

POPULATION DYNAMICS
BEYOND CLASSIC LOTKA-VOLTERRA MODELS

by

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This thesis was prepared under the direction of the candidate's thesis advisor, Dr. Eugene Belogay, and has been approved by the members of her supervisory committee. It was submitted to the faculty of The Harriet L. Wilkes Honors College and was accepted in partial fulfillment of the requirements for the degree of Bachelor of Arts in Liberal Arts and Sciences.

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Abstract

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Motivated by the brown tree snake invasion on Guam, we use mathematics to model the interaction between a predator species and several prey species. Starting with the basics, we present a hierarchy of models, which goes beyond the textbook classics of exponential growth and Lotka-Volterra predation. Each model is more realistic and more complicated than the one before.

After we justify each model and explain the biological meaning of its parameters, we turn our assumptions into a non-linear system of ordinary differential equations and analyze its nullclines and equilibrium points from a symbolic, numerical, and geometric point of view. We also study the long-term behavior of the solutions to each system, providing biological interpretation of the mathematical results and finding a few surprises along the way.

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1 Introduction

The motivation for the investigation in this thesis is an invading predator. The brown tree snake, *Boiga Irregulars*, was accidentally introduced to Guam in the late 1940s, when it was carried to the island by military cargo. The snake ate the most abundant species of birds, lizards, and mammals, and drove them to extinction. In an attempt to find a realistic mathematical model for this unusual situation—a model that describes the changing populations of predator and prey, we consider a hierarchy of population growth models.

We explain each model in words and translate assumptions into mathematical formulas. After working through a simple example, we analyze the long-term behavior of each population. We conclude the study of each model by discussing its advantages and drawbacks, as well as its relation to the simpler models in the hierarchy.

Chapter 2 provides a brief review of differential equations techniques, such as the use of Jacobian matrices and eigenvalues to analyze the equilibria of a system of differential equations. Chapter 3 presents two classic one-species population models: the exponential and the logistic growth models. In the next chapter, we study the interaction of two species—one predator and one prey. We begin with the classic Lotka-Volterra model and expand it by introducing more intricate terms. For example, in Chapter 6, we modify the predation term so that it accounts for the snakes getting more full with each rabbit they eat. We aim to make the models

“more realistic” by going beyond the textbook to discover the surprising change of behavior when a third species is added to the mix.

Most Calculus and Differential Equations textbooks end the discussion of population growth models at the classic Lotka-Volterra predator-prey models, creating the impression that population growth models do not exist beyond two species. As we will see, simple modifications of the classic model exhibit more interesting behavior and even a few surprises. We hope this thesis helps better the understanding of classic population growth models and the surprising behavior that occurs when small changes are made to these classic models.

2 Background

In this chapter, we review basic definitions and techniques covered in a traditional differential equations course. The presentation and notation here follows [BDH]. First, we briefly discuss linear systems and methods to analyze their equilibria. Then we explain how these linear techniques determine the behavior of non-linear systems, which are the focus of this investigation. This chapter is essentially a crash course in differential equations.

2.1 Linear Systems of Differential Equations

The simplest types of systems of differential equations are autonomous linear systems, such as the system

$$dx/dt = ax + by$$

$$dy/dt = cx + dy.$$

It is called linear because all functions on its right-hand side are linear; it is called autonomous because the independent variable t (usually time) does not appear on the right-hand side. The right-hand side can be rewritten in the matrix form:

$$\begin{bmatrix} dx/dt \\ dy/dt \end{bmatrix} = \begin{bmatrix} a & b \\ c & d \end{bmatrix} \begin{bmatrix} x \\ y \end{bmatrix}.$$

The only equilibrium point for a linear system is $(0, 0)$, and the behavior of solutions near the origin is determined by the eigenvalues of the matrix $\begin{bmatrix} a & b \\ c & d \end{bmatrix}$.

A standard approach to understand the behavior of a non-linear system near an equilibrium point is to approximate the non-linear system by a linear system (see Section 2.3).

2.2 Non-linear Systems of Differential Equations

A non-linear system is the set of non-linear differential equations such as

$$\begin{aligned}dx/dt &= ax^2 + by \\ dy/dt &= cx^2 + dy^3.\end{aligned}$$

It is rare to find explicit solutions to systems with more than two dependent variables, so we rely on qualitative, numeric, and geometric methods. We discuss the techniques for understanding the solutions and long-term behavior of autonomous linear systems and then explain how these linearization techniques can be used for autonomous non-linear systems.

2.3 Tricks in the Toolbox

We discuss some linear system “tricks” that help us understand the behavior of non-linear systems near equilibrium points.

2.3.1 Nullclines and Equilibrium Points

Nullclines are usually simple to compute; yet, they can often give us plenty of information about a system and the behavior of its solutions.

Definition 2.1. Consider the system

$$dx/dt = f(x, y)$$

$$dy/dt = g(x, y).$$

The set of points (x, y) such that $f(x, y)=0$ is called the ***x-nullcline***. Similarly, the set of points (x, y) where $g(x, y)=0$ is the ***y-nullcline***.

Along the x -nullcline, $dx/dt = 0$ and the x -component of the vector field is 0, so the vector field is vertical, that is, points up or down. We mark the x -nullcline with vertical tick marks. Note that the x -component is 0 *only* on the x -nullcline; it is positive or negative on the rest of the phase plane. If $dx/dt > 0$, then solutions move to the right; if $dx/dt < 0$, then solutions move to the left.

Similarly, along the y -nullcline, the y -component of the vector field is 0, so the vector field is horizontal, that is, points to the left or right and we mark the y -nullcline with horizontal tick marks. If $dy/dt > 0$, then solutions moves up. If $dy/dt < 0$, then solutions moves down.

Definition 2.2. An ***equilibrium point*** occurs when both $x(t)$ and $y(t)$ are constant, so $dx/dt = 0$ and $dy/dt = 0$. Therefore, we look for equilibrium points by finding points (x, y) where $dx/dt = f(x, y) = 0$ and $dy/dt = g(x, y) = 0$.

Since $f(x, y)=g(x, y)=0$ at an equilibrium point, the equilibrium points occur at the intersections of the x - and y -nullcline.

Example 1. Consider the non-linear autonomous system

$$dx/dt = 2x - xy$$

$$dy/dt = -y + 2xy.$$

The x -nullcline is the set of points where $2x - xy = 0$. Since this equation is equivalent to $x(2 - y) = 0$, the x -nullcline consists of two lines: $x = 0$ and $y = 2$ (see Figure 1). Similarly, the y -nullcline is the set of points where $-y + 2xy = y(-1 + 2x) = 0$, which also consists of two lines: $y = 0$ and $x = 1/2$. The equilibrium points occur where the x - and y -nullcline intersect. The x -nullcline intersects the y -nullcline at two points, $(0, 0)$ and $(1/2, 2)$, which are the only equilibrium points for this system.

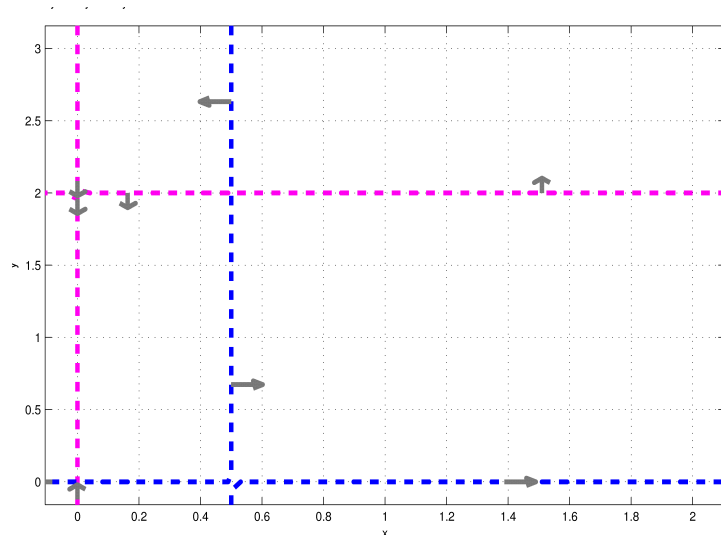


Figure 1: Nullclines and equilibrium points for Example 1.

2.3.2 The Jacobian Matrix

At an equilibrium point, the solution remains constant and nothing changes, but we want to understand the behavior of solutions *near* an equilibrium point. This behavior is determined by the Jacobian matrix of the system.

Definition 2.3. *The **Jacobian matrix** for the system*

$$dx/dt = f(x, y)$$

$$dy/dt = g(x, y)$$

is the matrix of partial derivatives

$$J(x, y) = \begin{bmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{bmatrix}.$$

Example 1. Computing the four partial derivatives for the system

$$dx/dt = 2x - xy$$

$$dy/dt = -y + 2xy,$$

we find that its Jacobian matrix is

$$J(x, y) = \begin{bmatrix} 2 - y & -x \\ 2y & -1 + 2x \end{bmatrix}.$$

At the equilibrium point $(0, 0)$, the Jacobian matrix evaluates to

$$J(0,0) = \begin{bmatrix} 2 & 0 \\ 0 & -1 \end{bmatrix},$$

and at $(1/2, 2)$, it evaluates to

$$J(1/2,2) = \begin{bmatrix} 0 & -1/2 \\ 4 & 0 \end{bmatrix}.$$

This means that near $(0, 0)$, our system behaves like the system

$$dx/dt = 2x$$

$$dy/dt = -y$$

and near $(1/2, 2)$, it behaves like the system

$$dx/dt = -y/2$$

$$dy/dt = 4x.$$

2.3.3 Eigenvalues

The **eigenvalues** of a Jacobian matrix help us understand the graphical behavior of solutions near equilibrium points. The eigenvalues of a matrix A are the values of λ such that

$$\det(A - \lambda I) = 0,$$

where I is the identity matrix.

The eigenvalues of the 2×2 matrix, $\begin{bmatrix} a & b \\ c & d \end{bmatrix}$, are the roots of its characteristic polynomial

$$\lambda^2 - (a + d)\lambda + (ad - bc) = 0.$$

Example 1. Recall the Jacobian matrix

$$J(0, 0) = \begin{bmatrix} 2 & 0 \\ 0 & -1 \end{bmatrix},$$

for the equilibrium point $(0, 0)$ that we computed earlier. This matrix has the characteristic polynomial

$$\lambda^2 - (1)\lambda + (-2 - 0) = \lambda^2 - \lambda - 2,$$

which has two real roots (eigenvalues) $\lambda_1 = -1$ and $\lambda_2 = 2$.

Recall that the system in our example has two equilibrium points. At the second equilibrium,

$$J(1/2, 2) = \begin{bmatrix} 0 & -1/2 \\ 4 & 0 \end{bmatrix}.$$

This matrix has the characteristic polynomial

$$\lambda^2 - (0)\lambda + (0 - (-2)) = \lambda^2 + 2,$$

which has two complex roots (eigenvalues) $\lambda_1 = i\sqrt{2}$ and $\lambda_2 = -i\sqrt{2}$.

2.3.4 Classification of Equilibrium Points

We classify equilibria by the behavior of the solutions that pass near them. To do this, we look at the sign and type (real or complex) of the eigenvalues that are associated with each equilibrium point.

Real Eigenvalues The sign of a real eigenvalue plays a key role in determining the behavior of solutions near the corresponding equilibrium point. We discuss three possible behaviors associated with real eigenvalues:

- A **saddle** occurs when there is at least one negative and at least one positive eigenvalue. Only few solutions are attracted to the equilibrium point over time; most are repelled away.
- A **sink** occurs when all eigenvalues are negative. Solutions are attracted to the equilibrium point over time.
- A **source** occurs when all eigenvalues are positive. Solutions are repelled away from the equilibrium point over time.

Complex Eigenvalues Complex eigenvalues come in conjugate pairs, and are of the form $a \pm ib$ where $b \neq 0$. There are three possible behaviors associated with complex eigenvalues, as well:

- A **spiral source** occurs when $a > 0$ and $b \neq 0$.
- A **spiral sink** occurs when $a < 0$ and $b \neq 0$.
- A **center** occurs when $a = 0$ and $b \neq 0$. Here, the solution will return to the initial condition in a periodic fashion; its trajectory is a closed curve, often called a cycle.

Stability An equilibrium point is **stable** if initial conditions (near the equilibrium) produce solutions that are attracted to the equilibrium point over time. This means that small changes in initial conditions will not affect the solutions, and they will still tend toward the equilibrium point. Sinks and spiral sinks are stable since nearby solutions are attracted toward the equilibrium over time.

An equilibrium point is **unstable** if initial conditions (near the equilibrium) produce solutions that repel away from the equilibrium point over time. Near unstable equilibria, small changes in initial conditions can drastically affect solutions. Saddles, sources, and spiral sources are unstable equilibrium points since they repel solutions over time. Note that a saddle cannot occur in one-dimension, since it needs at least one positive and one negative eigenvalue.

Figure 2 from [BDH] summarizes the different types of equilibrium points, based on the eigenvalues.

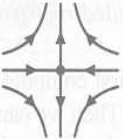

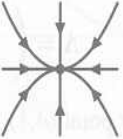

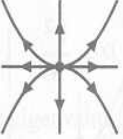

Type	Eigenvalues	Phase Plane	Type	Eigenvalues	Phase Plane
Saddle	$\lambda_1 < 0 < \lambda_2$		Spiral Sink	$\lambda = a \pm ib$ $a < 0, b \neq 0$	
Sink	$\lambda_1 < \lambda_2 < 0$		Spiral Source	$\lambda = a \pm ib$ $a > 0, b \neq 0$	
Source	$0 < \lambda_1 < \lambda_2$		Center	$\lambda = \pm ib$ $b \neq 0$	

Figure 2: Different types of equilibrium points, from [BDH].

2.3.5 The Phase Plane

Graphs can give us a good idea of how populations change over time. We can look at graphs of x and y against time t , but it is often easier to look at a graph of y against x . We plot a point (x, y) representing the population $x(t)$ and $y(t)$, at any given time t . As each population changes, the point (x, y) moves. This xy -plane is called the **phase plane**, and the path that this point follows is called the **phase trajectory**.

Example 1. Recall that the Jacobian matrix for the equilibrium $(0, 0)$ had eigenvalues $\lambda_1 = -1$ and $\lambda_2 = 2$, which are both real. Since there is one negative and one positive eigenvalue, $(0, 0)$ is a saddle point, and solutions originating near this point will be repelled away from $(0, 0)$ over time.

The Jacobian matrix for the equilibrium $(1/2, 2)$ has eigenvalues $\lambda_1 = i\sqrt{2}$ and $\lambda_2 = -i\sqrt{2}$, which are complex. Since the eigenvalues have no real part, this equilibrium point is a center; solutions follow a closed curve around the equilibrium point $(1/2, 2)$ over time, as in the phase plane seen in Figure 3.

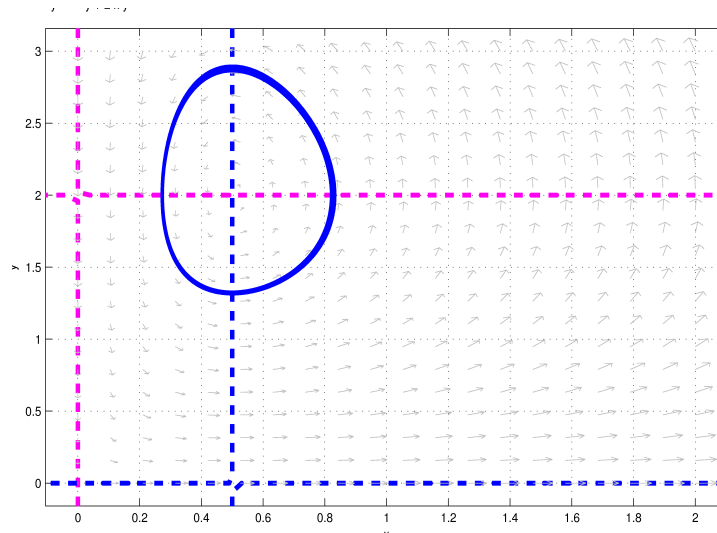


Figure 3: Closed curve trajectory around $(1/2, 2)$ for Example 1.

2.3.6 First Integrals

Definition 2.4. A function $H(x, y)$ is called a **first integral** if $H(x(t), y(t)) = C$, for some constant C and for all solutions $(x(t), y(t))$.

In some cases, we are able to compute the first integral of a system, by going from an autonomous system to a single differential equation. Consider the system

$$\begin{aligned} dx/dt &= f(x, y) \\ dy/dt &= g(x, y). \end{aligned}$$

We eliminate t by using the chain rule and rewriting the system as

$$\frac{dy}{dx} = \frac{dy/dt}{dx/dt} = \frac{g(x, y)}{f(x, y)}.$$

If this differential equation can be solved, we get the first integral of the system and a symbolic representation of the trajectories in the xy -plane.

Example 1. To compute a first integral for our system

$$\begin{aligned} dx/dt &= 2x - xy \\ dy/dt &= -y + 2xy, \end{aligned}$$

we rewrite it as a single differential equation, using the chain rule:

$$\frac{dy}{dx} = \frac{-y + 2xy}{2x - xy} = \frac{y(2x - 1)}{x(2 - y)}.$$

Separating the variables, we have

$$\int \frac{2x - 1}{x} dx = \int \frac{2 - y}{y} dy.$$

We integrate both sides to get

$$2x + y - \ln|x| - 2\ln|y| = C,$$

where C is the integration constant. Hence, we have a symbolic representation of the solution in the xy -plane for our system.

3 Population Growth Models for a Single Species

In this chapter, we examine classical population models, starting with the simple exponential model and adding more realistic assumptions to it. In the next chapter, we modify these classic models to include two species. Before we look into species interaction, let us consider the growth of a single species population, which we call “rabbits” throughout.

3.1 Exponential Growth

3.1.1 From Words to Math: Assumptions and Notation

Denote the size of the rabbit population at time t by $R(t)$. The rate of change, or the absolute growth rate, of a population R is measured by the derivative dR/dt .

In a single-species population, two things happen in a given time period:

(1) a certain fraction r_1R of the population procreates (has babies), and (2) a certain fraction r_2R of the population dies. Therefore, the population increases by r_1R and decreases by r_2R , so the net growth of the population in one time period is $(r_1 - r_2)R = rR$, for some positive constant r , called the “relative growth rate”. Since we want the rabbits to grow, we assume $r > 0$.

Example 2. Consider a petri dish, with no lid, of 20 bacteria. Assume that 20% of the bacteria split each day and 5% of them die each day. Then, the net relative growth rate of the bacteria is 20%-5%=15% per day. On Day 1, the dish will have 20 bacteria. On Day 2, the dish will have

$$.20(20) - .05(20) = (.20 - .05)(20) = (.15)(20) = 3$$

more bacteria than Day 1, i.e., there are 23 bacteria on Day 2. We can continue this technique for each day, but what if we want to know the number of bacteria on Day 50? It would be tedious to work out the number of new bacteria for each day and add it to the previous amount. For each day, we are calculating the rate of change of the number of bacteria, which is the derivative dR/dt . Thus, the rate of change of the bacteria population is

$$dR/dt = .15R,$$

with $R(0) = 20$.

3.1.2 Differential Equation

The differential equation for this situation is

$$dR/dt = rR,$$

where r is the net relative growth rate constant.

3.1.3 Equilibrium Analysis

First, we look for constant solutions (called equilibrium points) by solving

$$0 = dR/dt = rR,$$

which has $R = 0$ as its only solution. This special solutions makes sense: if there are no rabbits, then there will be no new babies and no one dies, so there will be no rabbits in the future. According to the model, if $R = 0$, then $dR/dt = r(0) = 0$, so the rabbit population R remains constant, namely, 0.

To understand the solutions that originate near $R = 0$, we compute the Jacobian matrix for the differential equation; here it is just the derivative of the right-hand side,

$$J(R) = [r].$$

Notice that in the one-species case, the Jacobian matrix is just a scalar. At the equilibrium, the Jacobian matrix is

$$J(0) = [r],$$

with eigenvalue r . Since we assume $r > 0$, the solutions diverge from the line $R = 0$, and the system is unstable. This makes sense because if the growth rate of the rabbits is positive, the rabbit population will increase.

3.1.4 General Solution and Long-term Behavior

Since the rabbit population grows when $r > 0$, we know that as time increases, the population gets larger and it grows faster as the population gets larger. Therefore, as the rabbit population increases, the absolute growth rate increases, and we expect the graph of the function $R(t)$ to be curving up as in Figure 4. The value of $R(t)$ at $t = 0$ is the initial condition $R(0)$. Changing the initial condition results in a different function $R(t)$. As seen in Figure 4, larger initial populations grow faster.

If $R(0) < 0$ and $r > 0$, then $dR/dt = rR < 0$, so the population is initially decreasing and continues to decrease as t increases. Biologically, of course, negative populations do not make sense.

What if we want to know the exact value of $R(t)$ for a given time, as in our bacteria example (Example 1.)? Given an initial condition, there is a unique solution

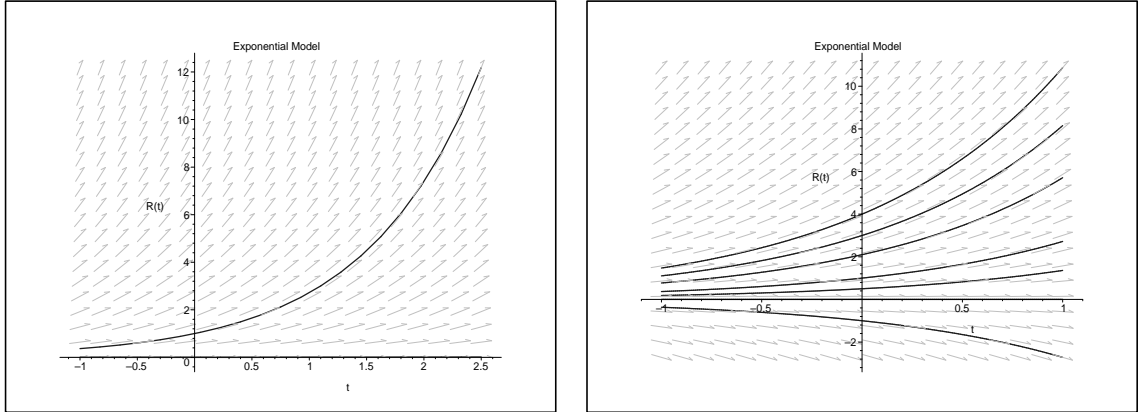


Figure 4: The graph of a function that satisfies $dR/dt = rR$ and the graph of several solutions of $dR/dt = rR$ with initial conditions $R(0) = -1, 0, .5, 1, 2, 3,$ and 4 .

$R(t)$ that satisfies

$$dR/dt = rR, \quad R(0) = R_0.$$

The general solution to $dR/dt = rR$ is the collection of functions $R(t) = Ce^{rt}$, where C is an arbitrary constant. In particular, there are infinitely many solutions to the differential equation when no initial condition is specified. Using the *general solution* $R(t) = Ce^{rt}$ and the *initial condition* $R(0) = R_0$, we can solve for C : $R_0 = R(0) = Ce^{r(0)} = C$, so the *particular solution* is $R(t) = R_0e^{rt}$. The symbolic form of the solution explains why this model is called exponential growth.

3.1.5 Limitations

A special feature of the exponential model is that $\frac{dR/dt}{R} = r = \text{constant}$. That is, the relative growth rate (in percent of rabbits per time) is constant.

An obvious limitation for this basic model is that it predicts a population explosion, which is only reasonable for relatively small populations in large environmental settings. For larger populations, we must take into account the lack of resources, so we look for a more realistic model in the next section.

3.2 Logistic Growth

3.2.1 From Words to Math: Assumptions and Notation

As earlier, we denote the size of the rabbit population at time t by $R(t)$. We expect small populations to grow as described by the exponential model, but as the population grows, we expect fewer babies to be born per adult because the environment cannot support too large a population. For such a case, the population grows more slowly as it approaches its carrying capacity, which is the maximum population the environment can sustain; we expect the growth rate to be positive, but decreasing with R . When the rabbit population is small, we can assume that its net growth rate is proportional to its population, as in the exponential growth model. As the rabbit population increases and approaches the carrying capacity K , the growth rate declines and eventually reaches 0 when $R = K$.

We must include a factor in this new model to account for these changes. As seen in Figure 5, the relative growth rate in the exponential model is constant. A better growth rate is the solid line, which decreases as the rabbit population increases; its initial growth rate (at $R = 0$) is equal to the exponential growth rate and its terminal growth rate (when $R = K$) is zero. The equation of this line is the factor we must include in the model, so the new net growth of the population is $r_0(1 - R/K)R$, where r_0 is the initial growth rate. For simplicity, we refer to this as $r(1 - R/K)R$.

Example 3. Recall our previous example of a petri dish of 20 bacteria with a relative growth rate of 15% per day. Assume now that the petri dish has a lid and can only hold 100 bacteria (this is the carrying capacity), that is, once the dish contains 100 bacteria, the bacteria population stops growing. Initially, the bacteria grow exponentially, as in the previous model: there will be 20 bacteria on Day 1 and

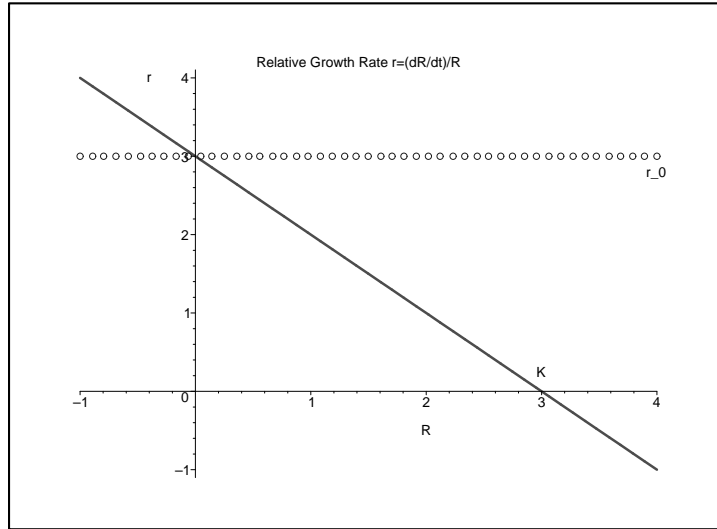


Figure 5: Graph of relative growth rate against population R for exponential (circles) and logistic models (solid).

23 bacteria on Day 2. Well, how many bacteria will there be on Day 50? Eventually, the petri dish will reach a total population of 100 and its growth will stop. So, the rate of change of the bacteria population is

$$dR/dt = .15(1 - R/100)R, \text{ with } R(0) = 20.$$

Let us compare this to the previous model where both petri dishes begin with 20 bacteria. The plot on the left in Figure 6 shows the population of bacteria from time $t = 0$ to $t = 16$, with unlimited growth. We see that at time $t = 10$, there are nearly 100 bacteria in the petri dish. The plot on the right shows the population of bacteria from time $t = 0$ to $t = 60$, but with carrying capacity 100. Notice that at time $t = 60$, there are only 100 bacteria in this dish. In fact, it seems that the bacteria in this dish stopped growing at time $t = 50$. We see that the bacteria in the first dish grow much faster than the bacteria subject to logistic growth.

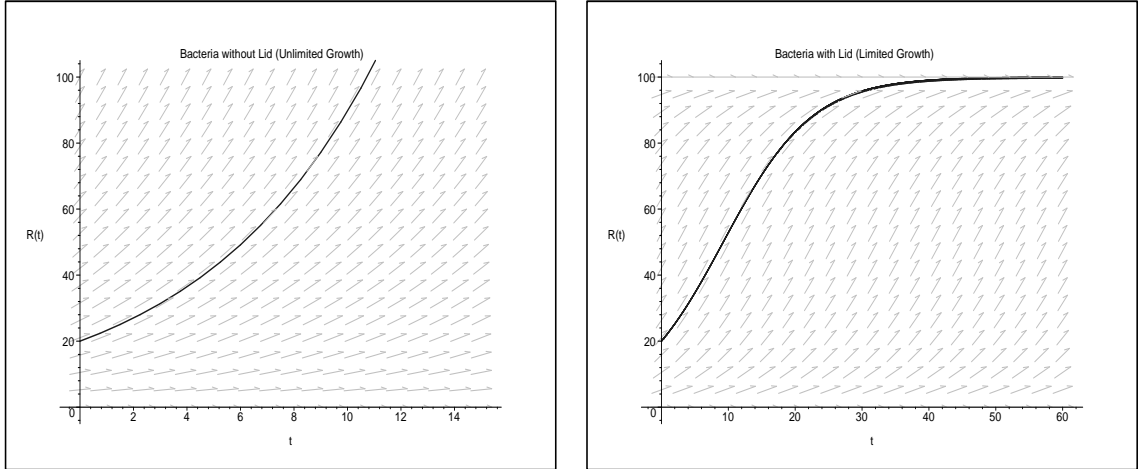


Figure 6: Left: Bacteria from previous example with unlimited growth. Right: Bacteria with carrying capacity.

3.2.2 Differential Equation

The assumption that $\frac{dR/dt}{R} = r(1 - R/K)$ leads to the differential equation

$$dR/dt = r(1 - R/K)R.$$

If the rabbit population is small ($R \approx 0$), then $1 - R/K \approx 1$, so $dR/dt \approx rR$, which is the exponential model. However, if the population gets close to its carrying capacity ($R \approx K$), then $(1 - R/K) \approx 0$, and $dR/dt \approx 0$, so the rate of change of the rabbit population is nearly 0, and R remains nearly constant.

3.2.3 Equilibrium Analysis

We find the equilibrium points of the differential equation by solving

$$0 = dR/dt = r(1 - R/K)R.$$

We now have two equilibrium points: $R = 0$ and $R = K$. Intuitively, if there are no rabbits or the environment is already supporting the maximum number of rabbits, then nothing changes and there will be no more rabbits in the future. To understand the solutions that originate near $R = 0$ and $R = K$, we compute the Jacobian matrix

$$J(R) = \left[\frac{-rR}{K} + r \left(1 - \frac{R}{K}\right) \right].$$

The Jacobian matrix at $R = 0$ is

$$J(0) = [r],$$

with eigenvalue r , so the system is unstable and solutions diverge from the line $R = 0$. Hence, if the rabbit population starts small, it will increase, just as in the previous model.

The Jacobian matrix at $R = K$ is

$$J(K) = [-r],$$

with eigenvalue $-r$. Since $r > 0$, then this equilibrium point is stable, and the solutions are attracted to the line $R = K$. As the population approaches the carrying capacity K , it levels off because the environment cannot sustain too large a population.

3.2.4 General Solution and Long-term Behavior

Since we assumed that $r > 0$ (that is, birth overcomes death), we know that if the initial population is between 0 and K , then the rate of its change is positive, so

the number of rabbits will increase. However, unlike the exponential model, the relative growth rate decreases as the population increases and the population levels off as it reaches its carrying capacity K , so $R = K$ is a stable equilibrium point. If $R(0) > K$, then some rabbits will die because the rabbit population is too large for the environment to support. We exclude the case where $R(0) < 0$ since negative populations do not make sense. Figure 7 shows four different functions at four initial conditions:

$$R(0) = 0, \quad 0 < R(0) < K, \quad R(0) = K, \quad \text{and} \quad R(0) > K.$$

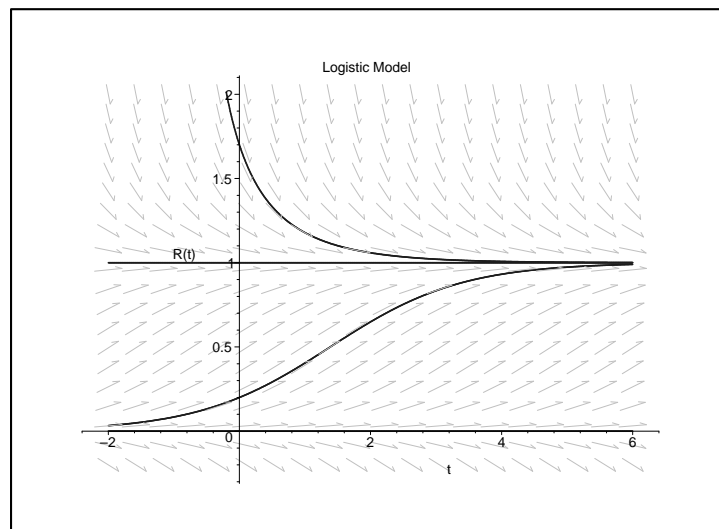


Figure 7: Solutions to $dR/dt = r(1 - R/K)R$ with initial conditions $R(0) = 0, 0.2, 1,$ and 1.7 .

What if we want the exact rabbit population for a given time? One can solve the differential equation

$$dR/dt = r(1 - R/K)R, \quad R(0) = R_0,$$

by separating the variables and integrating. We omit the tedious computations here and let the reader verify that the family of functions

$$R(t) = \frac{K}{1 + Ce^{-rt}},$$

solves the differential equation $dR/dt = r(1 - R/K)R$. The arbitrary constant C , of course, depends on the initial condition $R(0)$, namely, $C = \frac{K-R_0}{R_0}$.

3.2.5 Limitations

In this model, we assume that the relative growth rate is not constant, but a linear function of the population that decreases as the rabbit population increases. If the relative growth rate is not a straight line, but another decreasing function, such as $r = r_0e^{-\alpha R}$, for some positive α , as in Figure 8, the behavior may be different. The straight line was simple, but there are other ways to assume that the relative growth rate is not constant, which the logistic growth model does not take into account.

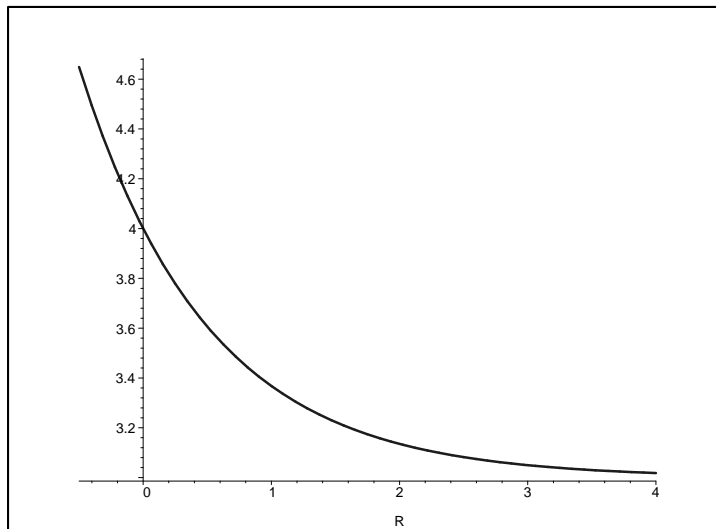


Figure 8: Possible decreasing relative growth rate $r = r_0e^{-\alpha R}$ as rabbit population increases.

3.2.6 Special Case

The logistic model has a special case: the exponential model. Notice that as $K \rightarrow \infty$, we get $dR/dt = rR$, which is the exponential model. We know that for small values of R , the logistic model looks and behaves like the exponential model. If the environment has plenty of food, resources, and space, the logistic model will also look and behave like the exponential model.

4 Population Growth Models for Two Species

This chapter is about two interacting species, for example, a predator and a prey. Since the words “predator” and “prey” begin with the same letter, let us call the predator “snake” and denote its population by $S(t)$; similarly, call the prey “rabbits” and denote its population by $R(t)$. Of course, our investigation applies to any predator-prey interaction.

4.1 Two Species: No Interaction

4.1.1 From Words to Math: Assumptions and Notation

In the previous chapter, we discussed the population changes of a single species. To get things started, consider an environment where two species, rabbits and snakes, live together, but do not interact with one another. The rabbits grow exponentially, as in Chapter 4, and their net growth is rR , with $r > 0$, so the rabbit population increases. It seems that the snake population would behave the same, but since the rabbits and snakes do not interact, the snakes have no food to eat so it is reasonable to assume that the death rate will overcome the birth rate. Thus, the snake population decreases exponentially, with net growth $-sS$, where s is the death rate due to starvation. Combining the two exponential models, we obtain the system of differential equations

$$\begin{aligned}dR/dt &= rR \\dS/dt &= -sS.\end{aligned}$$

4.1.2 Equilibrium Analysis

The R -nullcline is the set of points where $rR = 0$, so the R -nullcline is $R = 0$. Similarly, the S -nullcline is $S = 0$. The R - and S -nullclines intersect at the origin,

which is the only equilibrium point for this system. This trivial equilibrium makes sense: if no rabbits and no snakes exist now, then no rabbits or snakes will exist in the future.

To understand the behavior of solutions near $(0, 0)$, we compute the Jacobian matrix

$$J(R, S) = \begin{bmatrix} r & 0 \\ 0 & -s \end{bmatrix},$$

which has eigenvalues r and $-s$. Therefore, the origin is a repelling saddle: solutions approach the origin along the S -axis and repel from it along the R -axis.

4.1.3 Long-term Behavior

This model describes the change in populations of two species that do not interact with one another. Figure 9 suggests that the rabbit population grows forever while the snake population dies out from starvation.

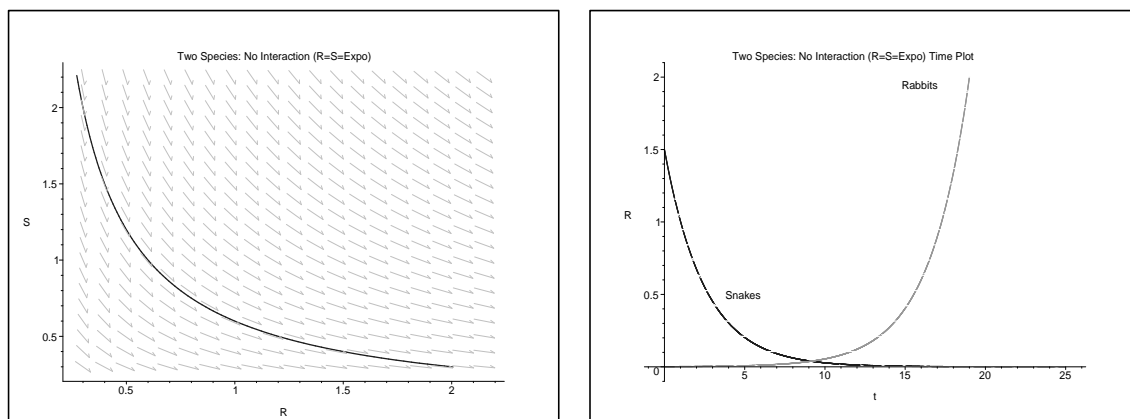


Figure 9: Direction field with a trajectory and corresponding time plot that satisfies the two-species system with no interaction.

4.2 Lotka-Volterra Predator-Prey

4.2.1 From Words to Math: Assumptions and Notation

The previous model shows how the rabbits grow exponentially while the snakes die exponentially from starvation without interacting with (eating) any rabbits. If the rabbits and snakes do interact, the model should look like

$$\begin{aligned}dR/dt &= rR + \text{effect of interaction on rabbits} \\dS/dt &= -sS + \text{effect of interaction on snakes.}\end{aligned}$$

An interaction between a rabbit and a snake has a negative effect on the rabbit population, but a positive effect on the snake population. How can we quantify those effects?

We assume that a certain fraction h of the meetings between a rabbit and a snake results in a dead rabbit. The number of meetings between a rabbit and a snake is proportional to the product RS . Note that h is the hunting rate in percent of rabbits that one snake can catch in one time period.

On the other hand, eating rabbits is healthy for the snakes; we expect that the healthy rabbit diet will boost the snake birth rate and decrease their death rate, thus reducing the net starvation rate for the snakes. To quantify it, each time a rabbit is eaten, the snake population increases its net growth rate by some amount, which we denote by u . In other words, u is the utility of each eaten rabbit to the snakes' net growth rate.

4.2.2 System of Differential Equations

Combining all the terms together, we obtain the system of differential equations

$$\begin{aligned}dR/dt &= rR - hRS \\dS/dt &= -sS + uhRS.\end{aligned}$$

In the last section, the snakes died out from starvation. What happens to the two species here, when the snakes eat the rabbits for survival? Will the snakes eat all the rabbits and still starve? As usual, the equilibrium points hold the answer.

4.2.3 Equilibrium Analysis

We solve the system

$$\begin{aligned}0 &= dR/dt = rR - hRS \\0 &= dS/dt = -sS + uhRS,\end{aligned}$$

which can be rewritten in the factored form

$$\begin{aligned}0 &= R(r - hS) \\0 &= S(-s + uhR).\end{aligned}$$

The first equation yields the two R -nullclines: $R = 0$ and $S = \frac{r}{h}$. The second equation is satisfied if either $S = 0$ or if $R = \frac{s}{uh}$, and so these two lines form the S -nullclines. Since equilibrium points occur at the intersections of the R - and S -nullclines, this system has two equilibrium points: $(0, 0)$ and $(\frac{s}{uh}, \frac{r}{h})$.

As we saw in the last section, the equilibrium point at $(0, 0)$ is trivial. The non-trivial equilibrium point $(\frac{s}{uh}, \frac{r}{h})$ is more interesting. It means that, if the snakes

eat enough rabbits to offset their starvation, then the two species could coexist in the same environment.

To understand the behavior of solutions near $(0, 0)$ and $(\frac{s}{uh}, \frac{r}{h})$, we compute the Jacobian matrix

$$J(R, S) = \begin{bmatrix} r - hS & -hR \\ uhS & -s + uhR \end{bmatrix}.$$

At the trivial equilibrium point,

$$J(0, 0) = \begin{bmatrix} r & 0 \\ 0 & -s \end{bmatrix},$$

with eigenvalues r and $-s$. This tells us that the origin is a repelling saddle, so solutions approach the origin along the S -axis and repel from the origin along the R -axis, as in the previous model. It is important to note that, for all our models, the origin is always a repelling saddle.

At the non-trivial equilibrium

$$J\left(\frac{s}{uh}, \frac{r}{h}\right) = \begin{bmatrix} 0 & \frac{-s}{u} \\ ur & 0 \end{bmatrix},$$

with eigenvalues $\pm i\sqrt{rs}$. Since the real part of the eigenvalues is 0, we need more information to classify this equilibrium point. As it turns out (Proposition 4.1), the solutions are indeed periodic and all orbits are closed (Figure 12), so this equilibrium point is a non-linear center.

4.2.4 Cyclical Behavior

When the rabbit and snake populations are small, the snakes do not have enough food (rabbits) to sustain their existence, so the snake population declines. At the same time, few snakes eat the rabbits, so the rabbit population increases, as in Figure 10. As the rabbit population (snake food) grows, the snake population starts to increase, as in the right plot in Figure 10.

When the snake population gets too large, the rabbits start to decline since they are eaten faster than they can reproduce. (See left plot of Figure 11.) If each population is fairly large, the snake population will increase, but the rabbit population decreases because the snakes are eating them. (See right plot of Figure 11.) Are the trajectories closed, or do the populations eventually spiral in and level off over time or spiral out (and explode)?

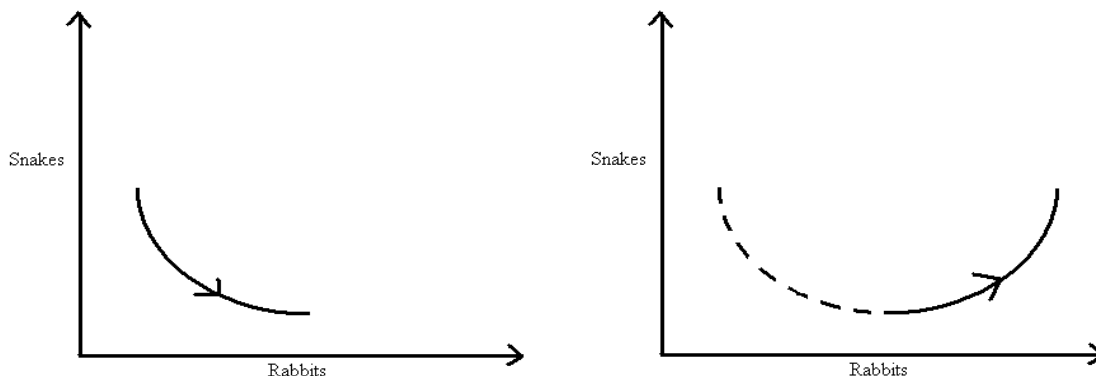


Figure 10: Left: Rabbit and snake populations begin small, rabbit population increases. Right: Rabbit population grows and snake population starts to increase.

Proposition 4.1. *All trajectories with positive initial conditions are closed.*

Proof. We prove the special case when $r = s = h = u = 1$, for simplicity. (The proof in the general case uses the same idea, but the constants get more cumbersome.)

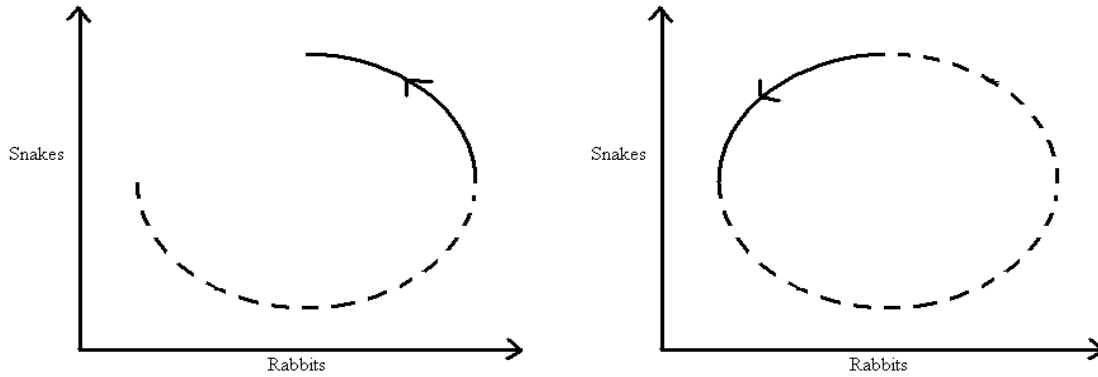


Figure 11: Left: Snake population gets large, rabbits begin to die. Right: Rabbit and snake populations large, rabbits decline.

We have

$$\begin{aligned} dR/dt &= R(1 - S) \\ dS/dt &= S(-1 + R). \end{aligned}$$

We eliminate t by using the chain rule:

$$\frac{dS}{dR} = \frac{S(-1 + R)}{R(1 - S)}.$$

Separating the variables, we get

$$\int \frac{(1 - S)}{S} dS = \int \frac{(R + 1)}{R} dR.$$

After integrating and rearranging, we have

$$S + R - \ln S - \ln R = C,$$

which provides a first integral for our simple system.

To see that the orbits are closed curves, denote the expression on the left above by $f(R,S)$ and plot its level curves, or contours, $f(R,S) = C$ for $R > 0, S > 0$ (see Figure 12).

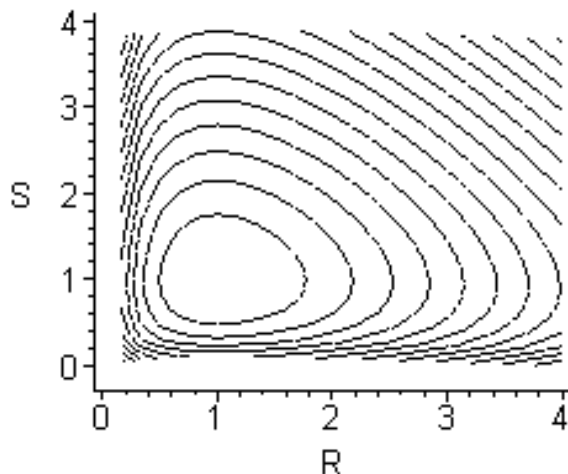


Figure 12: Contour plot of $f(R, S) = S + R - \ln S - \ln R$.

We see (and one can easily verify) that there is a global maximum at $S = R = 1$, and that the nearby contours are closed, which confirms that all solutions will be periodic closed orbits around the center $(1, 1)$. \square

4.2.5 New Behavior

In the previous model, the rabbit population grew forever and the snake population died out from starvation. This classic model predicts periodic oscillations near the equilibrium point $(\frac{s}{uh}, \frac{r}{h})$, so the rabbits and snakes coexist together, as seen in Figure 13.

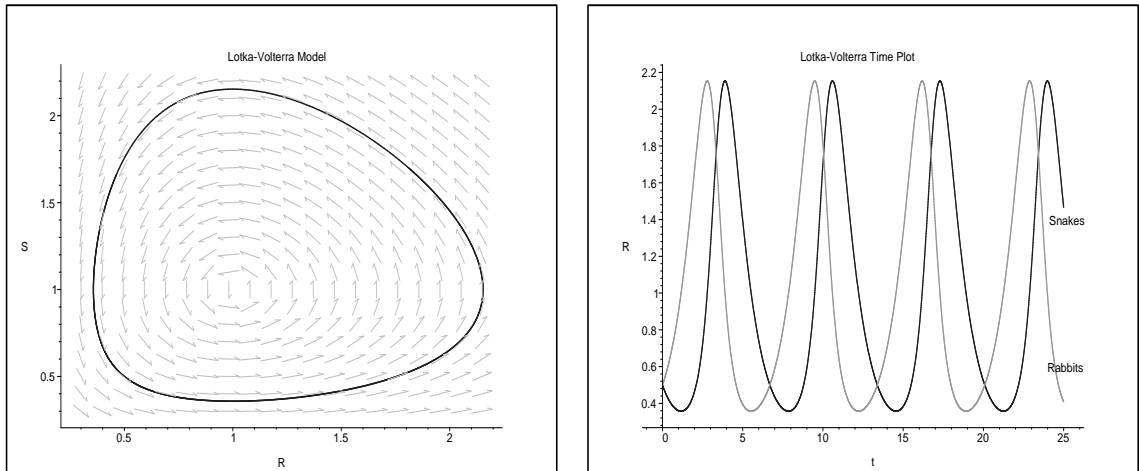


Figure 13: Direction field with a trajectory and time plot for the Lotka-Volterra system.

4.2.6 Special Cases

If a solution gets too close to either axis, a population may die out, despite what the model predicts. Ironically, this dangerous situation happens if the initial rabbit and snake populations are too large and thus, too far from the equilibrium point.

If the hunting rate h decreases to 0, we get the previous model, where the rabbits and snakes do not interact with one another. Note that without snakes, the rabbit population grows exponentially in this model. In this case, geometrically, the non-trivial equilibrium $(\frac{s}{uh}, \frac{r}{h})$ moves towards $(+\infty, +\infty)$.

4.2.7 Limitations

It is more realistic to assume that the rabbits have a carrying capacity to account for the rabbit population getting large and straining the sources, so we investigate this case in the next section.

4.3 Logistic Lotka-Volterra Predator-Prey

4.3.1 From Words to Math: Assumptions and Notation

In this model, we assume logistic growth for the rabbit population in the absence of snakes. Therefore, the only change is in the rabbit growth term; all other assumptions made about the growth rates of the rabbits and snakes and their interaction are the same as in the previous model. The improved model is

$$\begin{aligned}dR/dt &= r(1 - R/K)R - hRS \\dS/dt &= -sS + uhRS.\end{aligned}$$

4.3.2 Nullclines and Equilibria: Geometric Analysis

Using the same technique as in the previous model to find and analyze the equilibrium points, we solve the system

$$\begin{aligned}0 &= dR/dt = r(1 - R/K)R - hRS \\0 &= dS/dt = -sS + uhRS,\end{aligned}$$

which can be factored in the form

$$\begin{aligned}0 &= R(r(1 - R/K) - hS) \\0 &= S(-s + uhR).\end{aligned}$$

Solving each equation, we find the R -nullclines to be $R = 0$ or $S = \frac{r}{h}(1 - R/K)$ and the S -nullclines to be $S = 0$ or $R = \frac{s}{uh}$. Notice that the S -nullclines are the same as in the classic Lotka-Volterra system; this makes sense because we made no modifications to the dS/dt differential equation. In contrast, the R -nullcline, $S = \frac{r}{h}$

from the previous model is now the sloped line $S = \frac{r}{h} (1 - R/K)$, which crosses the R -axis at $R = K$, creating a new equilibrium.

Recall that the equilibrium points occur at the intersections of the R - and S -nullclines, so this system has three equilibrium points, $(0, 0)$, $(K, 0)$, and $(\frac{r}{h} (1 - \frac{s}{uhK}), \frac{s}{uh})$.

As in the previous model, the equilibrium $(0, 0)$ is trivial. At the new equilibrium $(K, 0)$, no snakes exist and the rabbits are at their carrying capacity, so no snakes and no rabbits exist in the future.

A geometric relationship exists between the equilibrium points $(K, 0)$ and $(\frac{r}{h} (1 - \frac{s}{uhK}), \frac{s}{uh})$ depending on the location of the nullclines, see Figure 14.

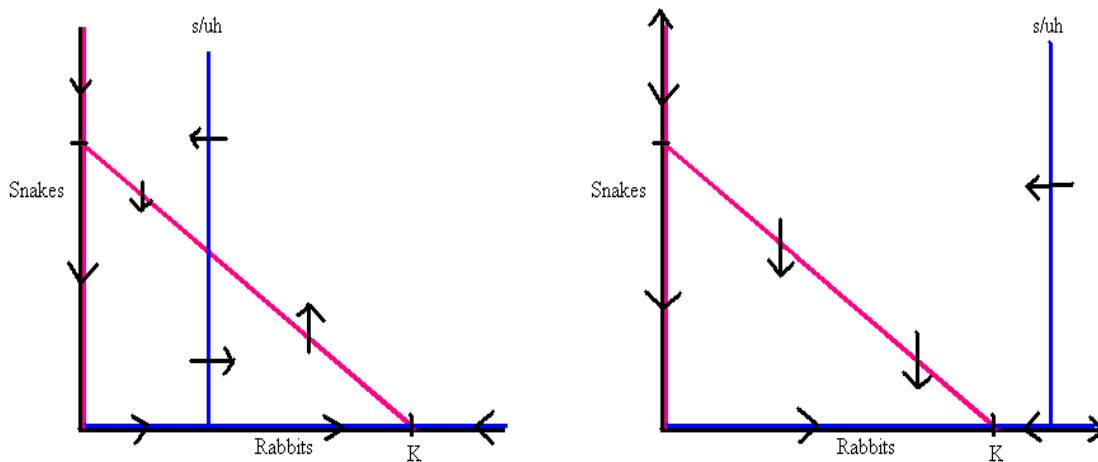


Figure 14: Nullclines for Lotka-Volterra with prey logics when $\frac{s}{uh} < K$ (left) and $\frac{s}{uh} > K$ (right).

If $\frac{s}{uh} > K$, then $\frac{s}{uh}$ is large. When $\frac{s}{uh}$ is large, then s is large or u and h are small. Does it make sense that the snakes die if one of these conditions holds? If the snake starvation rate s is large, then the snakes starve quickly and die out. If the hunting rate h is small, then the snakes are only catching a small number of rabbits in a given time, so the snakes do not have enough to eat and can die out. Also if the rabbits do not nourish the snakes enough (small u), then the snakes need to eat

more rabbits for their population to increase. Thus, if s is large, h is small, or u is small, then the snakes will die out.

If s is small, then the snakes do not starve quickly and can live longer without food. If h is large, then the snake hunts the rabbits well; if u is large, the rabbits are a good diet for the snakes. These conditions allow for a healthy snake, so we assume $\frac{s}{uh} < K$ for the rest of our study.

4.3.3 Equilibria: Stability Analysis

To understand the behavior of solutions near the equilibrium points, we compute the Jacobian matrix for the system:

$$J(R, S) = \begin{bmatrix} -\frac{rR}{K} + r \left(1 - \frac{R}{K}\right) - hS & -hR \\ uhS & -s + uhR \end{bmatrix}.$$

At the trivial equilibrium point,

$$J(0, 0) = \begin{bmatrix} r & 0 \\ 0 & -s \end{bmatrix},$$

with eigenvalues r and $-s$. This is a repelling saddle: solutions approach the origin, but then repel from $(0, 0)$ along the R -axis, as in all models in this chapter.

The Jacobian matrix at the equilibrium $(K, 0)$ is

$$J(K, 0) = \begin{bmatrix} -r & -hK \\ 0 & -s + uhK \end{bmatrix},$$

with eigenvalues $-r$ and $-s + uhK$. For the first time in our study, the sign of

an eigenvalue depends on the parameters: the equilibrium is stable if $\frac{s}{uh} < K$ and unstable if $\frac{s}{uh} > K$. Since we assume $\frac{s}{uh} < K$, the equilibrium $(K, 0)$ is unstable, so the snakes survive.

Instead of computing the Jacobian matrix at the equilibrium $(\frac{r}{h}(1 - \frac{s}{uhK}), \frac{s}{uh})$, we use geometric methods to determine its stability.

Lemma 4.2. *Consider a system with vertical S -nullcline $R = 0$ and a sloped R -nullcline $S = mR$. The equilibrium point at the intersection of the two nullclines is stable if m is negative and unstable if m is positive.*

Proof. We want a linear system such that $dS/dt = 0$ when $R = 0$ and $dR/dt = 0$ when $S = mR$ for some constant m . A simple linear system with this property is

$$\begin{aligned} dR/dt &= r(mR - S) \\ dS/dt &= sR. \end{aligned}$$

The (Jacobian) matrix for this system is

$$J(R, S) = \begin{bmatrix} mr & -r \\ s & 0 \end{bmatrix},$$

with eigenvalues $\frac{mr}{2} \pm \frac{1}{2}\sqrt{m^2r^2 - 4rs}$.

Since $r > 0$, the sign of the real parts of the eigenvalues depends on the sign of m . If $m > 0$, the slope of the R -nullcline is positive, as in Figure 15; the eigenvalues have positive real parts, so the equilibrium point is unstable. If $m = 0$, the slope of the R -nullcline is zero, so the nullcline is a horizontal line (see Figure 15). The

eigenvalues have no real part, so the equilibrium point is a center. If $m < 0$, the slope of the R -nullcline is negative (see Figure 15); the eigenvalues have negative real parts, so the equilibrium point is stable.

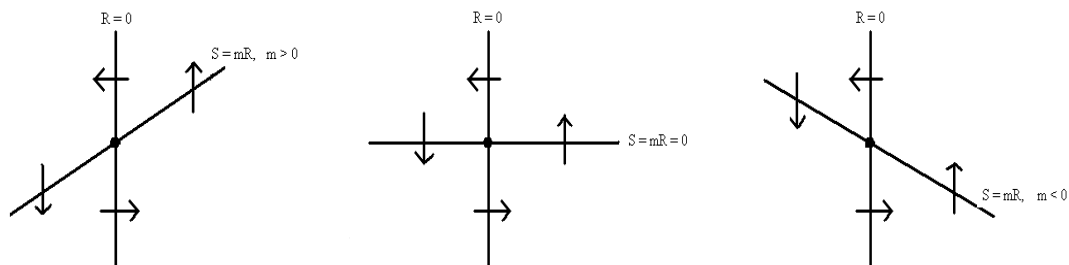


Figure 15: Slope of nullcline is positive (left); slope of nullcline is zero (middle); slope is negative (right).

Thus, if we know the slope of the nullcline, we can determine the behavior of solutions around a given equilibrium point. \square

For the most interesting (and most complicated) equilibrium point, we use Lemma 4.2 to determine the behavior of solutions near this equilibrium. The R -nullcline, $S = \frac{r}{h} (1 - R/K)$, crosses the S -nullcline, $R = \frac{s}{uh}$, at this non-trivial equilibrium. We know that $r > 0$, $h > 0$, and $K > 0$, so the slope $\frac{-r}{hK}$ of the R -nullcline is negative. By Lemma 4.2, the equilibrium $(\frac{r}{h} (1 - \frac{s}{uhK}), \frac{s}{uh})$ is stable. Figure 16 suggests that this point is an attracting spiral sink, so solutions originating near this point will be pulled into the stable equilibrium point.

4.3.4 New Behavior

As the rabbits increase, their growth rate decreases as they approach carrying capacity because they are limited by the environment. As in the previous model when the rabbit and snake populations are small, the snake population declines from a

lack of food (rabbits). As few snakes eat the rabbits, the snake population increases, but the rabbit population is not able to recover as quickly as in the Lotka-Volterra model, so the arc is curving up more, thus creating a spiral. In Figure 16, we see that when we consider limits to resources and include logistics in the model, a spiral emerges, which changes the overall behavior of the model. Also, this model does not predict periodic oscillations as in the previous model. Instead, the rabbit and snake populations eventually level off and the two species can coexist in the same habitat at a stable equilibrium point. This can be seen in the time plot in Figure 16. In some sense, imposing limited growth on the rabbits introduces “friction” or “damping” to the system.

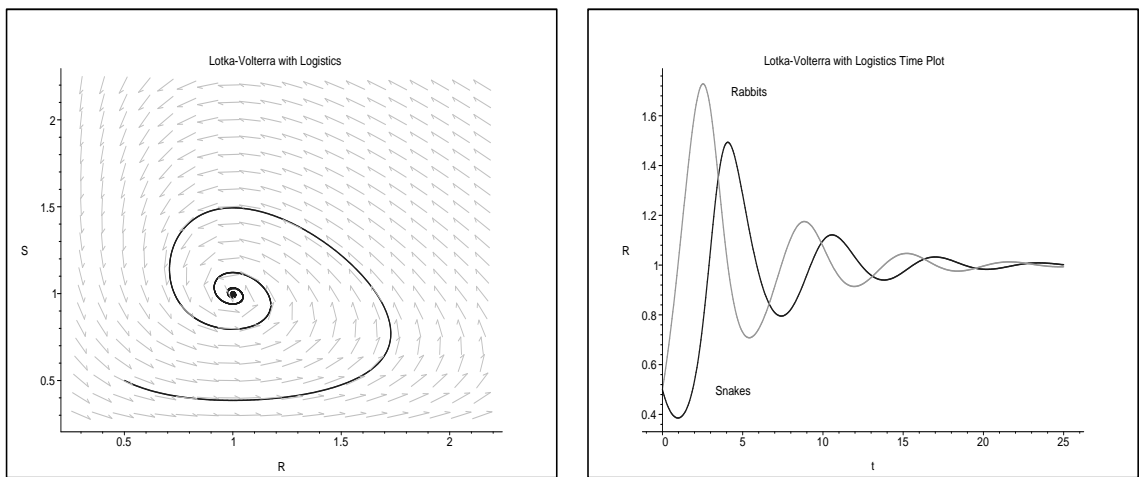


Figure 16: Direction field with a trajectory, spiraling towards the attractive non-trivial equilibrium and time plot for the Lotka-Volterra with prey logistics system.

4.3.5 Special Case

Recall from Section 3.2.6 that as $K \rightarrow \infty$, the logistic growth model becomes the exponential growth model. We notice that if we allow $K \rightarrow \infty$ in this model, then the slope of the R -nullcline, $S = \frac{r}{h} (1 - R/K)$, approaches zero and we get the classic Lotka-Volterra model from Section 4.2, whose solutions are closed curves.

5 Holling Predation

In 1959, C.S. Holling [H] suggested several ways to model a predator's consumption rate as a function the prey population. In the population growth models examined in Chapter 4, we assume a linear relationship between the predator's consumption rate and the prey population, that is, as the prey population gets larger, the number of prey eaten increases at a constant rate. The models in Chapter 4 include a Holling Type I predation term, although we do not explicitly name it as such earlier. This predation term, denoted hR , is the number of rabbits eaten per snake per time period, as seen in Figure 17. The Holling Type I predation term assumes that the snakes are always hungry and that each snake eats more rabbits if more rabbits exist.

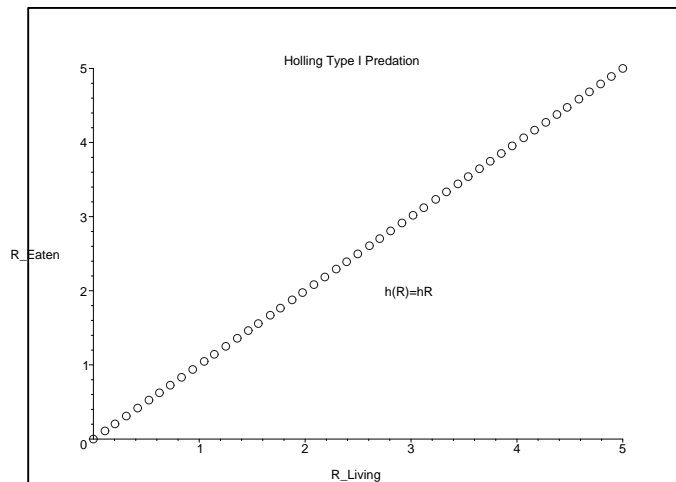


Figure 17: Graph of the Holling Type I predation term hR from the Lotka-Volterra models in Chapter 4.

A more realistic predation term accounts for the snakes eventually getting full. After all, how many rabbits can one snake eat in one time period, really? As the rabbit population increases, the number of rabbits eaten by each snake increases at a decreasing rate, as in Figure 18. Graphically, the function $h(r) = \frac{hHR}{H+R}$ has the desired shape, and the consumption rate cannot get arbitrarily large (as in Type I).

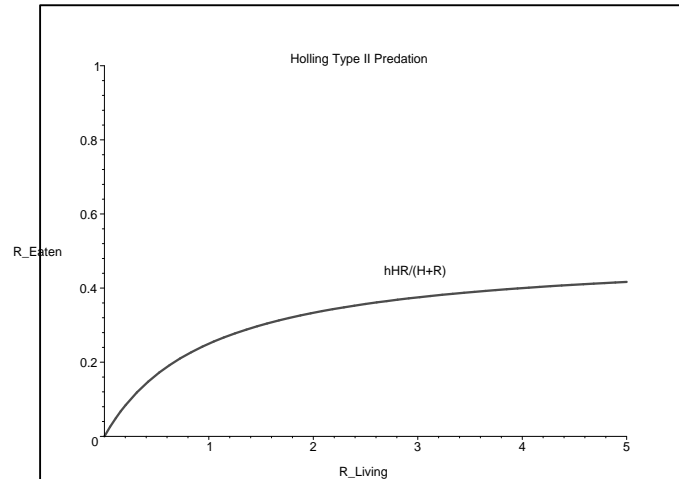


Figure 18: Graph of possible satiated predation term.

In this chapter, we describe Holling’s experiment and the basis for the Holling Type II predation, which develops a more complicated (and more realistic) relationship between a predator’s rate of consumption and the prey population. In the next chapter, we modify the classic Lotka-Volterra models from Chapter 4 to include Holling Type II predation.

5.1 Holling’s Experiment

Holling described an experiment where a blindfolded human represents the predator and sandpaper disks, measuring 4 centimeters in diameter, represent the prey. The disks were attached to a 3-foot by 3-foot table. The blindfolded “predator” stood in front of the table and searched for the “prey” by tapping on the table at one minute intervals. When a “prey” was found, the disk was removed from the table and the “predator” kept searching. The experiment was repeated for different “prey” populations, ranging from 4 to 256 disks per nine square feet.

5.2 Holling's Results

While we might expect a linear relationship between prey population and the number of prey found, this is not what Holling's experiment found. As seen in Figure 19 from [H], Holling's results showed that as the prey population increased, the number of disks picked up increased at a decreasing rate, so the total time taken to pick up and remove disks is higher at larger prey populations (when more disks are found). In contrast, the search time is longer and the total handling time is shorter at lower prey populations.

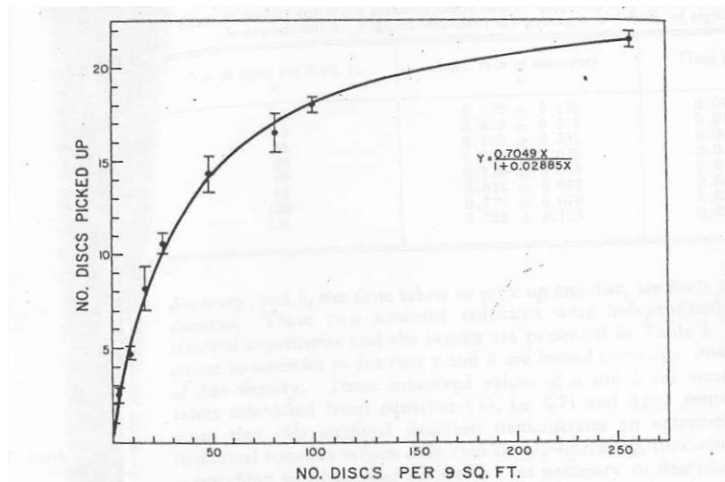


Figure 19: Functional response of a subject searching for sandpaper discs by touch, from [H].

Holling expressed his results in a simple form, often called the “disk equation”

$$h(R) = aT_s R,$$

where $h(R)$ represents the total number of disks collected, a is the rate of searching multiplied by the probability of finding a disk, and R is the density of the disks.

In the context of our study, $h(R)$ is the number of rabbits eaten per snake in one

time period, a is the instantaneous rate of discovery (the product of search rate and probability of finding a rabbit), T_s is the search time, and R is the rabbit population.

Handling time refers to the time it takes a snake to pursue, capture, and eat one rabbit. The search time is calculated by taking the total time available to search, denoted T , and subtracting the total handling time $T_h h(R)$, where T_h is the handling time per rabbit. Thus

$$T_s = T - T_h h(R).$$

Substituting this into the “disk equation,” we have

$$h(R) = aT_s R = a(T - T_h h(R))R,$$

which simplifies to

$$h(R) = \frac{aTR}{1 + aT_h R}.$$

The graph of the consumption rate that corresponds to this equation is shown in Figure 20 (left). We can further simplify this predation term by making the substitution $h = aT$ and $H = 1/aT_h$. Thus,

$$h(R) = \frac{aTR}{1 + aT_h R} = \frac{hHR}{H + R},$$

where h is the maximum percent of rabbits hunted per snake per time period and H is the number of living rabbits hunted by half-full snakes. Note that hH is the number of rabbits captured by one snake in one time period.

The consumption rate $h(R)$ rises as the prey population R increases, but levels off when all available time is spent handling the rabbits. That is, when the rabbit population is large, the snakes spend more time on handling the rabbits, and the

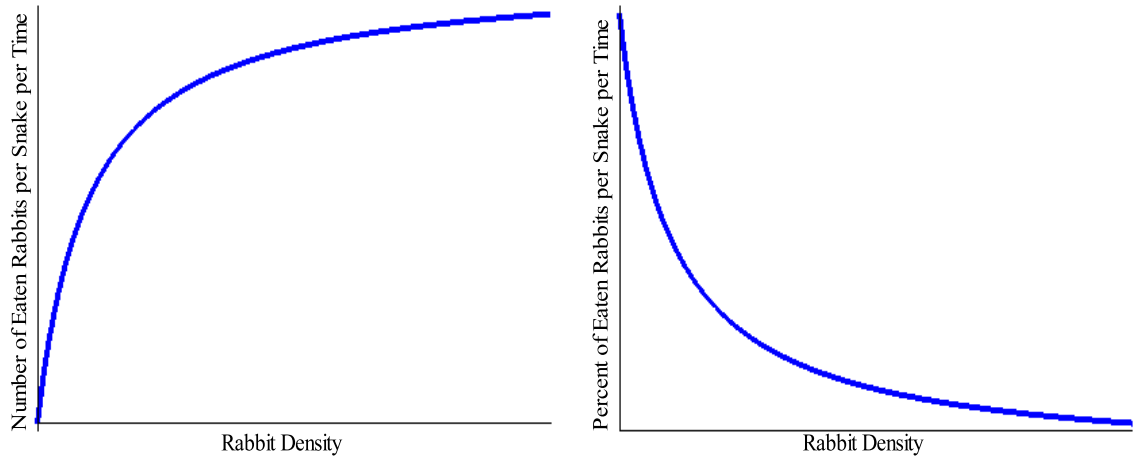


Figure 20: Graph of the number (left) and percent (right) of eaten rabbits per snake per time against rabbit population, for the Holling Type II predation term.

handling time limits the number of rabbits the snake can eat. At this point, the consumption rate remains constant when the prey population is large.

In Figure 20 (right), we see that the percent of rabbits being eaten per snake during one time period is decreasing as the rabbit population increases. Notice that the maximum percent of rabbit deaths occur when the rabbit population is small because the snakes spend more time searching for rabbits than on eating them.

The more realistic Holling Type II predation term accounts for the snakes getting full with each eaten rabbit. We will discuss the effects of Holling Type II predation on the classic Lotka-Volterra models (from Chapter 4) in the next chapter.

6 Holling Type II Predation in 2-D

In this chapter, we revisit the classic predator-prey models from Chapter 4 and modify the predation term to account for Holling Type II predation, as discussed in Chapter 5.

6.1 Lotka-Volterra with Holling Type II Predation

6.1.1 From Words to Math: Assumptions and Notation

Recall the classic Lotka-Volterra predator-prey model in Section 4.2,

$$\begin{aligned}dR/dt &= rR - hRS \\dS/dt &= -sS + uhRS,\end{aligned}$$

where r represents the relative growth rate of the rabbits in the absence of snakes, s is the starvation rate of the snakes in the absence of rabbits, h represents the constant predation rate, and u is the utility to the snake of each eaten rabbit. In this section we replace the linear (Holling Type I) predation term hRS with the non-linear (Holling Type II) predation term $\frac{hH}{H+R}RS$, as discussed in Chapter 5, and obtain the system of differential equations

$$\begin{aligned}dR/dt &= rR - \frac{hH}{H+R}RS \\dS/dt &= -sS + \frac{uhH}{H+R}RS.\end{aligned}$$

Recall from Chapter 5 that H is the number of living rabbits hunted by half-full snakes and hH is the number of rabbits captured by each snake in one time period.

Even though the snakes get full from eating more rabbits, we might expect the

rabbits and snakes to coexist and their populations to oscillate periodically, as in the Lotka-Volterra model (Chapter 4). As we shall see next, that is not that case.

6.1.2 Equilibrium Analysis

To find the equilibrium points of this system, we start by setting dR/dt and dS/dt equal to 0, obtaining the system

$$\begin{aligned} 0 &= dR/dt = R \left(r - \frac{hH}{H+R} S \right) \\ 0 &= dS/dt = S \left(-s + \frac{uhH}{H+R} R \right). \end{aligned}$$

The R -nullclines are $R = 0$ and $S = \frac{r}{hH}(H + R)$ and the S -nullclines are $S = 0$ and $R = \frac{sH}{uhH-s}$. A little algebra shows that this system has two equilibrium points at $(0, 0)$ and $(\frac{sH}{uhH-s}, \frac{ruH}{uhH-s})$, which can be verified for particular values of r , s , h , u , and H in Figure 21.

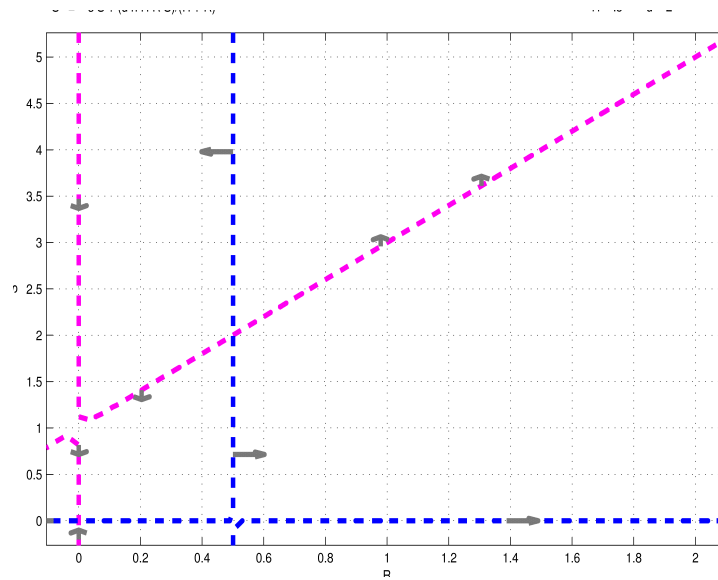


Figure 21: Nullclines for the Lotka-Volterra system with Holling Type II predation. (Parameter values $r = 2$, $s = 1$, $h = 2$, $u = 2$, and $H = 0.5$.)

The Jacobian matrix for the system is

$$J(R, S) = \begin{bmatrix} r - \frac{hHS}{H+R} + \frac{hHRS}{(H+R)^2} & -\frac{uHR}{H+R} \\ \frac{uhHS}{H+R} - \frac{uhHRS}{(H+R)^2} & -s + \frac{uhHR}{H+R} \end{bmatrix}.$$

At the origin,

$$J(0, 0) = \begin{bmatrix} r & 0 \\ 0 & -s \end{bmatrix},$$

with eigenvalues r and $-s$, so $(0, 0)$ is a saddle.

At the more complicated equilibrium $(\frac{sH}{uhH-s}, \frac{ruH}{uhH-s})$, we use Lemma 4.2 to determine the behavior of solutions near it. The R -nullcline, $S = \frac{r}{hH}(H + R)$, crosses the S -nullcline, $R = \frac{sH}{uhH-s}$, at this non-trivial equilibrium point. Since $r > 0$, $h > 0$, and $H > 0$, the slope $\frac{r}{hH}$ of the R -nullcline is always positive. By Lemma 4.2, the equilibrium is unstable; Figure 22 suggests that it is a repelling spiral source.

6.1.3 New Behavior

The classic Lotka-Volterra model predicts cyclical behavior between the rabbits and the snakes. This is not what happens in this model. Figure 22 suggests that the rabbit and snake populations coexist, but the model does not predict closed curves.

In fact, when the two populations are small, the snake population declines from a lack of food. Few snakes eat the rabbits, so the rabbit population increases. As the snakes eat more rabbits, the snakes get full, so the rabbit population can recover while the snakes get hungry. The rabbit population recovers before the snakes are hungry again, so the arc is curving up less than in the Lotka-Volterra model, thus creating a spiral source.

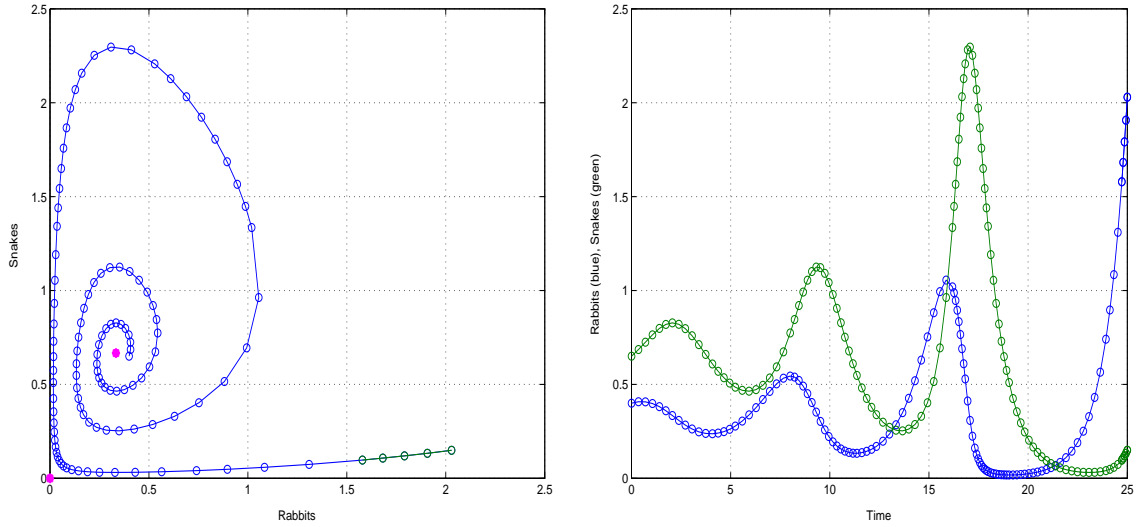


Figure 22: Trajectory spiraling away from the non-trivial equilibrium point and time plot for Lotka-Volterra with Holling Type II predation.

6.1.4 Special Cases

If a solution gets too close to either axis, one species may die, despite what the model predicts. In the Lotka-Volterra model, this situation occurs if the initial populations are too far from the equilibrium point. In this model, Figure 22 suggests that over time, a population may die out even if the initial populations are close to the equilibrium point.

As the snakes eat more and more, or as $H \rightarrow \infty$, this model turns into the classic Lotka-Volterra model from Chapter 4, which predicts closed curves. This makes sense, because the Lotka-Volterra with Holling Type I predation allows the snakes to eat forever without getting full.

6.2 Logistic Lotka-Volterra with Type II Predation

6.2.1 From Words to Math: Assumptions and Notation

In this model, the rabbit population obeys the logistic growth model from Section 3.2, in the absence of snakes. The only change from the previous model is in the rabbit growth term; all other assumptions remain the same, so the improved system of differential equations is

$$\begin{aligned}dR/dt &= r(1 - R/K)R - \frac{hH}{H+R}RS \\dS/dt &= -sS + \frac{uhH}{H+R}RS.\end{aligned}$$

Recall that, in the Logistic Lotka-Volterra model (Chapter 4), the addition of carrying capacity caused the neutral center to become a spiral sink. In the last model, the Holling Type II predation term caused the equilibrium point to repel solutions away from it. In this model, as the rabbit population reaches carrying capacity and the snakes get full due to Holling Type II predation, we might again expect closed curves, as in the classic Lotka-Volterra model. We look to the equilibrium points to find out.

6.2.2 Nullclines and Equilibria: Geometric Analysis

Setting dR/dt and dS/dt equal to 0 yields the system

$$\begin{aligned}0 &= dR/dt = R\left(r(1 - R/K) - \frac{hH}{H+R}S\right) \\0 &= dS/dt = S\left(-s + \frac{uhH}{H+R}R\right).\end{aligned}$$

From the logistic growth model in Section 3.2, we know that K will be some finite number, so we rescale the R -axis and let $K = 1$. Now R measures the number of

living rabbits as a percentage of their carrying capacity, at a given time t .

After some simple algebra, we find that the R -nullclines are $R = 0$ and $S = \frac{r}{hH}(1 - R)(H + R)$ and that the S -nullclines are $S = 0$ and $R = \frac{sH}{uhH-s}$. As in the Lotka-Volterra model (Section 4.2), the non-trivial R -nullcline, $S = \frac{r}{hH}(1 - R)(H + R)$, intersects the R -axis at $R = 1$ and the S -axis at $\frac{r}{h}$. In contrast, this nullcline is now a curving-down parabola (it was a line in Section 4.2), which intersects the non-trivial S -nullcline, $R = \frac{sH}{uhH-s}$, at the non-trivial equilibrium point.

Some algebra shows that this system has three equilibrium points, $(0, 0)$, $(1, 0)$, and $(\frac{sH}{uhH-s}, \frac{ruH[-s+H(uh-s)]}{(uhH-s)^2})$, see Figure 23.

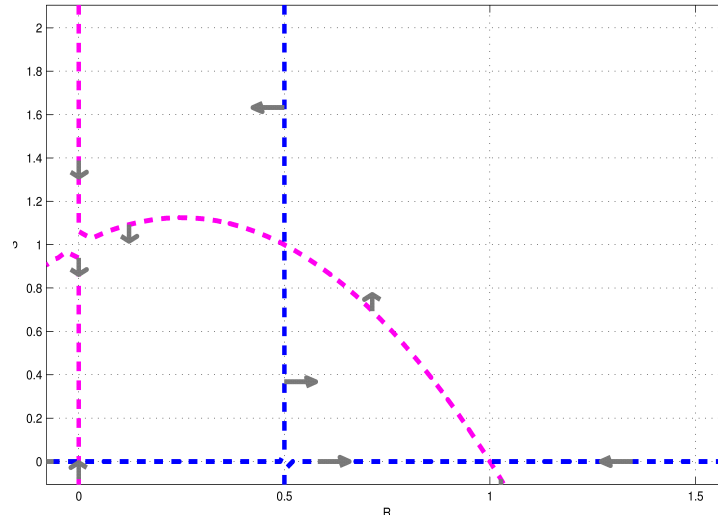


Figure 23: Nullclines for the Logistics Lotka-Volterra system with Holling Type II predation. (Parameter values $r = 2$, $s = 1$, $h = 2$, $u = 2$, $H = 0.5$, and $K = 1$.)

A geometric relationship exists between the nullclines. Since we already assumed $s < uh$ in Section 4.3, we know that the vertical line $R = \frac{sH}{uhH-s}$ crosses the parabola $S = \frac{r}{hH}(1 - R)(H + R)$, which has roots $R = 1$ and $R = -H < 0$. This model has two cases depending on whether the S -nullcline, $R = \frac{sH}{uhH-s}$, falls to the left or to the right of the peak of the parabola $S = \frac{r}{hH}(1 - R)(H + R)$ (the non-trivial

R -nullcline). Note that the peak of the parabola $S = \frac{r}{hH}(1-R)(H+R)$ is $R = \frac{1-H}{2}$. As we will see next, if the S -nullcline is to the left of the peak, then the equilibrium $(\frac{sH}{uhH-s}, \frac{ruH[-s+H(uh-s)]}{(uhH-s)^2})$ is unstable; if it falls to the right, the equilibrium is stable.

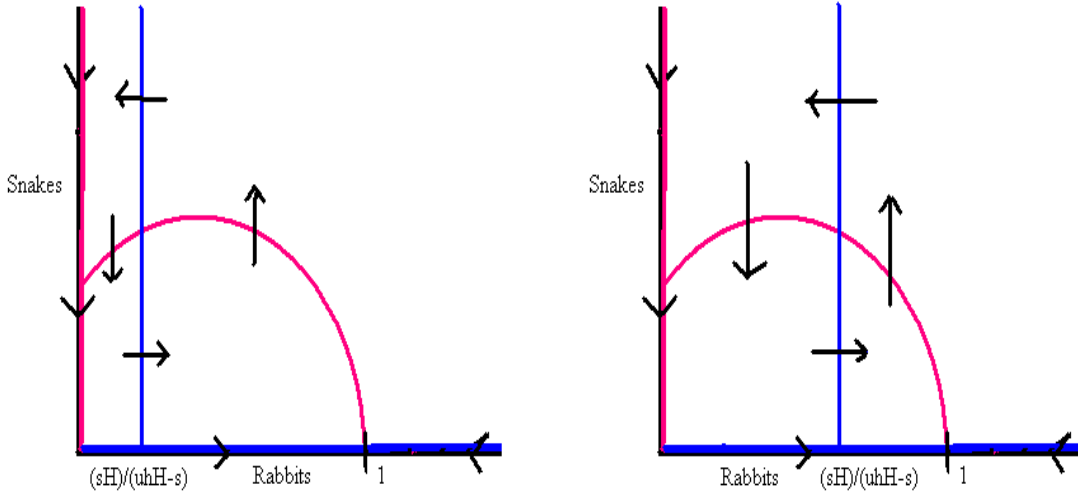


Figure 24: The S -nullcline intersects the R -nullcline at different positions, either to the left or right of the peak of the parabola.

6.2.3 Equilibria: Stability Analysis

The Jacobian matrix for the system is

$$J(R, S) = \begin{bmatrix} r(1-R) - \frac{hHS}{H+R} + R\left(-r + \frac{hHS}{(H+R)^2}\right) & -\frac{uHR}{H+R} \\ \frac{uhHS}{H+R} - \frac{uhHRS}{(H+R)^2} & -s + \frac{uhHR}{H+R} \end{bmatrix}.$$

At the origin,

$$J(0, 0) = \begin{bmatrix} r & 0 \\ 0 & -s \end{bmatrix},$$

with eigenvalues r and $-s$, which describes a saddle, as in all previous models.

At $(1, 0)$, we have

$$J(1, 0) = \begin{bmatrix} -r & -\frac{hH}{H+1} \\ 0 & \frac{-s+H(uh-s)}{H+1} \end{bmatrix},$$

with eigenvalues $-r$ and $\frac{-s+H(uh-s)}{H+1}$. Since we assume $s < uh$, $(1, 0)$ is a saddle, which pushes nearby solutions away.

Instead of computing the Jacobian matrix at $(\frac{sH}{uhH-s}, \frac{ruH[-s+H(uh-s)]}{(uhH-s)^2})$, we use Lemma 4.2 and Figure 24 to determine its stability. We can see that when the S -nullcline, $R = \frac{sH}{uhH-s}$, falls to the left of the peak of the parabola $S = \frac{r}{hH}(1-R)(H+R)$, as in Figure 24 (left), the slope of the R -nullcline is positive; it follows from Lemma 4.2 that the equilibrium is unstable. Figure 25 suggests that the equilibrium $(\frac{sH}{uhH-s}, \frac{ruH[-s+H(uh-s)]}{(uhH-s)^2})$ is a spiral source.

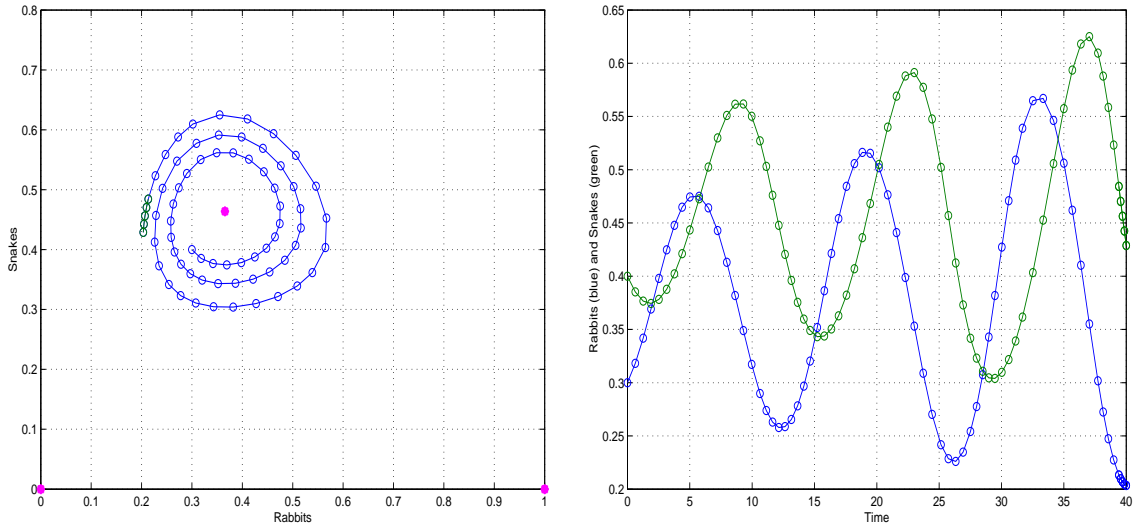


Figure 25: Direction field with trajectory spiralling away from the unstable equilibrium and corresponding time plot for the Lotka-Volterra system with Holling Type II predation.

When the S -nullcline, $R = \frac{sH}{uhH-s}$, falls to the right of the peak of the parabola as in Figure 24 (right), the slope of the R -nullcline is negative and it follows from

Lemma 4.2 that the non-trivial equilibrium is stable. Figure 26 suggests that the non-trivial equilibrium is a spiral sink.

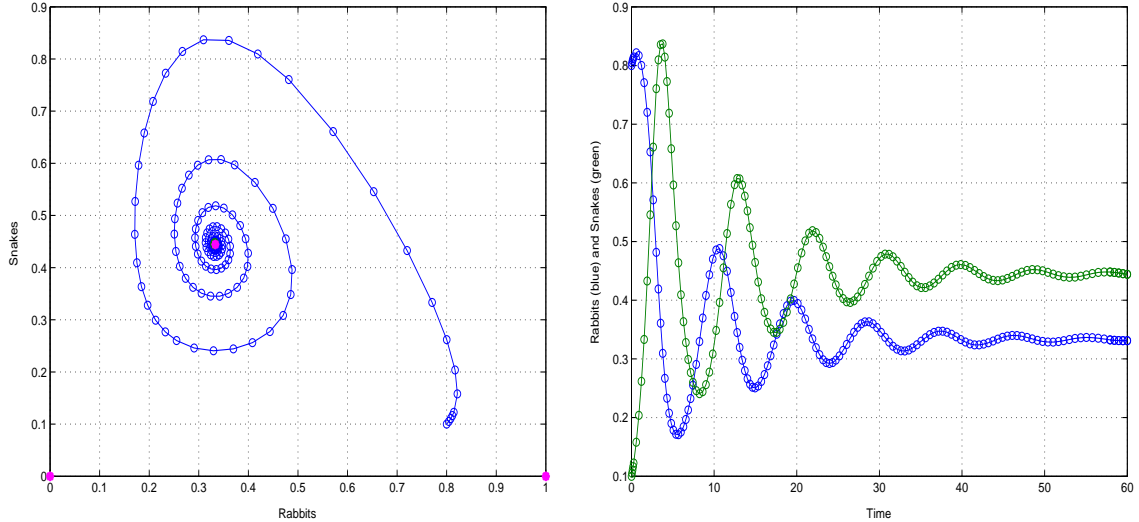


Figure 26: Direction field with trajectory spiraling in towards the attractive non-linear equilibrium and corresponding time plot for Logistic Lotka-Volterra and Holling II predation.

6.2.4 Long-term Behavior

This model produces two interesting behaviors depending on the parameter values. In the first case, when $\frac{1-H}{2} < \frac{sH}{uhH-s} < 1$ (Figure 24, left), the two species behave like the Logistic Lotka-Volterra model, and spiral in. Here, the rabbits cannot recover fast enough from the snakes' predation, thus creating a spiral.

In the second case, when $0 < \frac{sH}{uhH-s} < \frac{1-H}{2}$ (Figure 24, right), the model predicts oscillations. Let us follow a solution starting near $(1, 0)$, say $(1, 0.1)$, as in Figure 27. At $(1, 0.1)$, the direction field points northwest. This happens because $dR/dt < 0$ above the parabola, so solutions move to the left (rabbits dying) and $dS/dt > 0$ right of the S -nullcline, $R = \frac{sH}{uhH-s}$, so solutions move up (snake population increasing). The trajectory cannot cross itself and cannot escape, so it must either spiral toward

the equilibrium or wind around a closed orbit. Since the non-trivial equilibrium is unstable (see Figure 25), the trajectory cannot spiral toward it, so it must wind around a closed orbit, called a “limit cycle”. This cycle occurs because the snakes do not get hungry again fast enough, but the rabbits are able to recover quickly from being eaten.

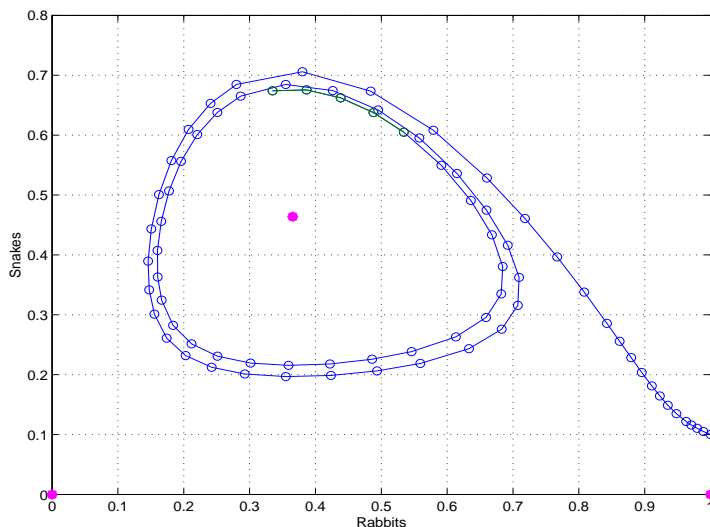


Figure 27: Direction field when $0 < \frac{sH}{uhH-s} < \frac{1-H}{2}$ and solutions wind around a limit cycle.

6.2.5 Special Cases

If we let $K \rightarrow \infty$ (before we assumed $K = 1$ for convenience), then we get the Lotka-Volterra model with Holling Type II predation, from the previous section. As $H \rightarrow \infty$, that is, the snakes can to eat rabbits without getting full, this model degenerates to the Logistics Lotka-Volterra model from Chapter 4.

7 Population Growth Models for Three Species

In Chapter 4, we studied the interaction of two species: a predator species (snakes) eating a prey species (rabbits) for survival. In this chapter, we add a second prey species—call it “squirrels”—to the “diet” of our predator and study the more complicated interactions among the three species.

Recall that we studied two models where rabbits and snakes interact in Chapter 4—the rabbit population grew exponentially in the first and logistically in the second model. Here we also consider several models, assuming that zero, one, or two prey species grow logistically; we refer to these models as EEE, EEL, and ELL.

In the EEE model, all populations grow exponentially in the absence of other species. Similarly, in the EEL model, the snakes and rabbits grow exponentially and the squirrels grow logistically in the absence of other species. The ELL model is when the rabbits and squirrels grow logistically in the absence of snakes.

As we shall see in this chapter, adding a second prey species allows for more complicated behavior and provides a few surprises, even in the simplest EEE case.

7.1 The EEE Model: Exponential Growth

7.1.1 From Words to Math: Assumptions and Notation

As in previous models, we denote the size of the rabbit and snake populations at time t by $R(t)$ and $S(t)$, respectively. We can think of the second prey as sQuirrels and denote its population by $Q(t)$. We assume that the rabbits and squirrels do not interact with each other, but both interact with the snakes. Apart from the predation by the snakes, the rabbit and squirrel populations increase exponentially, with growth rates rR and qQ , respectively. Similarly, in the absence of rabbits and

squirrels (snake food), the snakes starve and die exponentially at the net death rate sS . Assuming the snakes eat both rabbits and squirrels, the model becomes

$$\begin{aligned} dR/dt &= rR + \text{effect of snakes on rabbits,} \\ dQ/dt &= qQ + \text{effect of snakes of squirrels,} \\ dS/dt &= -sS + \text{effect of rabbits on snakes} + \text{effect of squirrels on snakes.} \end{aligned}$$

As in the Lotka-Volterra model, an interaction between a rabbit and snake has a negative effect on the rabbit population and a positive effect on the snake population. Similarly, an interaction between a squirrel and a snake has a negative effect on the squirrel population and a positive effect on the snakes.

How many rabbits and squirrels does each snake eat? A certain fraction h of the RS meetings between a rabbit and a snake results in a dead rabbit. Each eaten rabbit feeds the snakes and increases their net growth rate by some constant u ; thus u is the utility of each eaten rabbit to the snakes. Similarly, a certain fraction k of the QS meetings between a squirrel and a snake results in a squirrel death. Each squirrel eaten increases the snakes' net growth rate by some constant v , so v is the utility of each eaten squirrel.

7.1.2 System of Differential Equations

Combining all the terms, we obtain the system of differential equations

$$\begin{aligned} dR/dt &= rR - hRS \\ dQ/dt &= qQ - kQS \\ dS/dt &= -sS + uhRS + vkQS. \end{aligned}$$

Observe that the rabbits and squirrels do not interact, but contribute additively to the snake population growth. Also note that, in the absence of squirrels ($Q = 0$), we get the two-species Lotka-Volterra model from Chapter 4.

7.1.3 Nullclines and Equilibria: Geometric Analysis

In this chapter, we need to solve three equations to find the equilibrium points of the system. Note that in three-dimensional space the nullclines become surfaces (Figure 28). To find the nullclines of this system, we solve for R , Q , and S in the factored form of the system:

$$\begin{aligned} 0 &= R(r - hS) \\ 0 &= Q(q - kS) \\ 0 &= S(-s + uhR + vkQ). \end{aligned}$$

The R -nullclines are $R = 0$ and $S = \frac{r}{h}$. The Q -nullclines are $Q = 0$ and $S = \frac{q}{k}$. The S -nullclines are $S = 0$ and $uhR + vkQ = s$.

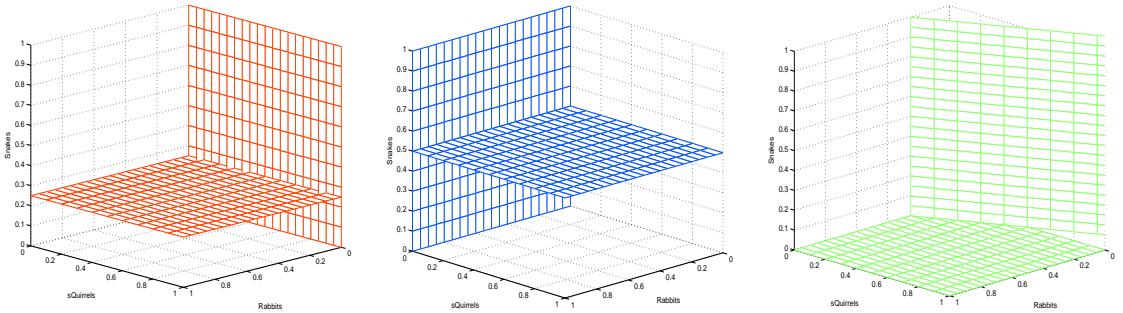


Figure 28: Left to right: The R -, Q -, and S -nullclines.

Some algebra and Figure 28 can convince us that the nullclines intersect at only three equilibrium points: $(0, 0, 0)$, $(\frac{s}{uh}, 0, \frac{r}{h})$, and $(0, \frac{s}{vk}, \frac{q}{k})$.

Geometrically, a dichotomy exists depending on the order of ratios $\frac{r}{h}$ and $\frac{q}{k}$,

which are the S -coordinates of the non-trivial R - and Q -nullclines, respectively. There are two cases: a special case when the two non-trivial horizontal nullclines coincide, that is $\frac{q}{k} = \frac{r}{h}$, and the generic case when they are disjoint ($\frac{q}{k} \neq \frac{r}{h}$). Note that the two prey species interact with the snake in exactly the same way; the only difference is in the rate constants. Because of this, without loss of generality, we can pick the squirrels to be the “superior” prey species, that is, we assume $\frac{q}{k} \geq \frac{r}{h}$ from now on. Geometrically, this means that the non-trivial Q -nullcline is “on top” of the non-trivial R -nullcline.

7.1.4 Equilibria: Stability Analysis

The Jacobian matrix for the system is

$$J(R, Q, S) = \begin{bmatrix} r - hS & 0 & -hR \\ 0 & q - kS & -kQ \\ uhS & vkS & -s + uhR + vkQ \end{bmatrix}.$$

At the origin, we have

$$J(0, 0, 0) = \begin{bmatrix} r & 0 & 0 \\ 0 & q & 0 \\ 0 & 0 & -s \end{bmatrix},$$

with eigenvalues r , q , and $-s$, so the origin is a saddle point, as usual. Solutions approach the origin along the S -axis and repel from it along the R - and Q -axes.

At $(\frac{s}{uh}, 0, \frac{r}{h})$, we have

$$J(\frac{s}{uh}, 0, \frac{r}{h}) = \begin{bmatrix} 0 & 0 & \frac{-s}{u} \\ 0 & q - \frac{rk}{h} & 0 \\ ru & \frac{rvk}{h} & 0 \end{bmatrix},$$

with eigenvalues $q - \frac{rk}{h}$ and $\pm i\sqrt{rs}$. If $\frac{q}{k} > \frac{r}{h}$, this equilibrium is a repelling center; if $\frac{q}{k} = \frac{r}{h}$, it is a neutral center (we study this case in Section 7.1.6).

Similarly, at $(0, \frac{s}{vk}, \frac{q}{k})$, we have

$$J(0, \frac{s}{vk}, \frac{q}{k}) = \begin{bmatrix} r - \frac{hq}{k} & 0 & 0 \\ 0 & 0 & \frac{-s}{v} \\ \frac{quh}{k} & qv & 0 \end{bmatrix},$$

with eigenvalues $r - \frac{hq}{k}$ and $\pm i\sqrt{qs}$. If $\frac{q}{k} > \frac{r}{h}$, this equilibrium is an attracting center; all nearby orbits will wind around it and approach a limit cycle in the QS -plane ($R = 0$).

We can confirm that one “wall” equilibrium, that is, one of $(\frac{s}{uh}, 0, \frac{r}{h})$ or $(0, \frac{s}{vk}, \frac{q}{k})$, is repelling and the other is attracting by examining the sign of the appropriate vector field coordinate near the appropriate wall. Since $\frac{q}{k} > \frac{r}{h}$, the equilibrium $(0, \frac{s}{vk}, \frac{q}{k})$ is above the R -nullcline, which means that the R -coordinate of the vector field near the equilibrium is negative, so nearby solutions are attracted to the “wall” $R = 0$.

For the same reason, the equilibrium $(\frac{s}{uh}, 0, \frac{r}{h})$ is below the Q -nullcline, which means that the Q -coordinate of the vector field near the equilibrium is positive, so nearby solutions are repelled away from the “wall” $Q = 0$.

7.1.5 Long-term Behavior

We already know what happens in the special case when there are no squirrels ($Q_0 = 0$, $R_0 > 0$, $S_0 > 0$): we get the classic predator-prey model, which predicts a cyclical coexistence between rabbits and snakes. Similarly, if $R_0 = 0$, $Q_0 > 0$ and $S_0 > 0$, the squirrels and snakes coexist in the Lotka-Volterra cycle. Now we can assume $R_0 > 0$, $Q_0 > 0$, $S_0 > 0$ and consider the special case $\frac{q}{k} = \frac{r}{h}$ first.

7.1.6 Long-term Behavior: “Twin Prey” ($\frac{q}{k} = \frac{r}{h}$)

What happens when $\frac{q}{k} = \frac{r}{h}$? If we start with more squirrels than rabbits, will the snakes eat all the squirrels and then eat all the rabbits? Will the snakes eat all the rabbits first if there are less rabbits than squirrels?

Let us first consider the special trivial case when $q = r$, $k = h$, and $v = u$. Biologically, it is as if we have two different colors of the same species, such as black and white rabbits. Essentially, we have a model with one predator and one prey species in a Lotka-Volterra cycle.

What happens if $\frac{q}{k} = \frac{r}{h}$, but $q \neq r$? Figure 29 suggests that all three species can coexist in the same environment and oscillate periodically along closed orbits, so even if there are initially more squirrels than rabbits, neither species dies. Notice that both prey species peak at the same time and the snakes peak later (see Figure 29, right).

The following proposition shows that this is, indeed, the case. Moreover, the closed orbit is confined to an invariant manifold.

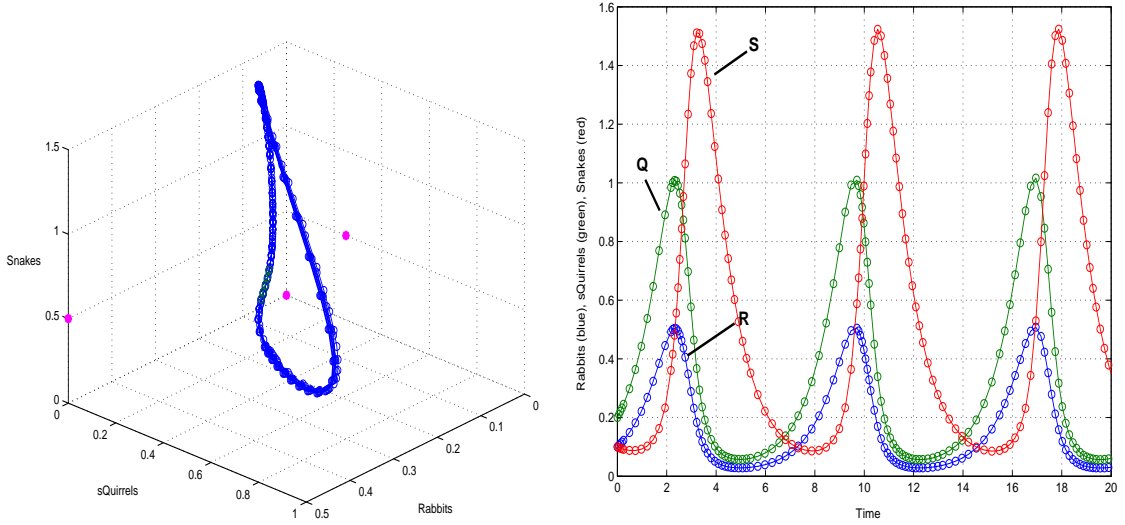


Figure 29: Closed orbit (rabbits, squirrels, and snakes coexist).

Proposition 7.1. Let $\frac{q}{k} = \frac{r}{h}$ and let $(R(t), Q(t), S(t))$ be a solution to the system

$$\frac{dR}{dt} = R(r - hS)$$

$$\frac{dQ}{dt} = Q(q - kS)$$

$$\frac{dS}{dt} = S(-s + uhR + vkQ),$$

with $R_0 > 0$, $Q_0 > 0$, and $S_0 > 0$. Then $Q(t)^{1/k} = CR(t)^{1/h}$ for some positive constant C .

Proof. We can find a first integral for the system by eliminating t :

$$\frac{dQ}{dR} = \frac{Q(q - kS)}{R(r - hS)} = \frac{kQ(q/k - S)}{hR(r/h - S)} = \frac{kQ}{hR},$$

since $\frac{q}{k} = \frac{r}{h}$. Separating the variables in the first-order differential equation

$$\frac{dQ}{dR} = \frac{kQ}{hR},$$

and integrating, we get

$$\frac{1}{k} \int \frac{dQ}{Q} = \frac{1}{h} \int \frac{dR}{R},$$

thus $Q(t)^{1/k} = CR(t)^{1/h}$, where the constant C depends only on the initial condition (R_0, Q_0, S_0) . Note that, in fact, we obtained an explicit formula for the trajectories in the RQ -plane (an explicit first integral), namely, $Q(t)^{1/k} = CR(t)^{1/h}$. \square

Note that the shape of the invariant manifold $Q(t)^{1/k} = CR(t)^{1/h}$ is a “vertical curtain,” so this model is essentially two-dimensional (the Lotka-Volterra model from Section 4.2). It is also important to note that the proof of Proposition 7.1 does not depend on the utility rates u and v , but on the equality of the “survival ratios” $\frac{q}{k}$ and $\frac{r}{h}$. Unfortunately, small changes in any of r , q , h , or k can alter the outcome of this special case $\frac{q}{k} = \frac{r}{h}$, so we do not expect to observe this “twin prey” behavior in the “real world” as this case is not *structurally stable*.

7.1.7 Long-term Behavior: Dominant Prey ($\frac{q}{k} > \frac{r}{h}$)

Recall our assumption that the squirrels are the “superior” prey: $\frac{q}{k} \geq \frac{r}{h}$. We now consider the generic case $\frac{q}{k} > \frac{r}{h}$. What happens if we start with plenty of rabbits and a few squirrels ($R_0 > Q_0$)? Will all three species coexist? Will the rabbits “win”? Figure 30 suggests a surprising answer: the rabbits die out, while the squirrels and

snakes coexist in a Lotka-Volterra limit cycle, as in Section 4.2.

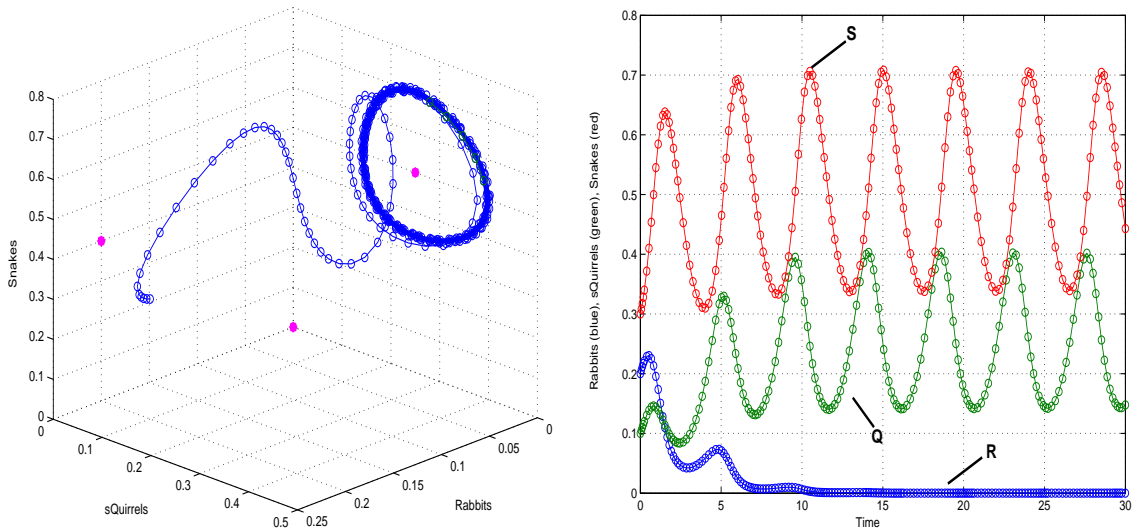


Figure 30: Attracting center with limit cycle (rabbits die out).

The following proposition shows that this is indeed the case.

Proposition 7.2. *Assume $\frac{q}{k} > \frac{r}{h}$ and let $R_0 > 0$, $Q_0 > 0$, $S_0 > 0$. Then, $\lim_{t \rightarrow \infty} R(t) = 0$, that is, the rabbits will die out and the squirrels will “win”.*

Proof. Our equilibrium analysis in Section 7.1.4 showed that only one of the three equilibria is stable; it attracts all the trajectories with positive initial conditions. When $\frac{q}{k} > \frac{r}{h}$, the equilibrium $(\frac{s}{wh}, 0, \frac{r}{h})$ is the stable one, which means that the rabbits die out, while the remaining species coexist. \square

The squirrels and snakes coexist and the rabbits die, which makes sense since we assume that the squirrels are the “superior” prey. The rabbits cannot reproduce fast enough, so they die out, while the squirrels and snakes coexist, as in the Lotka-Volterra model in Section 4.2.

7.1.8 New Behavior

In the classic Lotka-Volterra model, two species coexist in the same environment. While we might expect two prey and one predator to also coexist, this is not always the case. We find that all three species can cyclically coexist only if both prey species are essentially the same, such as black and white rabbits. When one species is “superior” to the other, the “weaker” species will eventually die out; in our model, the rabbits die out and the squirrels and snakes coexist in a cycle.

7.1.9 Special Case

Note that $Q = 0$ is not only a nullcline, but an invariant subspace for the system. As expected, in the absence of squirrels, our three-species model degenerates to the classic two-species Lotka-Volterra model in Section 4.2, which predicts cyclical coexistence. By Proposition 7.2, this cyclical coexistence is also the limit behavior of any trajectory with positive initial conditions.

7.2 The EEL Model

7.2.1 From Words to Math: Assumptions and Notation

In Section 4.3, we modified the Lotka-Volterra model from Section 4.2 by introducing carrying capacity for the prey species. We do the same here for the squirrels and replace the exponential growth term qQ with the logistic growth term $qQ(1 - Q/L)$. As we did in Section 6.2, for simplicity we rescale the Q -axis by letting $L = 1$, so Q now measures the number of living squirrels as a percentage of their carrying capacity at a given time t . We leave the rabbits to grow exponentially here, as in Section 7.1. The case when both prey species grow logistically is presented in the next section.

7.2.2 System of Differential Equations

Note that the addition of the carrying capacity affects only the differential equation for the squirrels:

$$\begin{aligned}dR/dt &= rR - hRS \\dQ/dt &= q(1 - Q/L)Q - kQS \\dS/dt &= -sS + uhRS + vkQS.\end{aligned}$$

7.2.3 Nullclines and Equilibria: Geometric Analysis

Again, we solve the factored form of the system

$$\begin{aligned}0 &= R(r - hS) \\0 &= Q(q(1 - Q/L) - kS) \\0 &= S(-s + uhR + vkQ).\end{aligned}$$

Since we only modified the second differential equation, the only difference is

in the non-trivial Q -nullcline: $S = \frac{q(1-Q)}{k}$; it now slopes down and intersects the RQ -plane (see Figure 31).

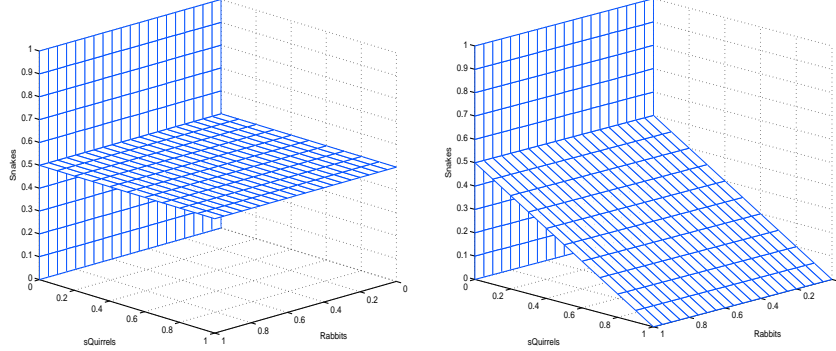


Figure 31: The Q -nullclines in the EEE model (left) and in the new EEL model (right).

With the help of Maple, we see that this system has five equilibrium points:

$$(0, 0, 0), \quad (0, 1, 0), \quad \left(\frac{s}{uh}, 0, \frac{r}{h} \right), \quad \left(0, \frac{s}{vk}, \frac{q}{k} \left(1 - \frac{s}{vk} \right) \right),$$

$$\text{and} \quad \left(\frac{vk^2r}{uh^2q} - \frac{vk-s}{uh}, 1 - \frac{kr}{qh}, \frac{r}{h} \right).$$

The first and third equilibrium points are the same as in the EEE model; the fourth has a different S -coordinate; the second and the last equilibriums are new—they have no analogies in the EEE model.

As we add more assumptions to the models, the formulas for the equilibrium points become more complicated. Looking at the coordinates of each equilibrium point, we now try to visualize where it lies in three-dimensional space.

The origin is trivial and $(0, 1, 0)$ occurs when the squirrels are at their carrying capacity, living by themselves with no rabbits and no snakes. The equilibrium point $(\frac{s}{uh}, 0, \frac{r}{h})$ occurs when no squirrels exist, so it lies on the RS -plane. Similarly, the equilibrium point $(0, \frac{s}{vk}, \frac{q}{k} (1 - \frac{s}{vk}))$ occurs when no rabbits exist, so it lies on the

QS -plane. At the most complicated equilibrium point $(\frac{vk^2r}{uh^2q} - \frac{vk-s}{uh}, 1 - \frac{kr}{qh}, \frac{r}{h})$, all species exist together; we refer to this point as the “truce equilibrium”.

A geometric relationship exists depending on the ratios $\frac{q}{k}$ and $\frac{r}{h}$, as well as the values of s , uh , and vk . Note that we always assume $s < uh$ and $s < vk$ (see Section 4.3). Since $s < vk$, we know that the S -coordinate of the fourth equilibrium is positive. We also know that the Q -coordinate, $1 - \frac{kr}{qh}$, of the equilibrium point $(\frac{vk^2r}{uh^2q} - \frac{vk-s}{uh}, 1 - \frac{kr}{qh}, \frac{r}{h})$ is positive, since we assumed $\frac{q}{k} > \frac{r}{h}$. Whether the fourth equilibrium is above or below the Q -nullcline depends on whether $\frac{r}{h} < \frac{q}{k}(1 - \frac{s}{vk})$ or $\frac{r}{h} > \frac{q}{k}(1 - \frac{s}{vk})$. As it turns out, the stability of the fourth equilibrium point depends on this geometric condition.

7.2.4 Equilibria: Stability Analysis

The Jacobian matrix for the system is

$$J(R, Q, S) = \begin{bmatrix} r - hS & 0 & -hR \\ 0 & q(1 - Q) - qQ - kS & -kQ \\ uhS & vkS & -s + uhR + vkQ \end{bmatrix}.$$

The coordinates and the Jacobian matrices of the two equilibria $(0, 0, 0)$ and $(\frac{s}{uh}, 0, \frac{r}{h})$ are the same as in Section 7.1, so the origin is again a saddle and $(\frac{s}{uh}, 0, \frac{r}{h})$ is again a repelling center.

The Jacobian matrix at $(0, 1, 0)$ is

$$J(0, 1, 0) = \begin{bmatrix} r & 0 & 0 \\ 0 & -q & -k \\ 0 & 0 & vk - s \end{bmatrix},$$

with eigenvalues r , $-q$, and $vk - s$. Since at least one eigenvalue is positive, and at least one is negative, this equilibrium point is always a saddle. In fact, since we assume $s < vk$ (see Section 4.3), solutions approach $(0, 1, 0)$ along the Q -axis and repel from $(0, 1, 0)$ along the R - and S -axes.

The Jacobian matrices for the equilibrium points $(0, \frac{s}{vk}, \frac{q}{k}(1 - \frac{s}{vk}))$ and $(\frac{vk^2r}{uh^2q} - \frac{vk-s}{uh}, 1 - \frac{kr}{qh}, \frac{r}{h})$ are too complicated to analyze, so we turn to geometric analysis to examine the behavior of solutions near these equilibrium points. First, let us look at the discriminant condition when $\frac{r}{h} < \frac{q}{k}(1 - \frac{s}{vk})$. Biologically, it means that the rabbits are “too weak” in comparison to the squirrels. This condition can be satisfied in a few ways: if r or s is small or if h or v is large. If r is small enough, then the rabbits are reproducing slowly and cannot recover from the snakes’ predation. If h is large enough, then the rabbits are hunted well by the snakes, causing a decline in the rabbit population. When s is small, the snakes can live for a while without food since they are not starving too fast. Note that if s is too small or if the squirrels are too good for the snakes (large v), then in practice, it is hard for $\frac{r}{h}$ to be between $\frac{q}{k}$ and $\frac{q}{k}(1 - \frac{s}{vk})$, unless the two prey are essentially the same species.

In any case, if the rabbits are “too weak,” that is, $\frac{r}{h} < \frac{q}{k}(1 - \frac{s}{vk})$, then the equilibrium $(0, \frac{s}{vk}, \frac{q}{k}(1 - \frac{s}{vk}))$ is above the R -nullcline, which means that the R -coordinate of the vector field near the equilibrium is negative. Thus nearby solutions are attracted to the “wall” $R = 0$ and the equilibrium $(0, \frac{s}{vk}, \frac{q}{k}(1 - \frac{s}{vk}))$ is stable; the rabbits die out and the squirrels and snakes coexist, as in Section 7.1.

If the rabbits are “strong,” that is, $\frac{q}{k} > \frac{r}{h} > \frac{q}{k}(1 - \frac{s}{vk})$, then the equilibrium $(0, \frac{s}{vk}, \frac{q}{k}(1 - \frac{s}{vk}))$ is below the R -nullcline, which means that the R -coordinate of the vector field near the equilibrium is positive, so nearby solutions are repelled from the equilibrium $(0, \frac{s}{vk}, \frac{q}{k}(1 - \frac{s}{vk}))$ and attracted to the “truce equilibrium”. Figure 32 suggests that the truce equilibrium is a sink, and all species coexist in a

stable equilibrium.

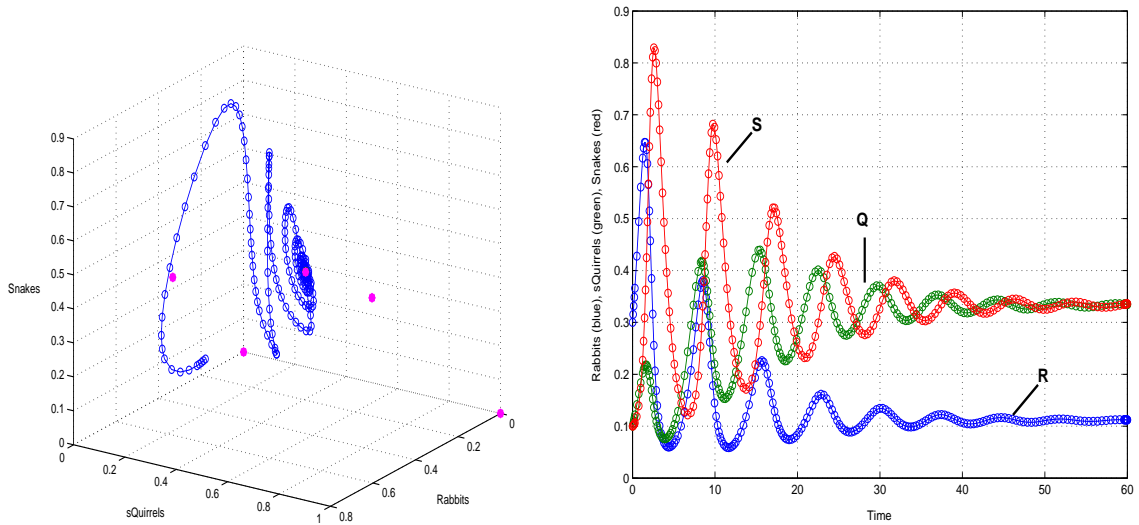


Figure 32: “Truce equilibrium” is a sink (all species coexist).

7.2.5 New Behavior

The two-species Logistic Lotka-Volterra model from Section 4.3 predicted that the rabbits and snakes can live together; we might expect that the addition of another prey species would still result in a peaceful coexistence. Surprisingly, this is not always the case! As we saw in the previous section, if the rabbits are “too weak,” they will die out, leaving the squirrels and snakes to coexist.

7.2.6 Special Case

As expected, in the absence of rabbits, our three-species model transforms into the two-species Logistic Lotka-Volterra model from Section 4.3. Similarly, in the absence of squirrels, this model degenerates to the classic Lotka-Volterra model in Section 4.2, which predicts cyclical behavior. If all three species exist and we let $L \rightarrow \infty$, this model becomes the previous model in Section 7.1, which predicts that

the “inferior” prey will die out, leaving the “superior” prey and the snakes to coexist (in this case, the rabbits have no chance).

7.3 The ELL Model

7.3.1 From Words to Math: Assumptions and Notation

In this section, we let both prey species grow logistically. We denote the rabbit carrying capacity by M and the squirrel carrying capacity by L . Again, for simplicity we let $L = M = 1$ by rescaling the R - and Q -axes (see Section 7.3).

7.3.2 System of Differential Equations

With the rabbits and squirrels growing logistically, the system of differential equations is symmetric with respect to R and Q :

$$\begin{aligned}dR/dt &= r(1 - R/M)R - hRS \\dQ/dt &= q(1 - Q/L)Q - kQS \\dS/dt &= -sS + uhRS + vkQS.\end{aligned}$$

7.3.3 Nullclines and Equilibria: Geometric Analysis

Solving the factored system

$$\begin{aligned}0 &= R(r(1 - R/M) - hS) \\0 &= Q(q(1 - Q/L) - kS) \\0 &= S(-s + uhR + vkQ),\end{aligned}$$

we see that the only new nullcline is the non-trivial R -nullcline: $S = \frac{r(1-R)}{h}$ (see Figure 33).

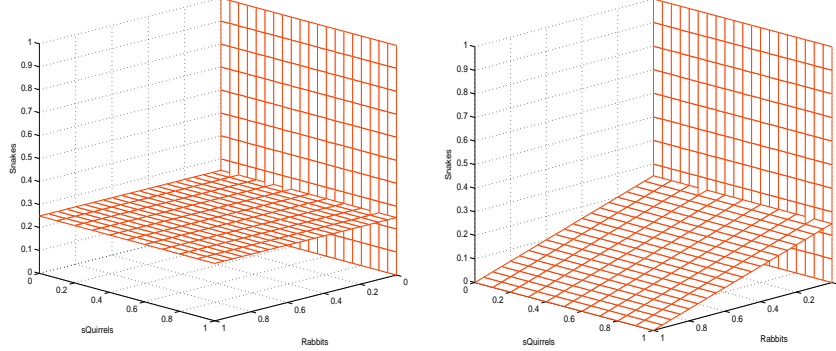


Figure 33: The R -nullclines in the EEE and EEL models (left) and in the new ELL model (right).

With the help of Maple, we see that this system has seven equilibrium points:

$$(0, 0, 0), \quad (1, 0, 0), \quad (0, 1, 0), \quad (1, 1, 0), \quad \left(\frac{s}{uh}, 0, \frac{r}{h} \left(1 - \frac{s}{uh} \right) \right), \quad \left(0, \frac{s}{vk}, \frac{q}{k} \left(1 - \frac{s}{vk} \right) \right),$$

$$\text{and} \quad \left(\frac{hq(s - vk) + vk^2r}{uh^2q + vk^2r}, \frac{kr(s - uh) + uh^2q}{uh^2q + vk^2r}, \frac{rq(-s + uh + vk)}{uh^2q + vk^2r} \right).$$

We have several new equilibrium points here, but none are unexpected. The new equilibrium $(1, 0, 0)$ corresponds to a carrying capacity of rabbits, living by themselves, with no squirrels and no snakes. Similarly, the new equilibrium $(1, 1, 0)$ corresponds to a carrying capacity of rabbits and squirrels, living together, in the absence of snakes.

Note that the S -coordinate of $(\frac{s}{uh}, 0, \frac{r}{h} (1 - \frac{s}{uh}))$ is positive as we assumed $s < uh$. Similarly, the S -coordinate of $(0, \frac{s}{vk}, \frac{q}{k} (1 - \frac{s}{vk}))$ is also positive since $s < vk$.

As in the EEL model, we see that the Q -coordinate of the truce equilibrium is positive if $\frac{q}{k} > \frac{r}{h} (1 - \frac{s}{uh})$, which is guaranteed as we assume $\frac{q}{k} > \frac{r}{h}$. Similarly, the

R -coordinate of this equilibrium is positive if $\frac{r}{h} > \frac{q}{k} \left(1 - \frac{s}{vk}\right)$, which may or may not happen, so we have to consider cases.

7.3.4 Equilibria: Stability Analysis

The Jacobian matrix for the system is

$$J(R, Q, S) = \begin{bmatrix} r(1-R) - rR - hS & 0 & -hR \\ 0 & q(1-Q) - qQ - kS & -kQ \\ uhS & vkS & -s + uhR + vkQ \end{bmatrix}.$$

The coordinates and Jacobian matrices of the two equilibria $(0, 0, 0)$ and $(0, 1, 0)$ are the same as in Section 7.2, so the origin and $(0, 1, 0)$ are again saddles. The situations at $(0, 1, 0)$ and $(1, 0, 0)$ are similar.

The Jacobian matrix at $(1, 0, 0)$ is

$$J(1, 0, 0) = \begin{bmatrix} -r & 0 & -h \\ 0 & q & -k \\ 0 & 0 & uh - s \end{bmatrix},$$

with eigenvalues $-r$, q , and $uh - s$. Since we assume $s < uh$, there are two positive eigenvalues and one negative eigenvalue. This equilibrium is a saddle, so solutions approach $(1, 0, 0)$ along the R -axis and repel from $(1, 0, 0)$ along the Q - and S -axes.

The Jacobian matrix at $(1, 1, 0)$ is

$$J(1, 1, 0) = \begin{bmatrix} -r & 0 & -h \\ 0 & -q & -k \\ 0 & 0 & -s + uh + vk \end{bmatrix},$$

with eigenvalues $-r$, $-q$, and $-s + uh + vk$. Since $s < uh$ and $s < vk$, there are two negative eigenvalues and one positive eigenvalue, so this equilibrium is also a saddle. Solutions approach $(1, 1, 0)$ along the R - and Q -axes and repel from $(1, 1, 0)$ along the S -axis.

The Jacobian matrices for the two “wall” equilibrium points $(\frac{s}{uh}, 0, \frac{r}{h}(1 - \frac{s}{uh}))$, and $(0, \frac{s}{vk}, \frac{q}{k}(1 - \frac{s}{vk}))$, and the “truce equilibrium” are too complicated to analyze, so we turn to geometric analysis.

Is it possible for the three species to coexist, or will one die out, while the other two live together? Since $\frac{q}{k} > \frac{r}{h}$, the equilibrium $(\frac{s}{uh}, 0, \frac{r}{h}(1 - \frac{s}{uh}))$ is below the Q -nullcline, which means that the Q -coordinate of the vector field near the equilibrium is positive, so nearby solutions are repelled from the “wall” $Q = 0$. Thus, the equilibrium $(\frac{s}{uh}, 0, \frac{r}{h}(1 - \frac{s}{uh}))$ is an unstable focus.

If the rabbits are “too weak,” that is, $\frac{q}{k}(1 - \frac{s}{vk}) > \frac{r}{h}$, the equilibrium $(0, \frac{s}{vk}, \frac{q}{k}(1 - \frac{s}{vk}))$ is above the R -nullcline, so the R coordinate of the vector field near the equilibrium is negative. Thus, solutions are attracted to the “wall” $R = 0$ and the equilibrium is stable; the rabbits die out and the squirrels and snakes coexist, as in Figure 34.

If the rabbits are “strong,” that is, $\frac{q}{k} > \frac{r}{h} > \frac{q}{k}(1 - \frac{s}{vk})$, the R -coordinate of the vector field near the equilibrium $(0, \frac{s}{vk}, \frac{q}{k}(1 - \frac{s}{vk}))$ is positive, so nearby solutions are attracted to the “truce equilibrium”. Figure 35 suggests that if the truce exists, it is a stable sink. We conjecture that this is always the case.

Conjecture 7.3. *The equilibrium point $(\frac{hq(s-vk)+vk^2r}{uh^2q+vk^2r}, \frac{kr(s-uh)+uh^2q}{uh^2q+vk^2r}, \frac{rq(-s+uh+vk)}{uh^2q+vk^2r})$ exists and is stable only if $\frac{q}{k} > \frac{r}{h} > \frac{q}{k}(1 - \frac{s}{vk})$.*

This conjecture says that if both wall equilibrium points are unstable, then the truce equilibrium exists and is stable. We believe the conjecture holds, but we need

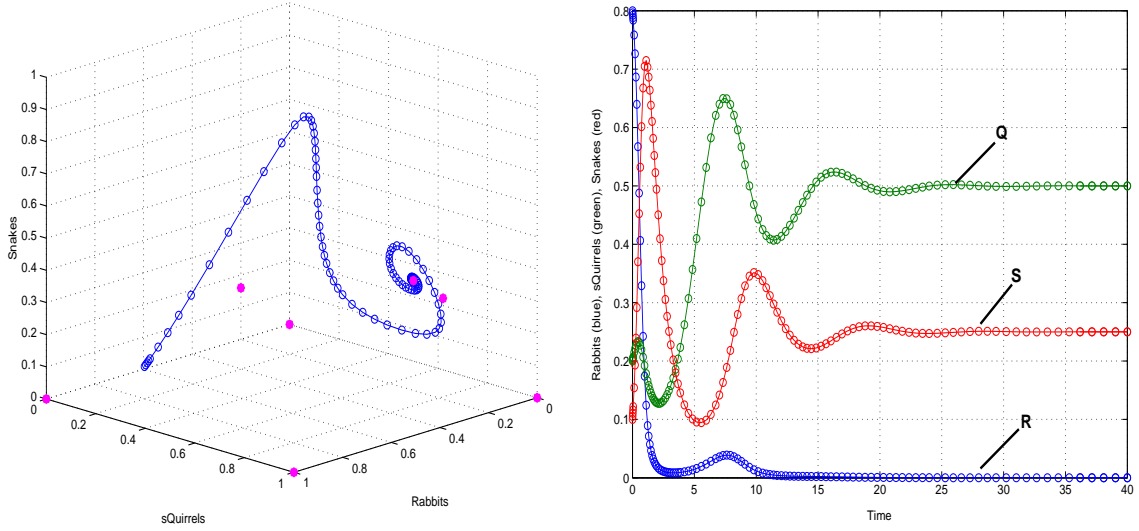


Figure 34: Stable sink (rabbits die out).

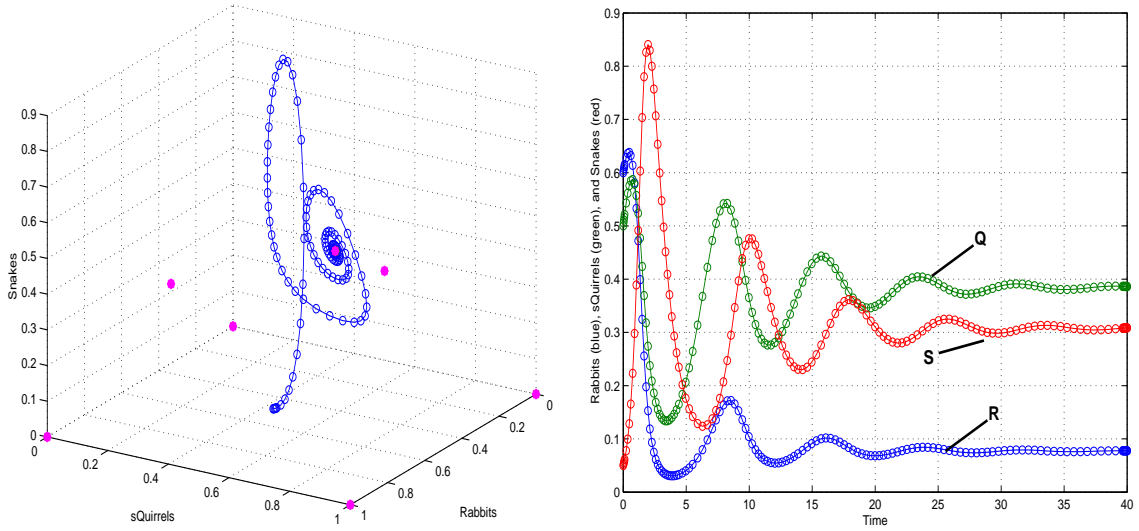


Figure 35: All species coexist and corresponding time plot.

more sophisticated theory to prove it. We ran a program that tested random values for the seven parameters r , q , s , h , k , u , and h , which satisfy the inequality stated in the conjecture. We tried over 6 million cases; in all of them the truce equilibrium was stable.

7.3.5 Long-term Behavior

This model predicts either a coexistence between the three species or a coexistence between the “superior” squirrels and snakes, which is the same behavior we saw in the EEL model. Adding logistic growth to the rabbit population in this model creates new equilibrium points, this model does not provide any new behavior.

7.3.6 Special Case

As expected, in the absence of either prey species, this three-species model degenerates to the two-species Logistic Lotka-Volterra model, which predicts a stable coexistence. If all three species exist, and we let $M \rightarrow \infty$, then this model degenerates to the EEL model in Section 7.2, where all three species coexist only if the “inferior” prey is strong enough to survive.. If we let $L \rightarrow \infty$ and $M \rightarrow \infty$, then we get the EEE model from Section 7.1, which predicts that the “superior” prey will coexist with the snakes.

8 Conclusion: Going Beyond the Textbook

Introducing more intricate terms makes population models more realistic, but also more complicated and messy, which is perhaps the reason most textbooks exclude models beyond the classic two-species Lotka-Volterra models. Our knowledge of the classic predator-prey models does not prepare us for the surprising change of behavior that occurs when a second prey is added to the predator's diet. In the last chapter, we discovered that three species can coexist only if the "inferior" rabbit species is strong enough to survive with the squirrels; otherwise, only the "superior" prey and predator coexist in the same environment.

The motivation for this investigation is the brown tree snake invasion in Guam. A study for more than two prey and one predator might provide a good explanation for the Guam invasion: we suspect a possible scenario where only the "superior" species can survive and coexist with the brown tree snakes.

What changes in behavior occur when a satiated (Holling Type II) predation term is incorporated in the three-species models? From our understanding of the effects of Holling Type II predation on the two-species models, it seems reasonable to assume that all three species could coexist only if the "inferior" prey was strong enough. Further investigation is necessary to support this claim.

We also suspect that the brown tree snakes might have conditioned themselves to learn how to hunt and kill the most abundant prey. It would be interesting to investigate a model in which the snakes have some learning ability that depends on the prey population.

With future research, we hope to find a mathematical model that explains the catastrophic changes in population on the island of Guam.

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