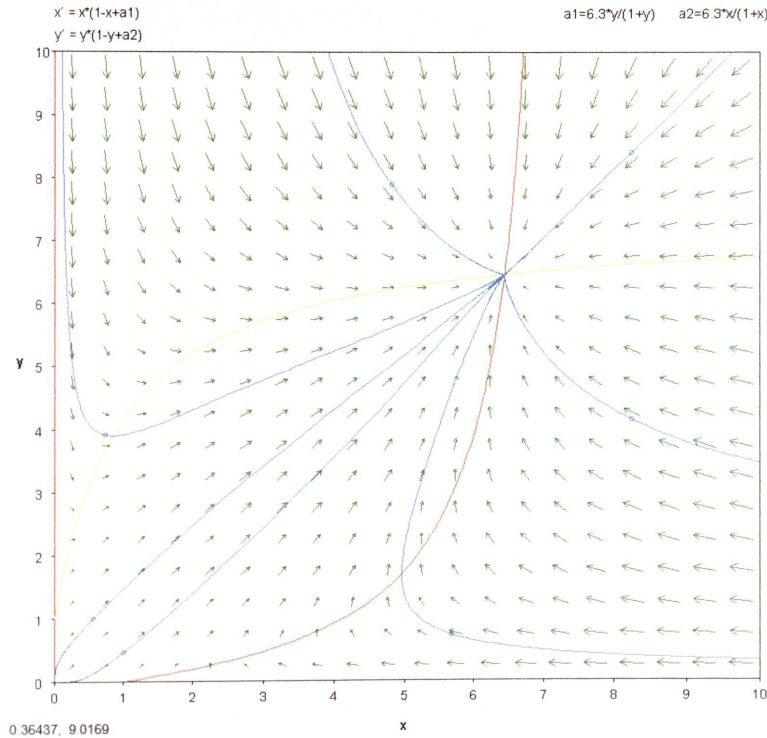
In these equations, “ $r$ ” is the growth rate, “ $b$ ” is the mutualism coefficient, and “ $A$ ” is Holling's instantaneous discovery rate, and “ $h$ ” is the handling time. The nullclines for Wright's model are:

$$x = 0, \quad y = \frac{r_1(c_1x - 1)}{A(r_1h + b_1 - r_1c_1hx)}$$

$$y = 0, \quad y = \frac{r_2 + (Ahr_2 + Ab_2)x}{r_2c_2(1 + Ahx)}$$

The equilibrium points  $(0, \frac{1}{c_2})$ ,  $(\frac{1}{c_1}, 0)$  are saddle points. The other equilibrium point will be the intersection of the nullclines. Finding the formula for the nullcline intersection point is a quadratic formula which will always have real numbers. However the symbolic formula is quite long. It is not important, however, it is only necessary to see under what conditions they will intersect, because that will determine if the this system is stable. This system has horizontal and vertical asymptotes. For the x-nullcline, it is at  $x = \frac{Ahr_1 + b_1A}{Ahr_1c_1}$ . For the y-nullcline, it is at  $y = \frac{Ahr_2 + b_2A}{Ahr_2c_2}$ . These asymptotes are positive, and they will always intersect in the first quadrant. Therefore, the nullclines

will intersect at point  $\left(\frac{1}{c_1} < x < \frac{Ahr_1+b_1A}{Ahr_1c_1}, \frac{1}{c_2} < y < \frac{Ahr_2+b_2A}{Ahr_2c_2}\right)$ . This system will always have a stable equilibrium. The intersection will be a sink point and the other equilibrium points will be saddle points, as in Figure 7.



**Figure 7. Wright Model**

The coefficient  $c$  could also be seen as  $1/K$ , where  $K$  is the carrying capacity in the absence of the other species. By representing the functional responses as functions, Wright's model is similar to the Pistorius and Utterback model.

$$\frac{dx}{dt} = r_1 x \left( 1 - \frac{x}{K_1} + f(y) \right)$$

$$\frac{dy}{dt} = r_2 y \left( 1 - \frac{y}{K_2} + g(x) \right)$$

Pistorius and Utterback used a Holling Type I functional response, and Wright used a Holling Type II functional response.

### Carrying capacity functions

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Dean [5] established a mutualism model based on the logistic growth equation. Instead of a constant, carrying capacity is a function of  $y$  for species  $x$ , and a function of  $x$  for species  $y$ . Dean derives exponential functions:

$$k_1(y) = K_1 \left( 1 - e^{\frac{-(ay+C_1)}{K_1}} \right)$$

$$k_2(x) = K_2 \left( 1 - e^{\frac{-(bx+C_2)}{K_2}} \right)$$

Dean establishes that the carrying capacity can be modeled as a functional response.

This carrying capacity function is put in the following logistic equations that describe the growth of the species:

$$\frac{dx}{dt} = \frac{r_1 x (k_1(y) - x)}{k_1(y)}$$

$$\frac{dy}{dt} = \frac{r_2 y (k_2(x) - y)}{k_2(x)}$$

The nullclines will be the carrying capacity functions. The nullclines for Dean's model are:

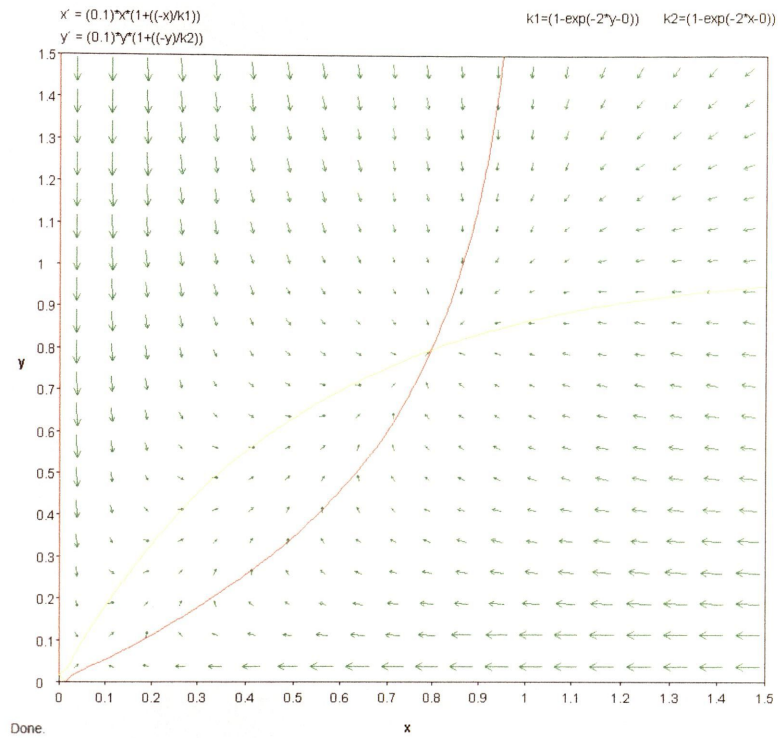
$$x = 0, \quad y = -\frac{1}{a} (K_1 \ln(K_1 - x) - K_1 \ln(K_1) + C_1)$$

$$y = 0, \quad y = K_2 \left( 1 - e^{\frac{-(bx+C_2)}{K_2}} \right)$$

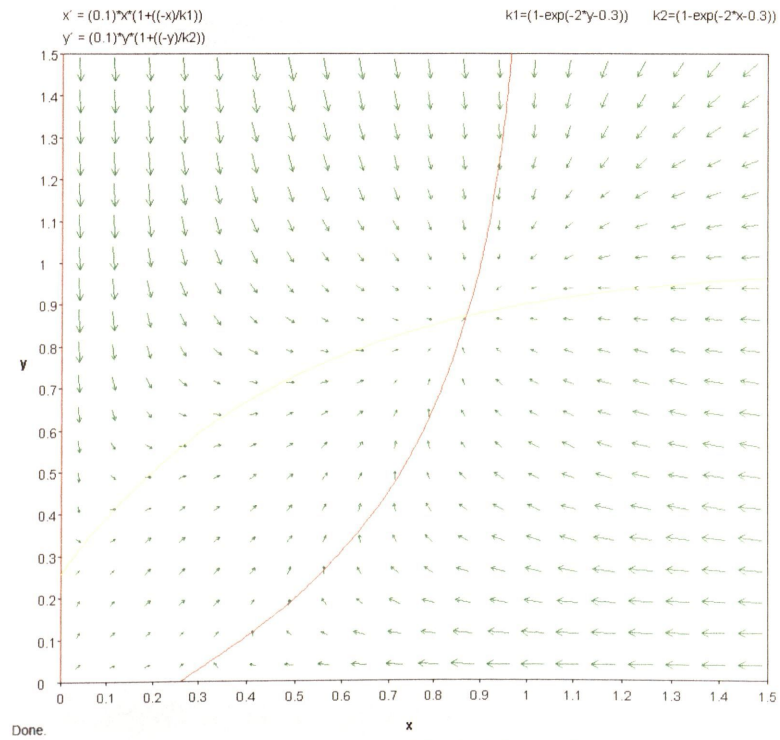
The equilibrium points are  $(0,0)$ ,  $(0, -\frac{c_1}{a})$ ,  $(-\frac{c_2}{b}, 0)$ ,  $(0, K_2(1 - e^{\frac{-c_2}{K_2}}))$ ,  $(K_1(1 - e^{\frac{-c_1}{K_1}}), 0)$  and the nullcline intersection points, if they exist. The points

$(0, -\frac{c_1}{a})$ ,  $(-\frac{c_2}{b}, 0)$ ,  $(0, K_2(1 - e^{\frac{-c_2}{K_2}}))$ ,  $(K_1(1 - e^{\frac{-c_1}{K_1}}), 0)$  will be saddle points, when

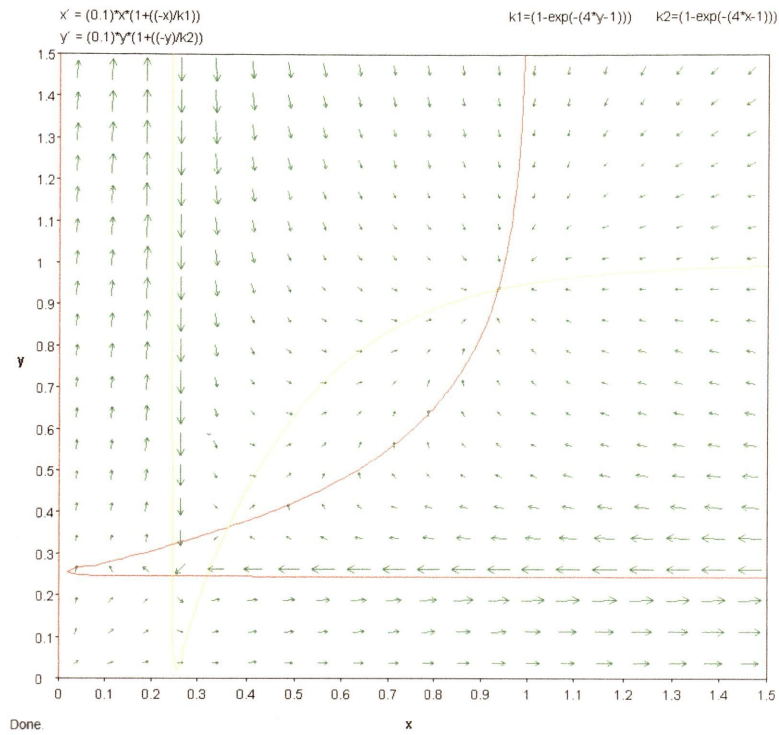
they exist in the first quadrant. When the integral constant is equal to zero (obligate mutualism), and the nullclines intersect in the first quadrant,  $(0,0)$  will be a saddle point and the intersection point will be a sink, as in Figure 8. When the integral constant is greater than zero (facultative mutualism), and the nullclines intersect in the first quadrant,  $(0,0)$  will be a source and the intersection point will be a sink, as in Figure 9. When the integral constants are less than zero (obligate mutualism), there is a threshold below the first intersection where there is unstable behavior, as in Figure 10. When the nullclines do not intersect, there will be no mutualism and the system will approach  $(0,0)$ , as in Figure 11.



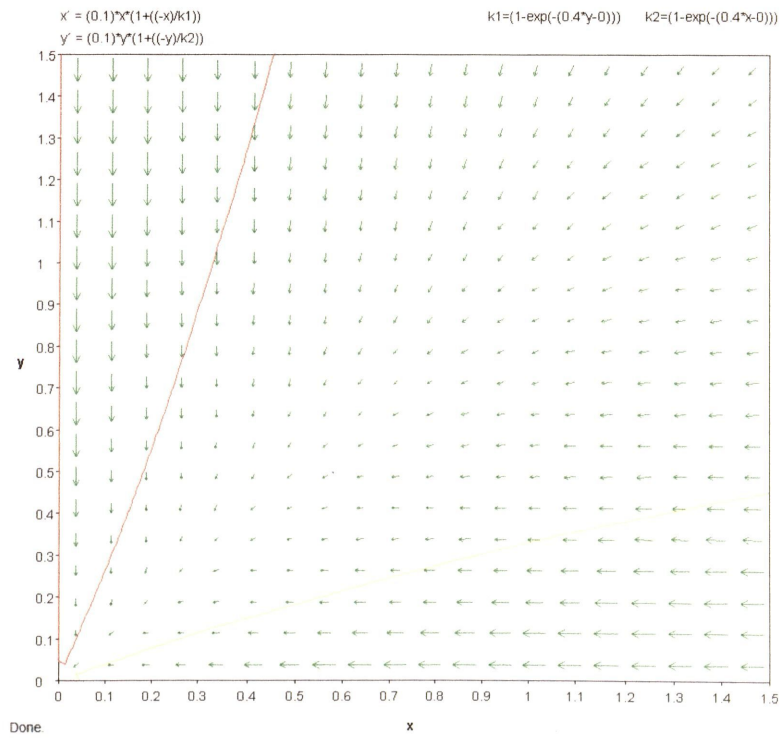
**Figure 8. Dean Model Case 1**



**Figure 9. Dean Model Case 2**



**Figure 10. Dean Model Case 3**



**Figure 11. Dean Model Case 4**

Yukalov et al. [6] also created a model of mutualism, which uses carrying capacities as a function in the logistic growth functions. The functions for the carrying capacities are:

$$k_1(x, y) = A_1 + B_1xy$$

$$k_2(x, y) = A_2 + B_2xy$$

Here,  $A$  is the carrying capacity of the given surrounding livelihood, and  $B$  is the intensity of producing, or destroying, the carrying capacity in the symbiotic process. These carrying capacities are substituted in the logistic growth equations:

$$\frac{dx}{dt} = r_1x - \frac{C_1x^2}{k_1(x, y)}$$

$$\frac{dy}{dt} = r_2y - \frac{C_2y^2}{k_2(x, y)}$$

Here  $r$  is the growth rate, and  $C$  is the intensity or intraspecies competition. The nullclines for Yukalov's model are:

$$x = 0, \quad y = \frac{c_1x - r_1A_1}{r_1B_1x}$$

$$y = 0, \quad y = \frac{r_2A_2}{c_2 - r_2B_2x}$$

The equilibrium points are  $\left(\frac{r_1A_1}{c_1}, 0\right)$ ,  $\left(0, \frac{r_2A_2}{c_2}\right)$ , and at most two nullcline intersection

points. The first two listed equilibrium points will be saddle points. The nullclines have vertical and horizontal asymptotes. For the  $x$ -nullcline, it is at  $y = \frac{c_1}{r_1B_1}$ . For the  $y$ -

nullcline, it is at  $x = \frac{c_2}{r_2B_2}$ . These asymptotes are positive, and they will always intersect

in the first quadrant. Therefore, the nullclines will intersect at point  $\left(\frac{c_2}{r_2 B_2} < x <$

$\frac{r_1 A_1}{c_1}, \frac{c_1}{r_1 B_1} < y < \frac{r_2 A_2}{c_2}\right)$ . Since the solution involves the quadratic formula, the

intersection will not exist when there are imaginary numbers. This intersection point

will not exist when  $2A_2 B_1 r_1 r_2 c_1 c_2 + 2A_2 B_1 r_1^2 r_2^2 A_1 B_2 + 2A_1 B_2 r_1 r_2 c_1 c_2 >$

$A_2^2 B_1^2 r_1^2 r_2^2 + c_1^2 c_2^2 + A_1^2 B_2^2 r_1^2 r_2^2$ . As Yukalov et al. observed, the system can

have exactly one stable equilibrium point in the first quadrant, the lesser of the two

intersection points, which will be a sink point. The other intersection point will be a

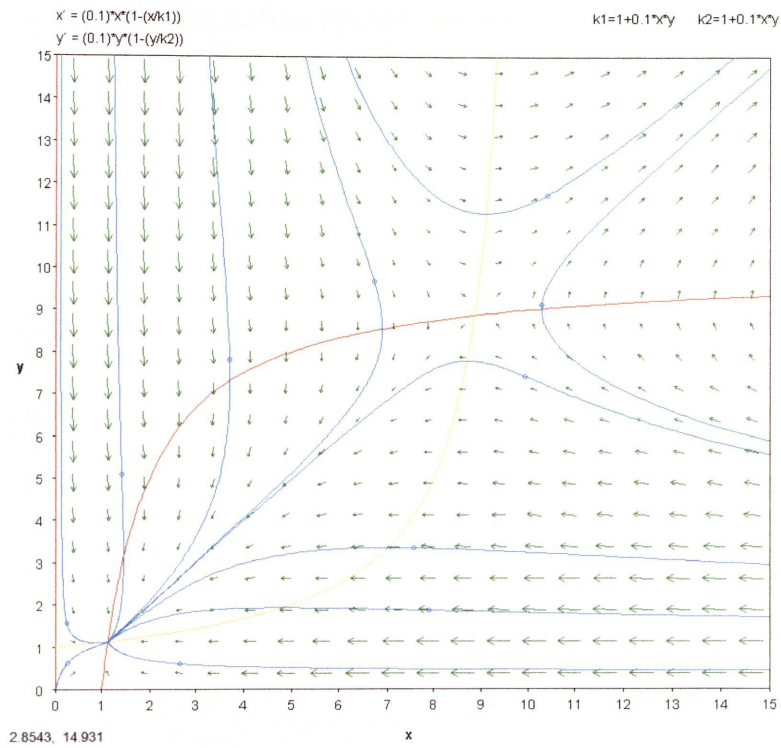
saddle point. This can be seen in Figure 12. Even when the stable equilibrium exists, a

threshold exists beyond which there can be unbounded growth. Furthermore, as they

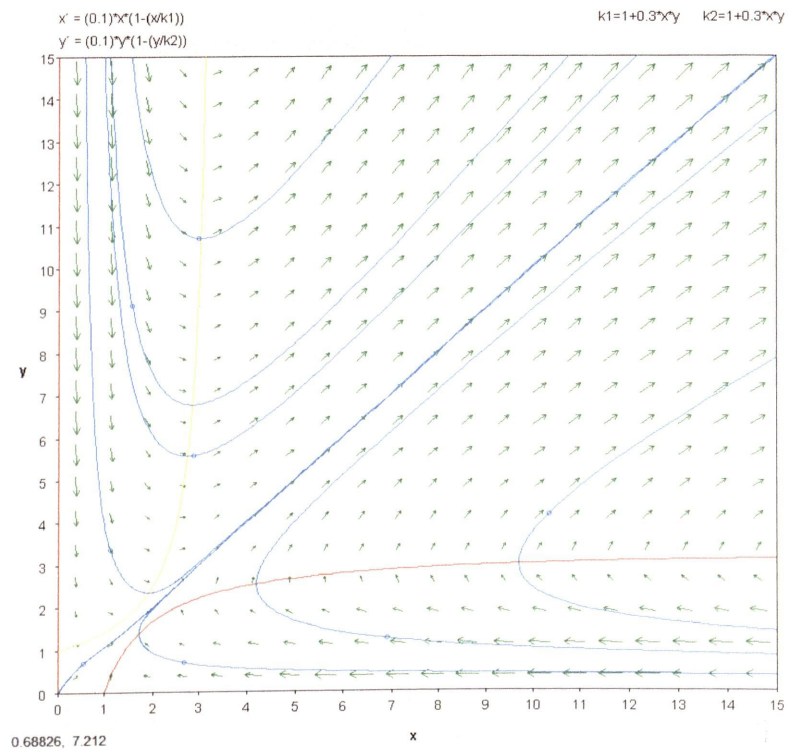
also observed, the system will have unbounded exponential growth when the nullclines

do not intersect in the first quadrant, as in Figure 13.





**Figure 12. Yukalov Model Case 1**



**Figure 13. Yukalov Model Case 2**

If  $C$  is taken to be equivalent to  $r$ , then these equations are the same as Dean's, but with different functions for the carrying capacities. Dean uses an exponential functional response, and Yukalov et al. use a linear functional response.

### Predator prey similarities

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According to Korobeinikov [7], the Leslie-Gower predator prey model defines the carrying capacity of the predator's environment to be a function that is proportional to the number of prey.

$$\frac{dx}{dt} = r_1 x \left( 1 - \frac{x}{K} - ay \right)$$

$$\frac{dy}{dt} = r_2 y \left( 1 - \frac{y}{mx} \right)$$

The nullclines for the Leslie-Gower model are:

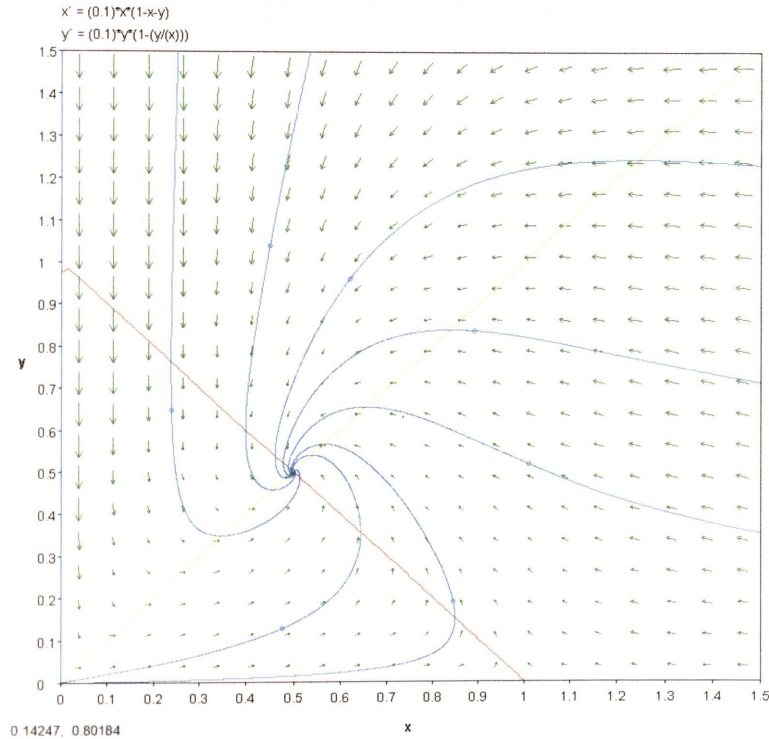
$$x = 0, \quad y = \frac{K - x}{Ka}$$

$$y = 0, \quad y = mx$$

The equilibrium points are  $(0,0)$ ,  $(K, 0)$ , and the nullcline intersection at

$\left(\frac{K}{maK+1}, \frac{mK}{maK+1}\right)$ . The points  $(0,0)$ ,  $(K,0)$  are saddle points, and the intersection point is

a spiral sink, as seen in Figure 14.



**Figure 14. Leslie-Gower Predator-Prey Model**

According to Nindjin et al. [8], the term  $y/mx$  of this equation is called the Leslie–Gower term, which measures the loss in the predator population due to the per capita rarity of its favorite food. Nindjin et al. model the case in which the predator can switch to another food source by adding a positive constant to the denominator.

Similarities between the symbiosis equations and these predator-prey equations can be seen when the equations are written another way:

$$\frac{dx}{dt} = r_1 x \left(1 - \frac{x}{K}\right) - af(y)\varphi(x)$$

$$\frac{dy}{dt} = r_2 y \left(1 - \frac{y}{k(x)}\right)$$

The first equation in the Leslie-Gower system is identical to the Lotka-Volterra competition equations and the symbiosis equations, if the sign on the last term is changed to positive. The Pistorius-Utterback, and Wright models are similar to this type of equation for species  $x$ , but for both species in mutualism. If  $\varphi(x) = x$  and instead  $f(y)$  is a functional response, because in mutualism the functional response is a function of the other species, then the Pistorius-Utterback and Wright models are obtained. As previously mentioned, Pistorius-Utterback use a Holling type I functional response, and Wright uses a Holling type II functional response. The second equation is identical to the logistic type symbiosis equations with a function for carrying capacity. Dean and Yukalov et al. use this type for their mutualism equations.

## CHAPTER III

### NEW SYMBIOSIS MODEL

In this paper, a new model of symbiosis is proposed. This new model uses the basic logistic growth differential equation that the Lotka-Volterra equation is based on. However, the carrying capacities are functions of the other species. For two symbionts M and N, the system will be:

$$\frac{dM}{dt} = r_1 M \left( 1 - \frac{M}{k_1(N)} \right)$$

$$\frac{dN}{dt} = r_2 N \left( 1 - \frac{N}{k_2(M)} \right)$$

The carrying capacity functions for the **obligate-obligate** model are:

$$k_1(N) = \frac{K_1 a_1 N}{K_1 + a_1 N}$$

$$k_2(M) = \frac{K_2 a_2 M}{K_2 + a_2 M}$$

The carrying capacity functions for the **facultative-facultative** model are:

$$k_1(N) = \frac{K_1(a_1 N + K_{10})}{K_1 + a_1 N}$$

$$k_2(M) = \frac{K_2(a_2 M + K_{20})}{K_2 + a_2 M}$$

The carrying capacity functions for the **obligate-facultative** model are:

$$k_1(N) = \frac{K_1 a_1 N}{K_1 + a_1 N}$$

$$k_2(M) = \frac{K_2(a_2 M + K_{20})}{K_2 + a_2 M}$$

The carrying capacity functions for the **commensal-obligate** model are:

$$k_1(N) = K_1$$

$$k_2(M) = \frac{K_2 a_2 M}{K_2 + a_2 M}$$

The carrying capacity functions for the **commensal-facultative** model are:

$$k_1(N) = K_1$$

$$k_2(M) = \frac{K_2(a_2 M + K_{20})}{K_2 + a_2 M}$$

The carrying capacity functions for the **parasitic** model are:

$$k_1(N) = \frac{K_1^2}{a_1 N + K_1}$$

$$k_2(M) = \frac{K_2 a_2 M}{K_2 + a_2 M}$$

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## Derivation

To derive the Holling Type II functional response for species  $z$ , Holling begins with the following equation [9]:

$$f(z) = AT_s z$$

$A$  is taken to be the attack rate, or the encounter rate, and  $T_s$  is the search time which is a function:

$$T_s = T - hf(z)$$

$T$  is the total time,  $h$  is the handling time, so  $hf(z)$  is the time spent handling all prey items. If the total time is taken to be equal to one unit of time, such as one day, the equation is:

$$T_s = 1 - hf(z)$$

Substituting gives the Holling Type II functional response:

$$f(z) = \frac{Az}{1 + Ahz}$$

This is the same functional response used by Wright [4] in their modified Lotka-Volterra type equations.

For the new model, the functional response is actually a carrying capacity. If the species cannot survive without the other species (i.e. obligate mutualists) then the carrying capacity function is:

$$k(z) = ak'z$$

Here,  $a$  is the symbiotic coefficient (a constant), and  $k'$  is the rate at which the carrying capacity grows with respect to species  $z$ . This is given by Dean [5] to be:

$$k' = \frac{K - k(z)}{K}$$

where  $K$  is the maximum carrying capacity. Substituting gives the new functional response for carrying capacity:

$$k(z) = \frac{Kaz}{K + az}$$

However, if the species can survive without the other species (i.e. facultative mutualists) then the carrying capacity function is:

$$k(z) = ak'z + K_0$$

where  $K_0$  is the carrying capacity in the absence of the other species, which is assumed to be less than the maximum carrying capacity. Substituting in the same equation for  $k'$  gives the new functional response for carrying capacity:

$$k(z) = \frac{K(az + K_0)}{K + az}$$

In a commensal relationship, where one species benefits but the other has no effect, the carrying function would be the facultative mutualists equation with  $K_0 = K$

$$k(z) = K$$

For parasitic relationships, another carrying capacity equation must be made. If the 'a' coefficient is changed to negative, there would be a vertical asymptote at  $x=K/a$ , where the carrying capacity would approach negative infinity from the left and positive infinity from the right. This makes no sense biologically. Instead, there is a kind of function similar to Holling's type II functional response, which is Langmuir's equation. Langmuir's equation is used in physiology and pharmacology to describe molecular binding. This is where an agonist binds to a receptor. This is analogous to a molecular symbiosis. According to Bindslev [10] Langmuir's equation is:

$$y = f(S) = \frac{y_{max}}{\frac{K_s}{S} + 1}$$



Here  $S$  is the agonist concentration, and  $K_S$  is the dissociation constant, and  $y_{max}$  is the maximum number of binding sites. The reverse of this is the concentration of inhibitors,  $I$ , to the binding. This is sometimes called the reverse Langmuir equation or hyperbolic decay [10].

$$y = f(I) = \frac{y_{max}}{\frac{I}{K_I} + 1}$$

This transformation was done by creating a new logistic equation with an exponent of  $\ln(K_S) - \ln(S)$ , and then reversing the sign of the exponent [10]. If mutualist symbionts are the agonists, then parasitic symbionts are the inhibitors. The same kind of transformation is used to obtain an equation for how the parasites affect the carrying capacity of the other species.

$$k(z) = \frac{K^2}{az + K}$$

The carrying capacity will begin at  $K$  and then decrease asymptotically to zero and the number of parasites,  $x$ , approaches infinity. The symbiotic coefficient ' $a$ ' has the same kind of meaning, and must be greater than zero.

## **Nondimensionalization**

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To reduce the number of parameters, a nondimensionalization scheme similar to Maiti and Pathak [11] was used. The following substitution of variables is used:

$$x = \frac{N}{K_1}, y = \frac{M}{K_2}, \tau = r_1 t$$

For the **obligate-obligate** model, the following equations are obtained:

$$\frac{dx}{d\tau} = x \left( 1 - x \left( \frac{y + \alpha}{y} \right) \right)$$

$$\frac{dy}{d\tau} = \gamma y \left( 1 - y \left( \frac{x + \beta}{x} \right) \right)$$

where  $\alpha = \frac{K_1}{K_2 a_1}$ ,  $\beta = \frac{K_2}{K_1 a_2}$ ,  $\gamma = \frac{r_2}{r_1}$ . In other words,  $\alpha$  is the ratio of the carrying

capacities  $K_1$  to  $K_2$  multiplied by  $1/a_1$ , and  $\beta$  is the ratio of  $K_2$  to  $K_1$  multiplied by  $1/a_2$ , and  $\gamma$  is the ratio of the growth rates  $r_1$  and  $r_2$ .

For the **facultative-facultative** model, the following equations are obtained:

$$\frac{dx}{d\tau} = x \left( 1 - x \left( \frac{y + \alpha}{y + \delta} \right) \right)$$

$$\frac{dy}{d\tau} = \gamma y \left( 1 - y \left( \frac{x + \beta}{x + \varepsilon} \right) \right)$$

where  $\delta = \frac{K_{10}}{K_2 a_1}$ ,  $\varepsilon = \frac{K_{20}}{K_1 a_2}$ . In other words,  $\delta$  is the ratio of the carrying capacity of

species one without the other species  $K_{10}$  to  $K_2$  multiplied by  $1/a_1$ , and  $\varepsilon$  is the ratio of carrying capacity of species one without the other species  $K_{20}$  to  $K_1$  multiplied by  $1/a_2$ .

For the **obligate-facultative** model, the following equations are obtained:

$$\frac{dx}{d\tau} = x \left( 1 - x \left( \frac{y + \alpha}{y} \right) \right)$$

$$\frac{dy}{d\tau} = \gamma y \left( 1 - y \left( \frac{x + \beta}{x + \varepsilon} \right) \right)$$

For the **commensal-obligate** model, the following equations are obtained:

$$\frac{dx}{d\tau} = x(1 - x)$$

$$\frac{dy}{d\tau} = \gamma y \left( 1 - y \left( \frac{x + \beta}{x} \right) \right)$$

For the **commensal-facultative** model, the following equations are obtained:

$$\frac{dx}{d\tau} = x(1 - x)$$

$$\frac{dy}{d\tau} = \gamma y \left( 1 - y \left( \frac{x + \beta}{x + \varepsilon} \right) \right)$$

For the **parasitic** model, the following equations are obtained:

$$\frac{dx}{d\tau} = x(1 - x(1 + \eta y))$$

$$\frac{dy}{d\tau} = \gamma y \left( 1 - y \left( \frac{x + \beta}{x} \right) \right)$$

where  $\eta = a_1 K_2$

## Phase plane analysis

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For the phase plane analysis, it is only necessary to analyze the first quadrant of the Cartesian x-y plane. This is because the population of species will never be negative. Phase plane analysis will be done by finding the nullclines and the intersections of the nullclines, or the equilibrium points, and analyzing the behavior of the system around the equilibrium points.

The nullclines for **obligate-obligate** model are:

$$x = 0, \quad y = \frac{\alpha x}{1 - x}$$

$$y = 0, \quad y = \frac{x}{x + \beta}$$

Equilibrium points are  $(0,0), \left(\frac{1-\alpha\beta}{\alpha+1}, \frac{1-\alpha\beta}{\beta+1}\right)$ . The nullclines will always intersect at  $(0,0)$ .

However, the intersection point  $\left(\frac{1-\alpha\beta}{\alpha+1}, \frac{1-\alpha\beta}{\beta+1}\right)$  will only be positive when  $\alpha\beta > 1$ , that is

when both  $\alpha$  and  $\beta$  are greater than one. When  $\alpha\beta > 1$ , the intersection point

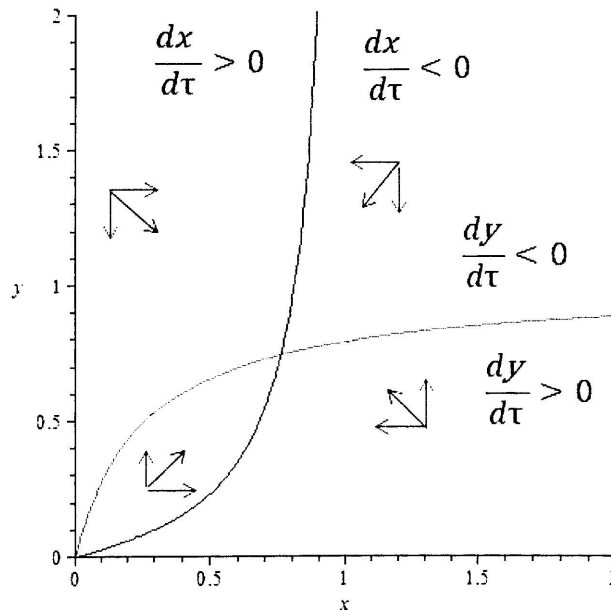
$\left(\frac{1-\alpha\beta}{\alpha+1}, \frac{1-\alpha\beta}{\beta+1}\right)$  will be a sink point, and  $(0,0)$  will be a saddle point. Otherwise, the

nullclines will not intersect in the first quadrant and  $(0,0)$  will be a sink point, and all

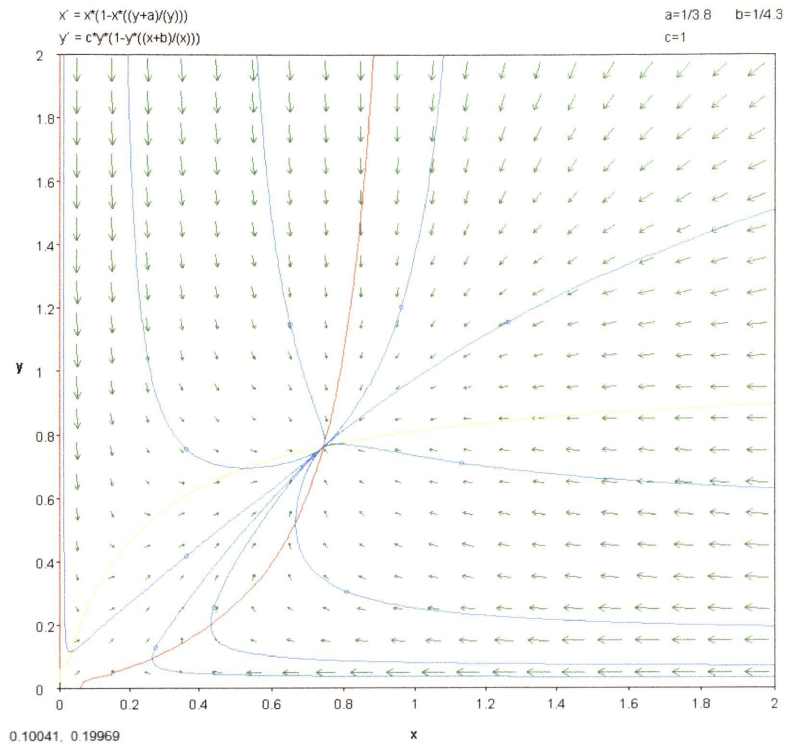
solutions to  $x$  and  $y$  will approach zero. The phase plane analysis and phase portrait

when  $\alpha\beta > 1$  are in Figure 15 and Figure 16 respectively. The phase plane analysis and

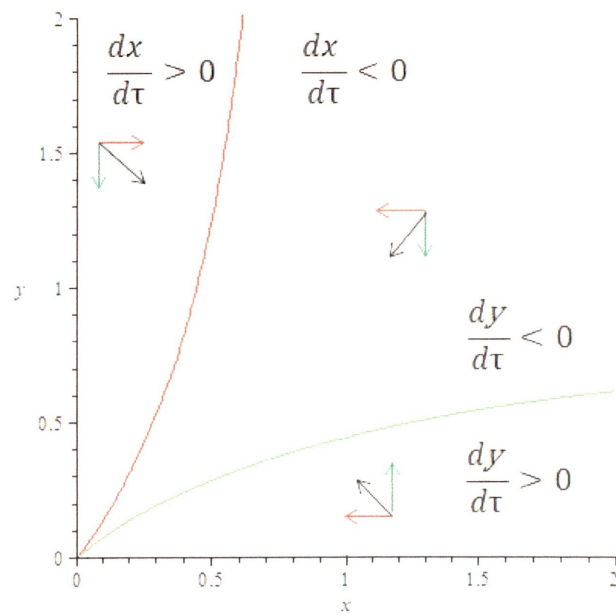
phase portrait when  $\alpha\beta < 1$  are in Figure 17 and Figure 18 respectively.



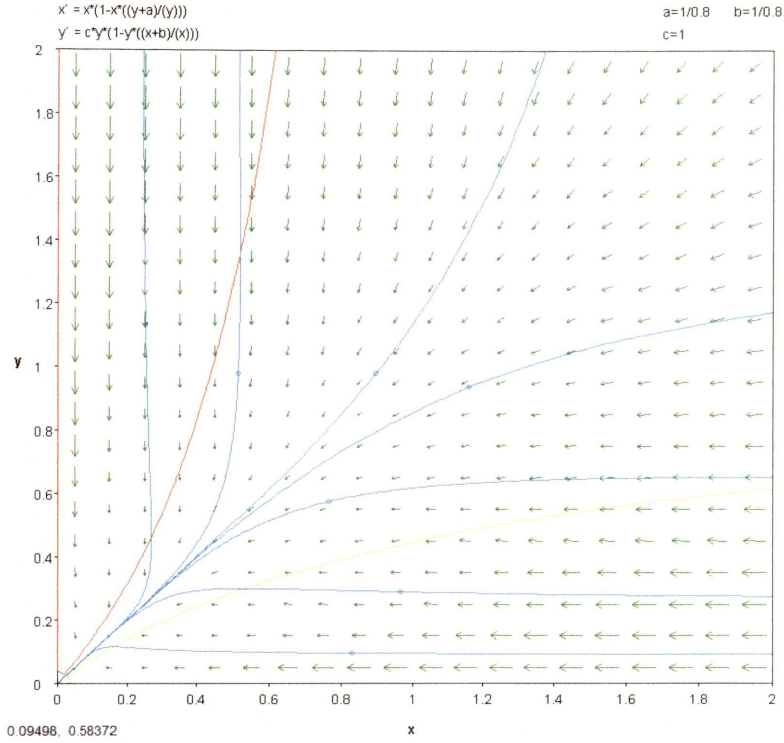
**Figure 15. Obligate-Obligate Case 1 Phase Plane Analysis**



**Figure 16. Obligate-Obligate Phase Case 1 Phase Portrait**



**Figure 17. Obligate-Obligate Case 2 Phase Plane Analysis**



**Figure 18. Obligate-Obligate Phase Case 2 Phase Portrait**

The nullclines for **facultative-facultative** model are:

$$x = 0, \quad y = \frac{\alpha x - \delta}{1 - \varepsilon}$$

$$y = 0, \quad y = \frac{x + \varepsilon}{x + \beta}$$

Equilibrium points are

$$(0, 0), \left( \frac{-(\alpha\beta + \varepsilon - \delta - 1) + \sqrt{(\alpha\beta + \varepsilon - \delta - 1)^2 + 4(\alpha + 1)(\beta\delta + \varepsilon)}}{2(\alpha + 1)}, \frac{-(\alpha\beta + \varepsilon - \delta - 1) + 2\alpha\varepsilon + \sqrt{(\alpha\beta + \varepsilon - \delta - 1)^2 + 4(\alpha + 1)(\beta\delta + \varepsilon)}}{\alpha\beta - \varepsilon + \delta + 1 + 2\beta + \sqrt{(\alpha\beta + \varepsilon - \delta - 1)^2 + 4(\alpha + 1)(\beta\delta + \varepsilon)}} \right)$$

,  $\left(\frac{\delta}{\alpha}, 0\right), \left(0, \frac{\varepsilon}{\beta}\right)$ . The nullclines will always intersect in the first quadrant at the point

$$\left( \frac{-(\alpha\beta + \varepsilon - \delta - 1) + \sqrt{(\alpha\beta + \varepsilon - \delta - 1)^2 + 4(\alpha + 1)(\beta\delta + \varepsilon)}}{2(\alpha + 1)}, \frac{-(\alpha\beta + \varepsilon - \delta - 1) + 2\alpha\varepsilon + \sqrt{(\alpha\beta + \varepsilon - \delta - 1)^2 + 4(\alpha + 1)(\beta\delta + \varepsilon)}}{\alpha\beta - \varepsilon + \delta + 1 + 2\beta + \sqrt{(\alpha\beta + \varepsilon - \delta - 1)^2 + 4(\alpha + 1)(\beta\delta + \varepsilon)}} \right).$$

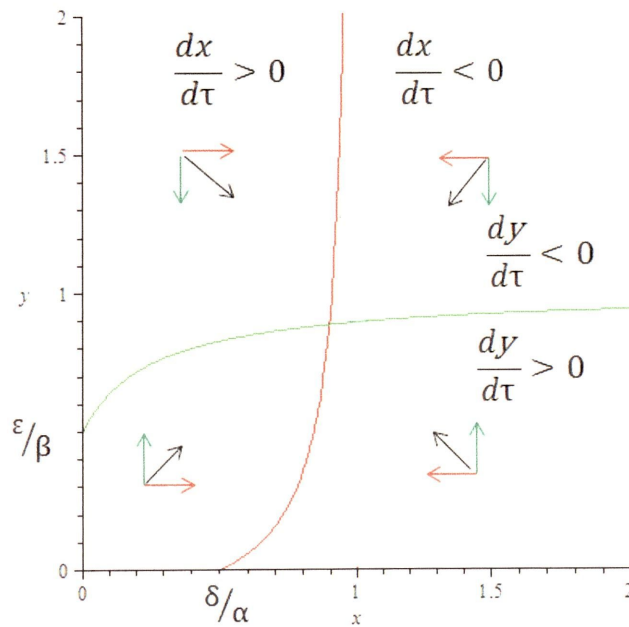
This is because the nullclines will start at  $y = \varepsilon/\beta$  and increase asymptotically to  $y = 1$  for

the y-nullcline, and start at  $x = \delta/\alpha$  increase asymptotically to  $x = 1$  for the x-nullcline.

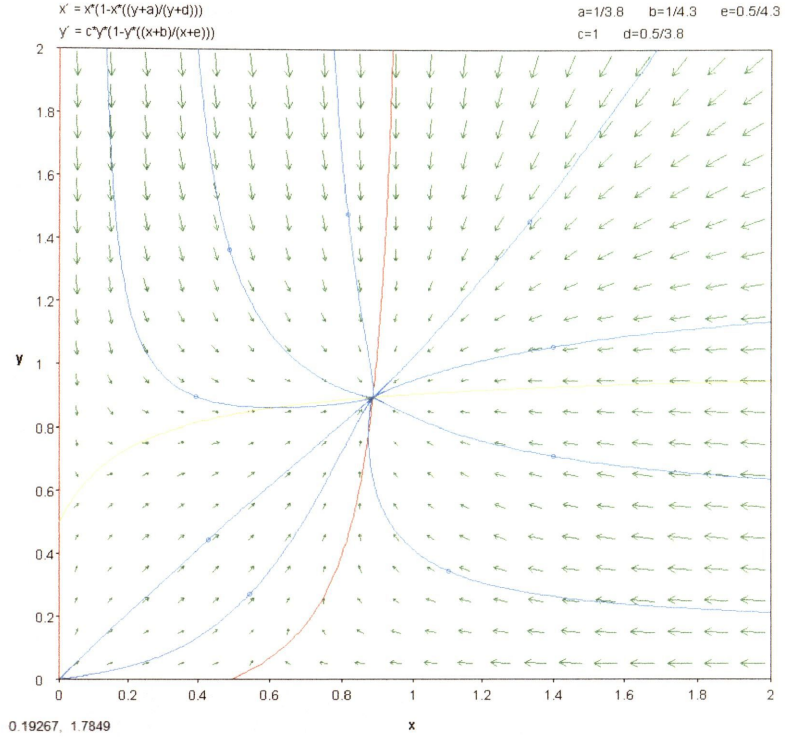
The intersection will be  $(\delta/\alpha < x < 1, \varepsilon/\beta < y < 1)$ . Furthermore the intersection will be a

sink point, while  $(\frac{\delta}{\alpha}, 0)$ ,  $(0, \frac{\varepsilon}{\beta})$  will be saddle points, and  $(0,0)$  will be a source. The

phase plane analysis and phase portrait are in Figure 19 and Figure 20 respectively.



**Figure 19. Facultative-Facultative Phase Plane Analysis**



**Figure 20. Facultative-Facultative Phase Portrait**

The nullclines for **obligate-facultative** model are:

$$x = 0, \quad y = \frac{\alpha x}{1 - x}$$

$$y = 0, \quad y = \frac{x + \varepsilon}{x + \beta}$$

Equilibrium points are

$$(0, 0), \left( \frac{-(\alpha\beta + \varepsilon - 1) + \sqrt{(\alpha\beta + \varepsilon - 1)^2 + 4(\alpha + 1)(\varepsilon)}}{2(\alpha + 1)}, \frac{-(\alpha\beta + \varepsilon - 1) + 2\alpha\varepsilon + \sqrt{(\alpha\beta + \varepsilon - 1)^2 + 4(\alpha + 1)(\varepsilon)}}{\alpha\beta - \varepsilon + 1 + 2\beta + \sqrt{(\alpha\beta + \varepsilon - 1)^2 + 4(\alpha + 1)(\varepsilon)}} \right), \left( 0, \frac{\varepsilon}{\beta} \right).$$

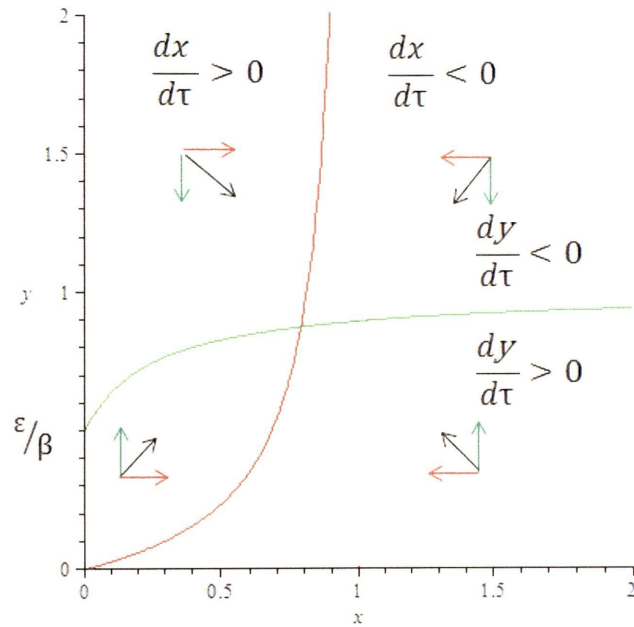
The nullclines will always intersect in the first quadrant at the

$$\text{point} \left( \frac{-(\alpha\beta + \varepsilon - 1) + \sqrt{(\alpha\beta + \varepsilon - 1)^2 + 4(\alpha + 1)(\varepsilon)}}{2(\alpha + 1)}, \frac{-(\alpha\beta + \varepsilon - 1) + 2\alpha\varepsilon + \sqrt{(\alpha\beta + \varepsilon - 1)^2 + 4(\alpha + 1)(\varepsilon)}}{\alpha\beta - \varepsilon + 1 + 2\beta + \sqrt{(\alpha\beta + \varepsilon - 1)^2 + 4(\alpha + 1)(\varepsilon)}} \right). \text{ This is}$$

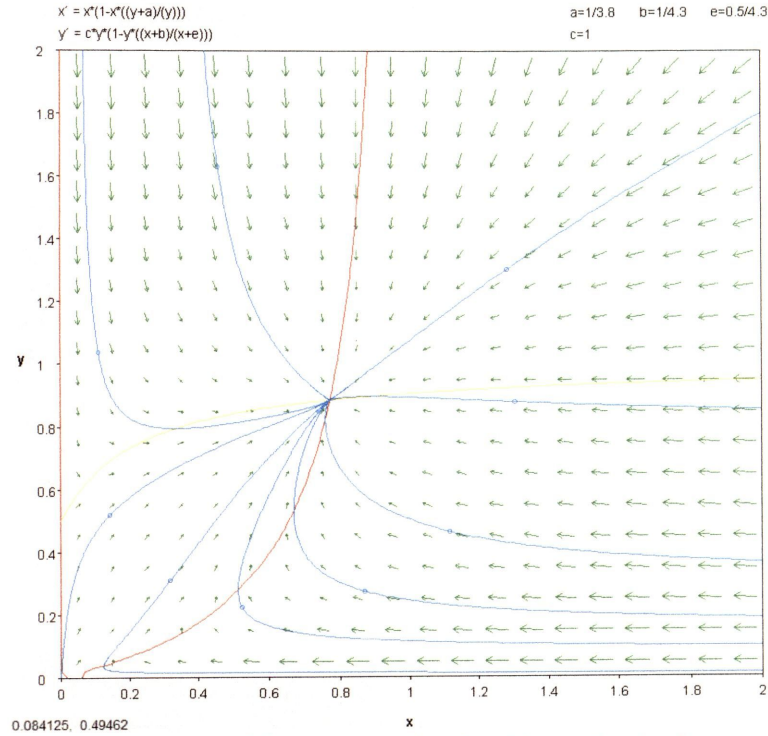
because the nullclines will start at  $y = \varepsilon/\beta$  and increase asymptotically to  $y = 1$  for the  $y$ -nullcline, and start at  $x = 0$  and increase asymptotically to  $x = 1$  for the  $x$ -nullcline. The



intersection will be  $(0 < x < 1, \varepsilon/\beta < y < 1)$ . Furthermore the intersection will be a sink point, while  $(0,0), (0, \frac{\varepsilon}{\beta})$  will be saddle points. The phase plane analysis and phase portrait are in Figure 21 and Figure 22 respectively.



**Figure 21. Obligate-Facultative Phase Plane Analysis**



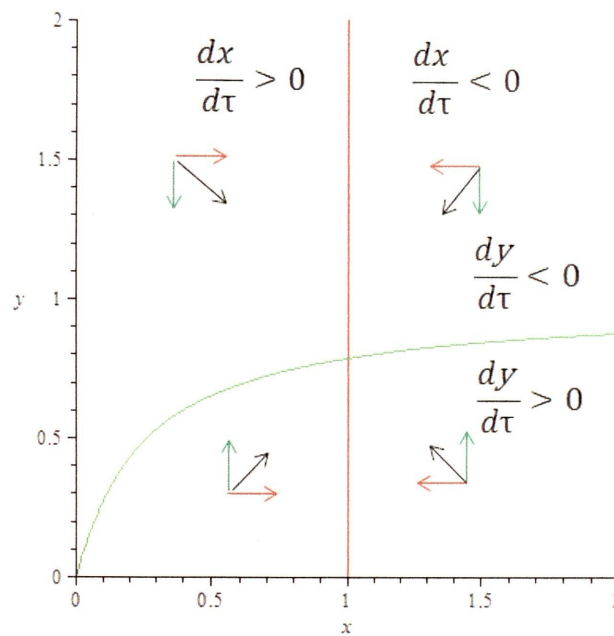
**Figure 22. Obligate-Facultative Phase Portrait**

The nullclines for **commensal-obligate** model are:

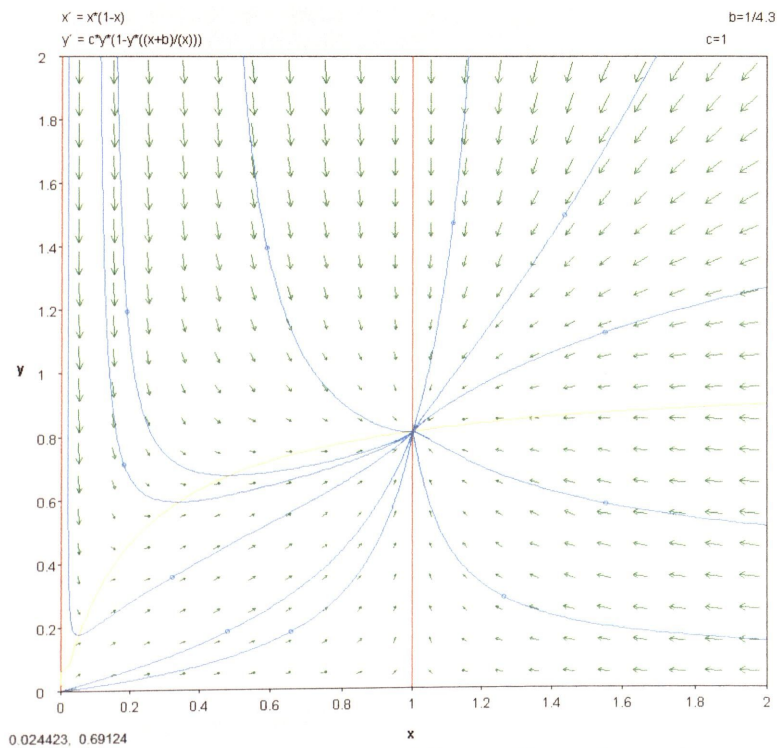
$$x = 0, \quad x = 1$$

$$y = 0, \quad y = \frac{x}{x + \beta}$$

Equilibrium points are  $(0, 0)$ ,  $(1, \frac{1}{1+\beta})$ ,  $(1, 0)$ . The intersection point  $(1, \frac{1}{1+\beta})$  will always be in the first quadrant, and will be a sink. Points  $(0, 0)$ ,  $(1, 0)$  will be saddle points. The phase plane analysis and phase portrait are in Figure 23 and Figure 24 respectively.



**Figure 23. Commensal-Obligate Phase Plane Analysis**



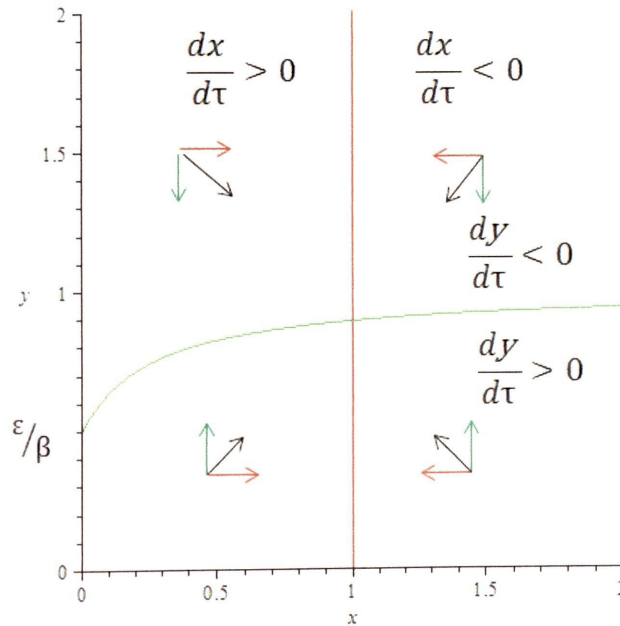
**Figure 24. Commensal-Obligate Phase Portrait**

The nullclines for **commensal-facultative** model are:

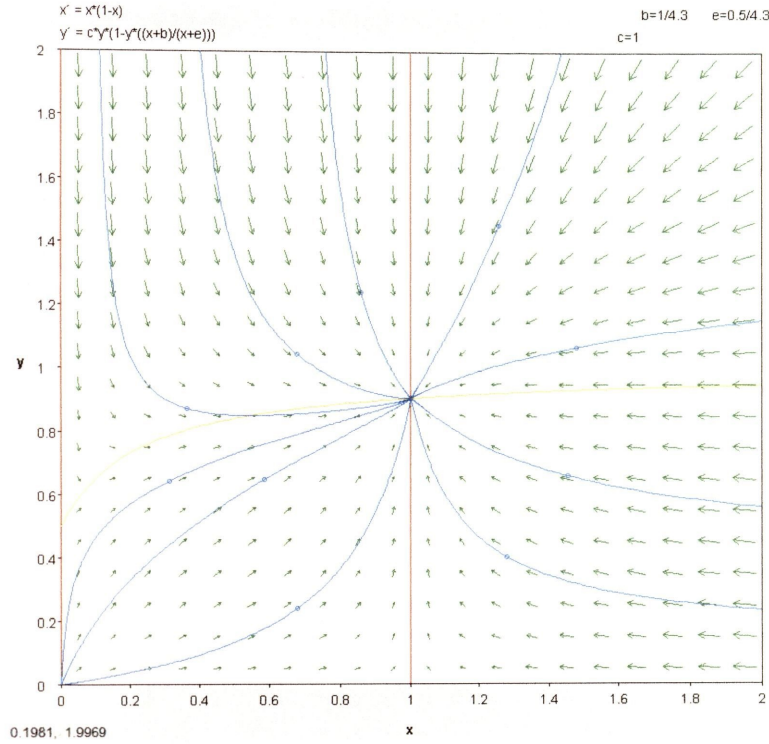
$$x = 0, \quad x = 1$$

$$y = 0, \quad y = \frac{x + \varepsilon}{x + \beta}$$

Equilibrium points are  $(0, 0)$ ,  $(1, \frac{1+\varepsilon}{1+\beta})$ ,  $(1, 0)$ ,  $(0, \frac{\varepsilon}{\beta})$ . The intersection point  $(1, \frac{1+\varepsilon}{1+\beta})$  will always be in the first quadrant, and will be a sink. Points  $(0, 0)$ ,  $(1, 0)$  will be saddle points. The phase plane analysis and phase portrait are in Figure 25 and Figure 26 respectively.



**Figure 25. Commensal-Facultative Phase Plane Analysis**



**Figure 26. Commensal-Facultative Phase Portrait**

The nullclines for **parasitic** model are:

$$x = 0, \quad y = \frac{1-x}{\eta x}$$

$$y = 0, \quad y = \frac{x}{x + \beta}$$

Equilibrium points are  $(0, 0), \left( \frac{1-\beta+\sqrt{\beta^2+2\beta+4\beta\eta+1}}{2(\eta+1)}, \frac{1-\beta+\sqrt{\beta^2+2\beta+4\beta\eta+1}}{1+\beta+2\beta\eta+\sqrt{\beta^2+2\beta+4\beta\eta+1}} \right), (1, 0)$ . The

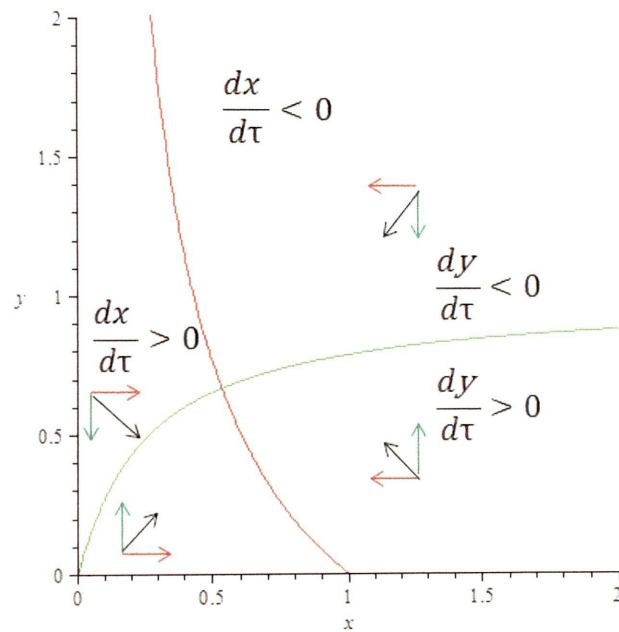
intersection point  $\left( \frac{1-\beta+\sqrt{\beta^2+2\beta+4\beta\eta+1}}{2(\eta+1)}, \frac{1-\beta+\sqrt{\beta^2+2\beta+4\beta\eta+1}}{1+\beta+2\beta\eta+\sqrt{\beta^2+2\beta+4\beta\eta+1}} \right)$  will always be in the

first quadrant. This is because the nullclines will start at  $y = 0$  and increase

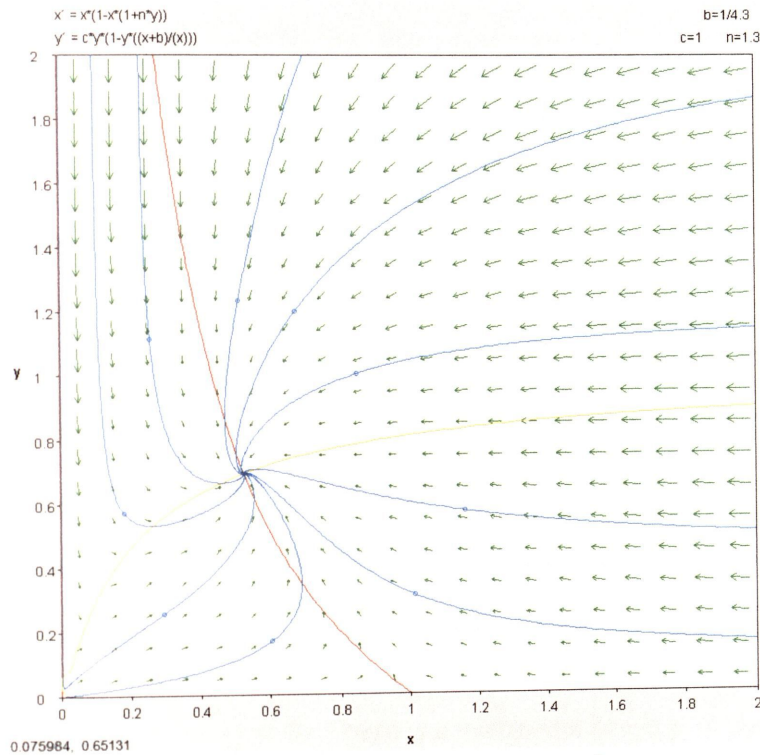
asymptotically to  $y = 1$  for the  $y$ -nullcline, and start at  $x = 1$  and decrease asymptotically

to  $x = 0$  for the  $x$ -nullcline. The intersection will be  $(0 < x < 1, 0 < y < 1)$ . Furthermore,

the intersection will be a sink point, while (0,0), (1,0) will be saddle points. The phase plane analysis and phase portrait are in Figure 27 and Figure 28 respectively.



**Figure 27. Parasitic Phase Plane Analysis**



**Figure 28. Parasitic Phase Portrait**

### Limits for obligate mutualism

For obligate mutualism, in either  $x$  or  $y$ , the equations can be written in a simplified way:

$$\frac{dx}{d\tau} = x - x^2 - \frac{\alpha x^2}{y}$$

$$\frac{dy}{d\tau} = \gamma y - \gamma y^2 - \frac{\gamma \beta y^2}{x}$$

Neither  $x$  nor  $y$  can be equal to zero. To find out what is happening at  $x = 0$  or  $y = 0$ , the limits must be found. The limits as  $x$  and  $y$  approach zero from the right are:

$$\lim_{x \rightarrow 0^+} \frac{dx}{d\tau} = 0, \quad \lim_{y \rightarrow 0^+} \frac{dx}{d\tau} = -\infty$$

$$\lim_{x \rightarrow 0^+} \frac{dy}{d\tau} = -\infty, \quad \lim_{y \rightarrow 0^+} \frac{dy}{d\tau} = 0$$

The limits as x and y approach zero from the left are:

$$\lim_{x \rightarrow 0^-} \frac{dx}{d\tau} = 0, \quad \lim_{y \rightarrow 0^-} \frac{dx}{d\tau} = +\infty$$

$$\lim_{x \rightarrow 0^-} \frac{dy}{d\tau} = +\infty, \quad \lim_{y \rightarrow 0^-} \frac{dy}{d\tau} = 0$$

To get a better idea of what will happen when the system approaches (0,0), the nullcline will be analyzed again. The equation for the y-nullcline for an obligate mutualist or is  $\gamma y \left( 1 - y \left( \frac{x+\beta}{x} \right) \right) = 0$ . There is a horizontal line is  $y = 0$ , and the line  $y = \frac{x}{x+\beta}$  has an asymptote at  $x = 0$  where the limit as x approaches zero from the right is negative infinity and from the left positive infinity. The equation for the x-nullcline for an obligate mutualist is  $x \left( 1 - x \left( \frac{y+\alpha}{y} \right) \right) = 0$ . There is a vertical line is  $x = 0$ , and the line  $y = \frac{\alpha x}{1-x}$  has an asymptote at  $y = 0$  where the limit as y approaches zero from the right is negative infinity and from the left is positive infinity. Therefore, the limit as (x,y) approaches (0,0) does not exist.

To get a better idea of what is happening at the equilibrium point at (0,0), the Jacobian matrix will be analyzed:



$$\begin{bmatrix} 1 - 2x - \frac{2\alpha x}{y} & \frac{\alpha x^2}{y^2} \\ \frac{\gamma\beta y^2}{x^2} & \gamma - 2\gamma y - \frac{2\gamma y}{x} \end{bmatrix}$$

The limit as x approaches zero from the right for the Jacobian matrix:

$$\begin{bmatrix} \lim_{x \rightarrow 0^+} \left( 1 - 2x - \frac{2\alpha x}{y} \right) & \lim_{x \rightarrow 0^+} \frac{\alpha x^2}{y^2} \\ \lim_{x \rightarrow 0^+} \frac{\gamma\beta y^2}{x^2} & \lim_{x \rightarrow 0^+} \left( \gamma - 2\gamma y - \frac{2\gamma y}{x} \right) \end{bmatrix} = \begin{bmatrix} 0 & 0 \\ +\infty & -\infty \end{bmatrix}$$

The limit as y approaches zero from the right for the Jacobian matrix:

$$\begin{bmatrix} \lim_{y \rightarrow 0^+} \left( 1 - 2x - \frac{2\alpha x}{y} \right) & \lim_{y \rightarrow 0^+} \frac{\alpha x^2}{y^2} \\ \lim_{y \rightarrow 0^+} \frac{\gamma\beta y^2}{x^2} & \lim_{y \rightarrow 0^+} \left( \gamma - 2\gamma y - \frac{2\gamma y}{x} \right) \end{bmatrix} = \begin{bmatrix} +\infty & -\infty \\ 0 & 0 \end{bmatrix}$$

The limit as x approaches zero from the left for the Jacobian matrix:

$$\begin{bmatrix} \lim_{x \rightarrow 0^-} \left( 1 - 2x - \frac{2\alpha x}{y} \right) & \lim_{x \rightarrow 0^-} \frac{\alpha x^2}{y^2} \\ \lim_{x \rightarrow 0^-} \frac{\gamma\beta y^2}{x^2} & \lim_{x \rightarrow 0^-} \left( \gamma - 2\gamma y - \frac{2\gamma y}{x} \right) \end{bmatrix} = \begin{bmatrix} 0 & 0 \\ -\infty & +\infty \end{bmatrix}$$

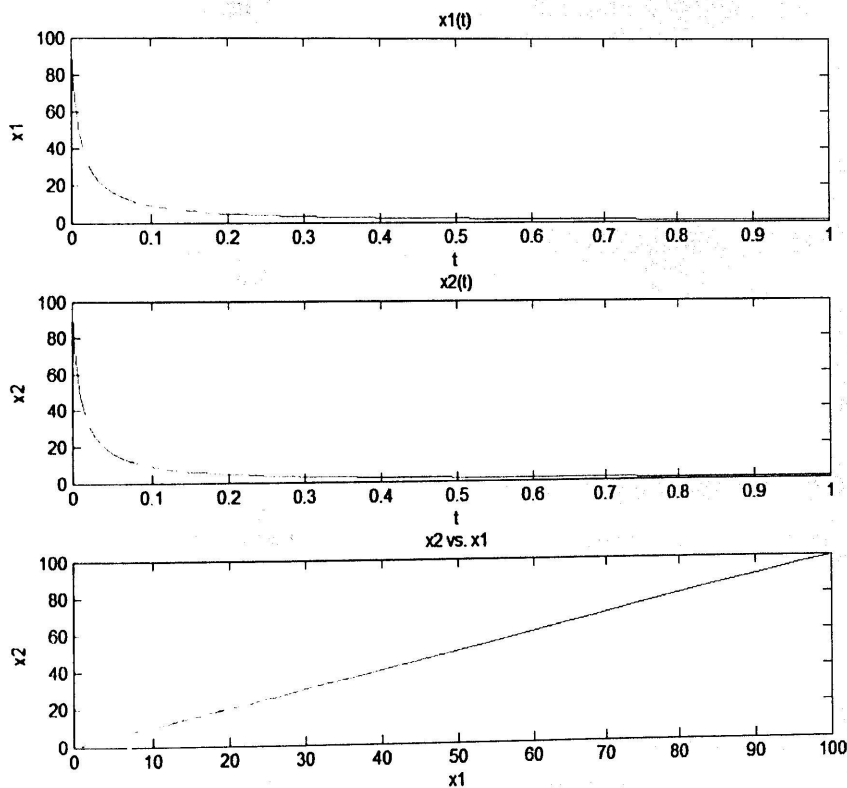
The limit as y approaches zero from the left for the Jacobian matrix:

$$\begin{bmatrix} \lim_{y \rightarrow 0^-} \left( 1 - 2x - \frac{2\alpha x}{y} \right) & \lim_{y \rightarrow 0^-} \frac{\alpha x^2}{y^2} \\ \lim_{y \rightarrow 0^-} \frac{\gamma\beta y^2}{x^2} & \lim_{y \rightarrow 0^-} \left( \gamma - 2\gamma y - \frac{2\gamma y}{x} \right) \end{bmatrix} = \begin{bmatrix} -\infty & +\infty \\ 0 & 0 \end{bmatrix}$$

Since the limits as x and y approach zero are not equal, and the limits from the left and right are not equal, the limit for the Jacobian matrix at (0,0) does not exist.

Since the limits do not exist, the nullcline and Jacobian provide useful information, but tell nothing of what the trajectories will approach if x and y approach

zero. The only case where this would happen is in the obligate-obligate model where  $\alpha\beta < 1$ , or Case 2 seen in Figures 17 and 18. To investigate further, the numerical solution will be found for this case. This is done using Matlab's fourth/fifth order Runge-Kutta method. The results can be seen in Figure 29.



**Figure 29. Numerical Solution to Obligate-Obligate**

The solutions for  $x$  and  $y$  will decrease asymptotically to zero. This would be a collapse for both populations. Therefore, if two species are both obligate mutualists in relation to each other, and the constants  $a_1$  and  $a_2$  are less than one, then both species will become extinct.

## CHAPTER IV

### CONCLUSION

Since symbiosis is a complex phenomenon with different types of relationship for each species, a mathematical model of symbiosis needs the same characteristics. Some of the models in Chapter II did not address this, such as Pistorius-Utterback and Wright. Yukalov's model does address the different types of symbiosis, but not whether a species is obligate or facultative. However, like Pistorius-Utterback it can exhibit unlimited growth which is biologically unrealistic. Dean's model does address obligate or facultative mutualism, but not the other types of symbiosis, commensalism or parasitism. Dean's model can also lead to unstable behavior for certain values of the coefficients.

The new model of symbiosis, presented in Chapter III, does address the different types of symbiosis, as well as obligate and facultative species. Furthermore, the models have stable positive equilibria. The parasitic model is similar to the Leslie-Gower predator prey model, except that there is an extra term added to the predator (parasite) for intra-species competition. This changes the phase portrait significantly. There is an issue with the models that have obligate species, in which the system cannot be zero for either species. However, the solutions will only converge to zero in one particular case, which is in the obligate-obligate model in Case 2. As shown, the limits of the system at

the origin do not exist. However, in the numerical solution, it is shown that in this case, that the solution will asymptotically fall to zero. This would effectively be an extinction of both species. In all other types of symbiosis, whether with obligate or facultative species, there will be a positive solution for both species, as shown in the existence of positive stable equilibria. Therefore, this new model can be a useful model for symbiosis.

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