Bachelor’s degree in Bioinformatics

Systems of Differential Equations

Prof. Renato Bruni

bruni@diag.uniroma1.it

Department of Computer, Control, and Management Engineering (DIAG)

“Sapienza” University of Rome

Parametric Curves

Imagine that a particle moves along the curve *C* shown in Figure 1.

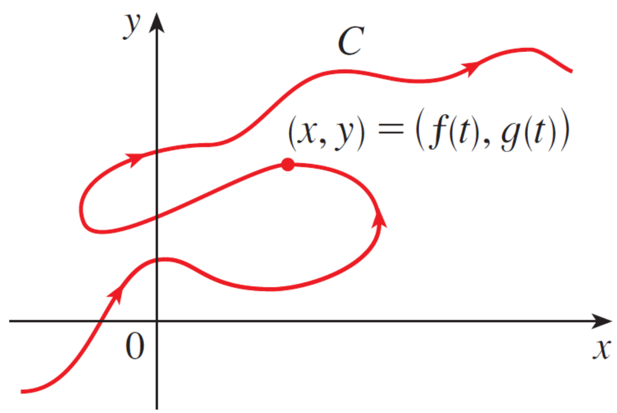


Figure 1

It is impossible to describe *C* by an equation of the form $y = f(x)$ because *C* fails the Vertical Line Test. But the *x*- and *y*-coordinates of the particle are functions of time and so we can write $x = f(t)$ and $y = g(t)$.

Parametric Curves

Such a pair of equations is often a convenient way of describing a curve and gives rise to the following definition.

Suppose that *x* and *y* are both given as functions of a third variable *t* (called a **parameter**) by the equations

$$x = f(t) \qquad y = g(t)$$

(called **parametric equations**). Each value of *t* determines a point (*x*, *y*) that we can plot in a coordinate plane. As *t* varies, the point (*x*, *y*) = (*f*(*t*), *g*(*t*)) varies and traces out a curve *C*, which we call a **parametric curve**.

Parametric Curves

The parameter t does not necessarily represent time and, in fact, we could use a letter other than t for the parameter.

But in the applications of parametric curves to systems of differential equations the parameter will be time and therefore we can interpret $(x, y) = (f(t), g(t))$ as the position of a particle at time t.

Example 1

Sketch and identify the curve defined by the parametric equations

$$x = t^2 - 2t \qquad y = t + 1$$

Solution:

Each value of *t* gives a point on the curve, as shown in the table.

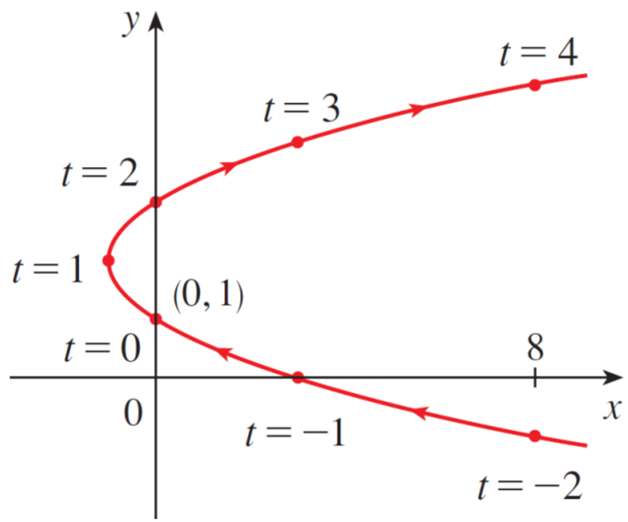
t	x	y
−2	8	−1
−1	3	0
0	0	1
1	−1	2
2	0	3
3	3	4
4	8	5

Example 1 – *Solution*

cont'd

For instance, if $t = 0$, then $x = 0$, $y = 1$ and so the corresponding point is (0, 1).

We plot the points (x, y) determined by several values of the parameter t and we join them to produce a curve.



Example 1 – *Solution*

cont'd

A particle whose position is given by the parametric equations moves along the curve in the direction of the arrows as t increases.

Notice that the consecutive points marked on the curve appear at equal time intervals but not at equal distances.

That is because the particle slows down and then speeds up as t increases.

It appears from the figure that the curve traced out by the particle may be a parabola.

Example 1 – *Solution*

cont'd

This can be confirmed by eliminating the parameter t as follows. We obtain $t = y – 1$ from the second equation and substitute into the first equation.

This gives

$$x = t^2 - 2t = (y - 1)^2 - 2(y - 1) = y^2 - 4y + 3$$

and so the curve represented by the given parametric equations is the parabola $x = y^2 - 4y + 3$.

Systems of Two Autonomous Diff. Eq.

Let $R(t)$ be the number of prey (using R for rabbits) and $W(t)$ be the number of predators (with W for wolves) at time t.

In the absence of predators, the ample food supply would support exponential growth of the prey, that is,

$$\frac{dR}{dt} = rR$$ where r is a positive constant

In the absence of prey, we assume that the predator population would decline through mortality at a rate proportional to itself, that is,

$$\frac{dW}{dt} = -kW$$ where k is a positive constant

Systems of Two Autonomous Diff. Eq.

With both species present, however, we assume that the principal cause of death among the prey is being eaten by a predator, and the birth rate of the predators depends on their available food supply, namely, the prey.

We also assume that the two species encounter each other at a rate that is proportional to both populations and is therefore proportional to the product RW.

This is referred to as the **principle of mass action**: the rate of encounter of two entities is proportional to the densities of each.

Systems of Two Autonomous Diff. Eq.

A system of two *coupled* differential equations that incorporates these assumptions is as follows:

(1) $$\frac{dR}{dt} = rR - aRW \qquad \frac{dW}{dt} = -kW + bRW$$

where *k*, *r*, *a*, and *b* are positive constants.

Notice that the term $-aRW$ decreases the growth rate of the prey and the term bRW increases the growth rate of the predators.

Systems of Two Autonomous Diff. Eq.

The equations in (1) are known as the **predator-prey equations**, or the **Lotka-Volterra equations**.

A **solution** of this system of equations is a pair of functions $R(t)$ and $W(t)$ that describe the populations of prey and predator as functions of time.

Therefore a solution can be represented as a parametric curve $(x, y) = (R(t), W(t))$ in the plane.

Example 2 – *Lotka-Volterra equations*

Suppose that populations of rabbits and wolves are described by the Lotka-Volterra equations (1) with $r = 0.08$, $a = 0.001$, $k = 0.02$, and $b = 0.00002$. The time t is measured in months.

(a) Use the system of differential equations to find an expression for dW/dR.

(b) Draw a direction field for the resulting differential equation in the RW-plane. Then use that direction field to sketch some parametric curves representing solutions of Equations 1.

Example 2 – *Lotka-Volterra equations*

cont'd

(c) Suppose that, at some point in time, there are 1000 rabbits and 40 wolves. Draw the corresponding parametric curve representing the solution for these initial conditions. Use it to describe the changes in both population levels.

(d) Use part (c) to make sketches of R and W as functions of t.

Example 2(a) – *Solution*

We use the Chain Rule to eliminate *t* :

$$\frac{dW}{dt} = \frac{dW}{dR}\frac{dR}{dt}$$

so

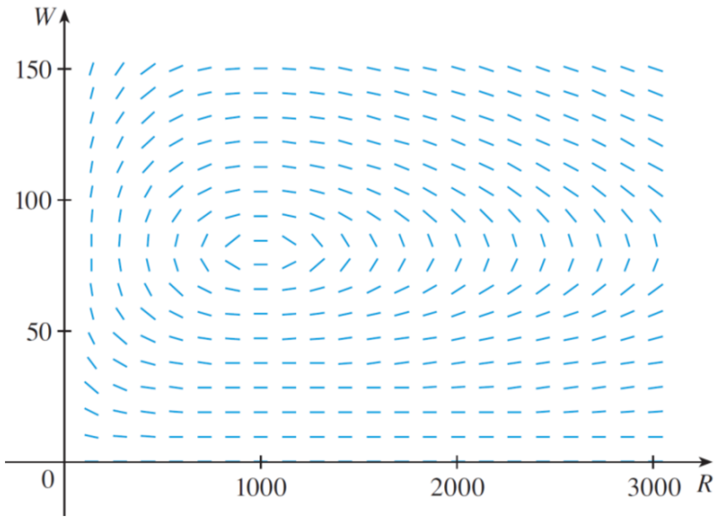
$$\frac{dW}{dR} = \frac{\frac{dW}{dt}}{\frac{dR}{dt}} = \frac{-0.02W + 0.00002RW}{0.08R - 0.001RW}$$

Example 2(b) – *Solution*

If we think of W as a function of R, we have the differential equation

$$\frac{dW}{dR} = \frac{-0.02W + 0.00002RW}{0.08R - 0.001RW}$$

We draw the direction field for this differential equation

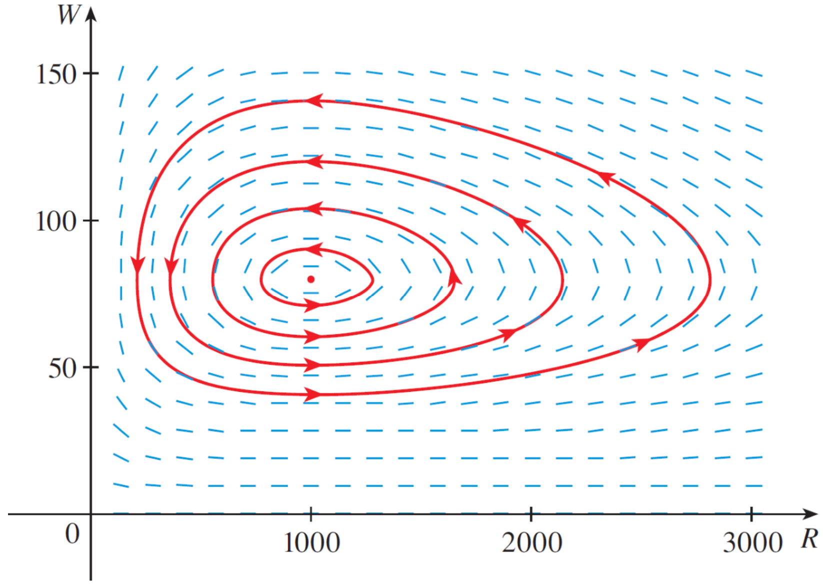


Direction field for the predator-prey system

Example 2(b) – *Solution*

cont'd

This direction field is always tangent to the parametric curves representing solutions to Equations 1



Phase portrait of the system

Example 2(b) – *Solution*

cont'd

If we move along a curve, we observe how the relationship between R and W changes as time passes.

Although it is not obvious from the direction field, it can be shown that the curves are closed in the sense that if we travel along a curve, we always return to our starting point.

When we represent solutions of a system of differential equations as parametric curves in the figure, we refer to the RW-plane as the **phase plane**.

Example 2(b) – *Solution*

cont'd

There, when we had a single variable, we plotted arrows on a line corresponding to the variable.

Movement could be in either direction along the line and the arrows indicated the direction of this movement. Now, with two variables, we plot arrows in the plane corresponding to the two variables.

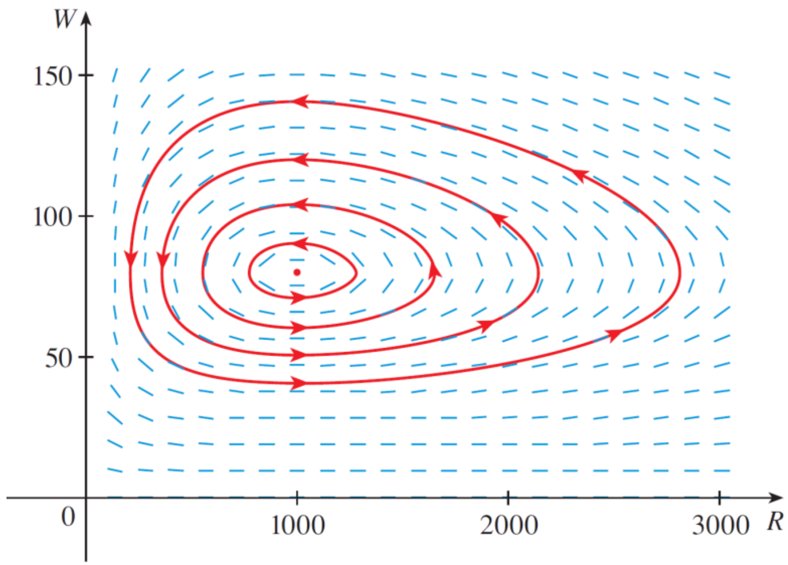
Movement can now be in any direction in the plane and again the arrows indicate the direction of this movement.

Example 2(b) – *Solution*

cont'd

The parametric curves in the phase plane are called **phase trajectories**, and so a phase trajectory is a path traced out by solutions (*R*, *W*) as time goes by.

A **phase portrait** consists of typical phase trajectories:

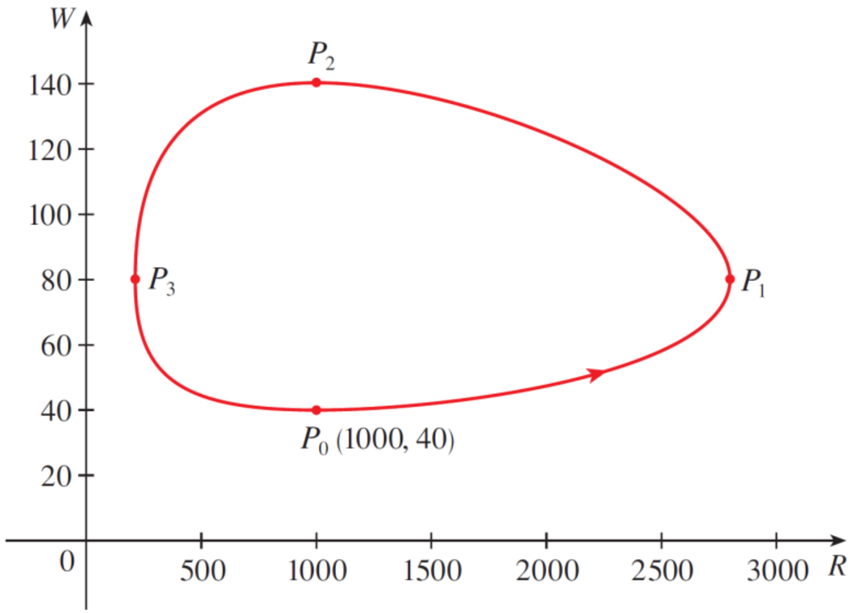


Phase portrait of the system

Example 2(c) – *Solution*

cont'd

Starting with 1000 rabbits and 40 wolves corresponds to drawing the parametric curve through the point $P_0(1000, 40)$.



Phase trajectory through (1000, 40)

Example 2(c) – *Solution*

cont'd

Starting at the point P_0 at time $t = 0$ and letting t increase, do we move clockwise or counterclockwise around the phase trajectory?

If we put $R = 1000$ and $W = 40$ in the first differential equation, we get

$$\frac{dR}{dt} = 0.08(1000) - 0.001(1000)(40) = 80 - 40 = 40$$

Since $dR/dt > 0$, we conclude that R is increasing at P_0 and so we move counterclockwise around the phase trajectory.

Example 2(c) – *Solution*

cont'd

We see that at P_0 there aren't enough wolves to maintain a balance between the populations, so the rabbit population increases.

That results in more wolves and eventually there are so many wolves that the rabbits have a hard time avoiding them.

So the number of rabbits begins to decline (at P_1, where we estimate that R reaches its maximum population of about 2800).

Example 2(c) – *Solution*

cont'd

This means that at some later time the wolf population starts to fall (at P_2, where $R = 1000$ and $W \approx 140$). But this benefits the rabbits, so their population later starts to increase (at P_3, where $W = 80$ and $R \approx 210$).

As a consequence, the wolf population eventually starts to increase as well.

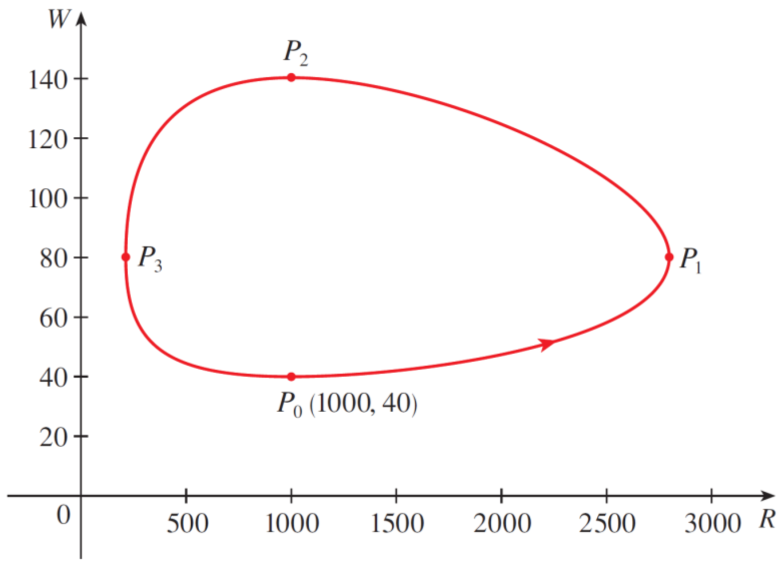
This happens when the populations return to their initial values of $R = 1000$ and $W = 40$, and the entire cycle begins again.

Example 2(d) – *Solution*

cont'd

From the description in part (c) of how the rabbit and wolf populations rise and fall, we can sketch the graphs of $R(t)$ and $W(t)$.

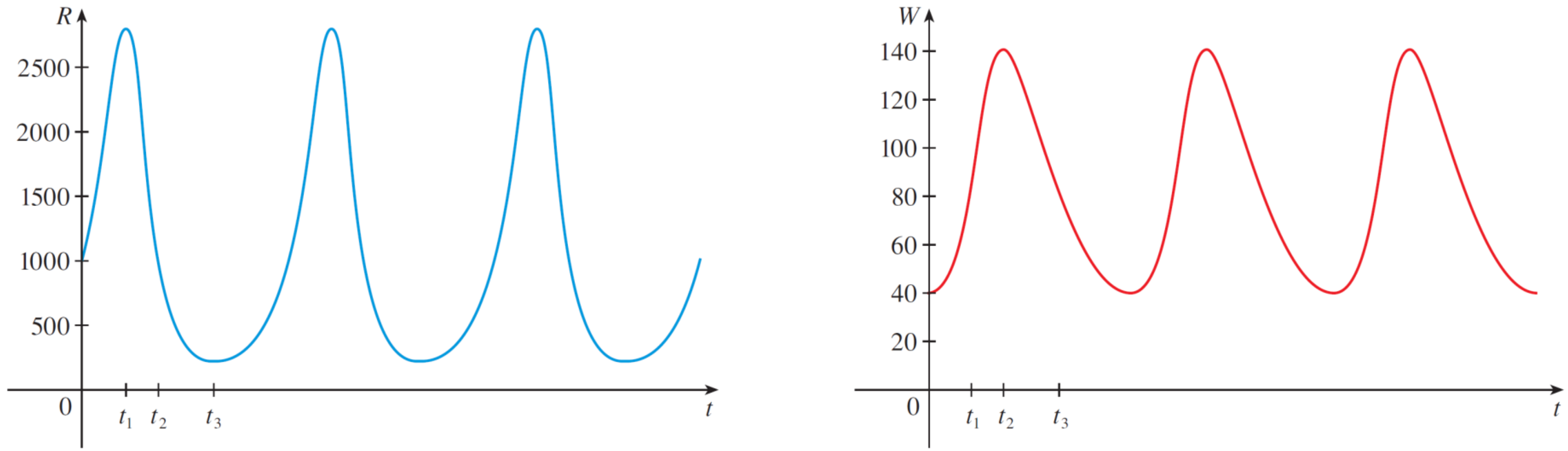
Suppose the points P_1, P_2, P_3 are reached at times t_1, t_2, t_3



Phase trajectory through (1000, 40)

Example 2(d) – *Solution*

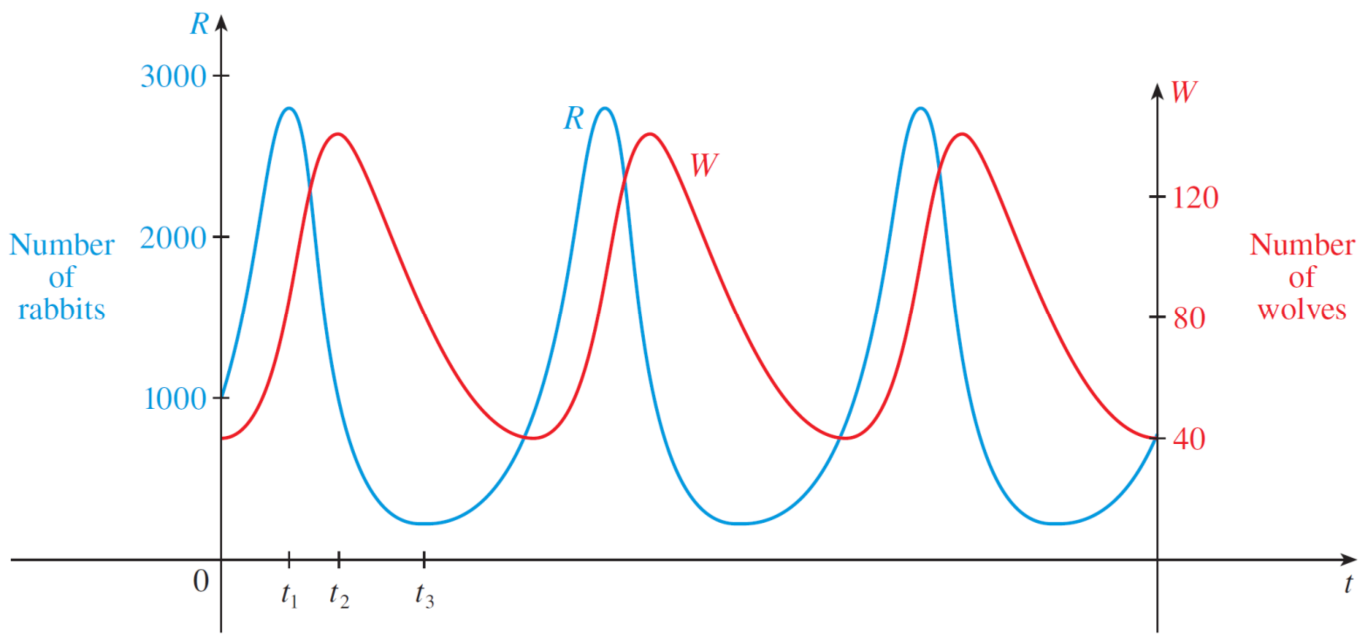
Then we can sketch graphs of *R* and *W* as follows.



Graphs of the rabbit and wolf populations as functions of time

Example 2(d) – *Solution*

To make the graphs easier to compare, we draw the graphs on the same axes but with different scales for *R* and *W*. Notice that the rabbits reach their maximum population size about a quarter of a cycle before the wolves.



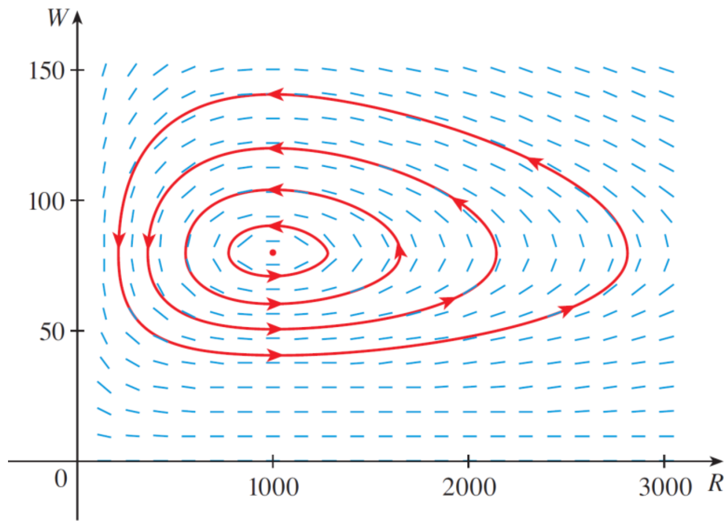
Comparison of the rabbit and wolf populations

Equilibria

The predator-prey equations or the population sizes of rabbits and wolves:

(1) $$\frac{dR}{dt} = rR - aRW \qquad \frac{dW}{dt} = -kW + bRW$$

The corresponding phase plane is shown here:



The predator-prey phase plot when

r = 0.08, *a* = 0.001, *k* = 0.02, and *b* = 0.00002

Equilibria

An *equilibrium* of this system of differential equations is a constant population size of rabbits $\hat{R}$ and of wolves $\hat{W}$ at which no further change in either occurs. This requires that both $dR/dt = 0$ and $dW/dt = 0$.

Using Equations 1, this gives two equations in two unknowns: $rR - aRW = 0$ and $-kW + bRW = 0$

Definition Consider the autonomous system of differential equations

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

An **equilibrium** is a pair of values $(\hat{x}, \hat{y})$ such that both $dx/dt = 0$ and $dy/dt = 0$ when $x = \hat{x}$ and $y = \hat{y}$. This gives a pair of equations $f(\hat{x}, \hat{y}) = 0$ and $g(\hat{x}, \hat{y}) = 0$ that define the values of $\hat{x}$ and $\hat{y}$.

Equilibria

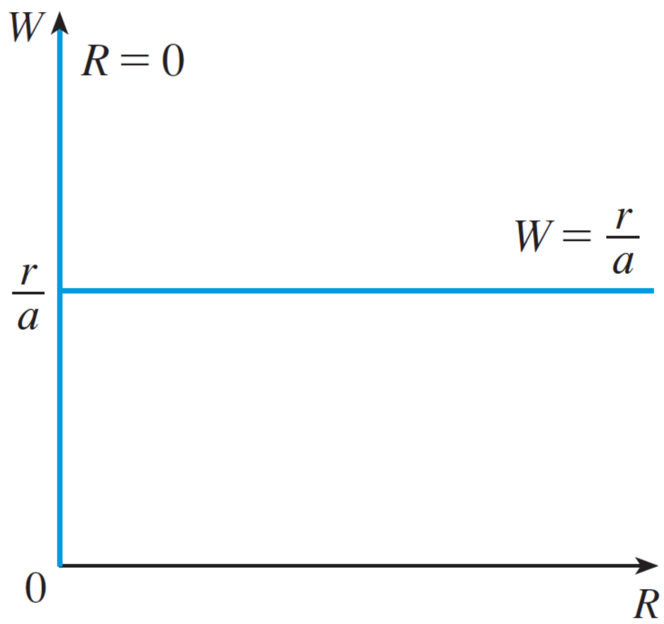
We can connect the pair of equations defining the equilibria of the predator-prey model to the phase plane in Figure 1. The equation $rR - aRW = 0$ must hold if the population size of rabbits is to remain constant; it can be factored to give $R(r - aW) = 0$.

Therefore the population size of rabbits will remain constant if either $R = 0$ or $W = r/a$

The first of these equations corresponds to absence of rabbits altogether. The second corresponds to the population size of wolves at which the birth rate of rabbits is exactly balanced by their death rate through predation.

Equilibria

The lines defined by these equations are called the *R-nullclines* and are plotted on the phase plane here:

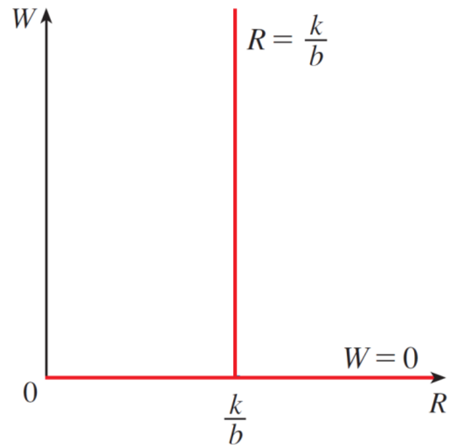


R-nullclines are blue, *W*-nullclines are red, and equilibria are black dots.

Equilibria

The second equation, $-kW + bRW = 0$, must hold if the population size of wolves is to remain constant; it can be factored and solved to give $W = 0$ and $R = k/b$. The first of these equations corresponds to absence of wolves. The second corresponds to the population size of rabbits at which the birth rate of wolves (through consumption of rabbits) is exactly balanced by their death rate.

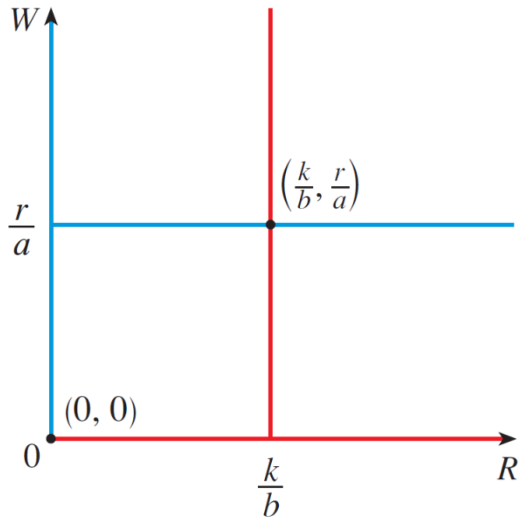
The lines defined by these equations are the *W-nullclines* and are plotted here



R-nullclines are blue, *W*-nullclines are red, and equilibria are black dots.

Equilibria

This figure shows the *R*- and *W-nullclines* plotted together.



R-nullclines are blue, *W*-nullclines are red, and equilibria are black dots.

Definition The ***x*-nullclines** of differential equations (2) are the curves in the xy-plane that satisfy the equation $f(x, y) = 0$. Along these curves, $dx/dt = 0$. The ***y*-nullclines** of differential equations (2) are the curves in the xy-plane that satisfy the equation $g(x, y) = 0$. Along these curves, $dy/dt = 0$.

Equilibria

Whenever a trajectory in the phase plane crosses a nullcline, it must do so either horizontally or vertically, depending on the nullcline in question. This is because movement in either the vertical or horizontal direction is zero on a nullcline since either *dy*/*dt* = 0 or *dx*/*dt* = 0.

> **Finding Equilibria Graphically** For differential equations (2) any point at which an x-nullcline intersects a y-nullcline is an equilibrium.

In addition to this visualization of equilibrium points and nullclines, we can sometimes derive expressions for the equilibria algebraically. The predator-prey model has two equilibria: (i) $\hat{R} = 0, \hat{W} = 0$ and (ii) $\hat{R} = k/b, \hat{W} = r/a$.

Example 1 – *Lotka-Volterra competition equations*

The differential equation for logistic population growth can be extended to model competitive interactions between two species. Let's use $N_1(t)$ and $N_2(t)$ to denote the population size of species 1 and 2 at time t. Suppose that the per capita growth rate of each species decreases linearly with the population size of each species. Specifically, the per capita growth rate of species 1 is

$$r\left(1 - \frac{N_1 + \alpha N_2}{K_1}\right)$$

where α , r, and K_1 are positive constants. Likewise, the per capita growth rate of species 2 is

$$r\left(1 - \frac{N_2 + \beta N_1}{K_2}\right)$$

Example 1 – *Lotka-Volterra competition equations*

where β and K_2 are positive constants. This gives the system

$$\frac{dN_1}{dt} = r\left(1 - \frac{N_1 + \alpha N_2}{K_1}\right)N_1 \qquad \frac{dN_2}{dt} = r\left(1 - \frac{N_2 + \beta N_1}{K_2}\right)N_2 \tag{3}$$

(a) Suppose $r = 1$, $K_1 = 1000$, $K_2 = 600$, $\alpha = 2$, and $\beta = 1$. Find the N_1- and N_2-nullclines and plot them on the phase plane. Indicate all equilibria.

(b) Calculate the equilibria algebraically.

(c) Suppose instead that $\beta = 0$, but all other constants have the same values as in part (a). Calculate the equilibria algebraically.

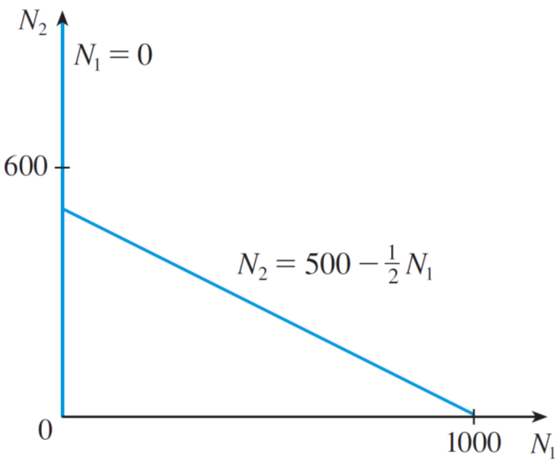
Example 1(a) – *Solution*

The N_1-nullclines satisfy $dN_1/dt = 0$ or

$$\left(1 - \frac{N_1 + 2N_2}{1000}\right)N_1 = 0$$

Therefore the N_1-nullclines are $N_1 = 0$ and $N_1 + 2N_2 = 1000$. The second equation can be rewritten as $N_2 = 500 - \frac{1}{2}N_1$.

It is plotted in Figure 3(a).



N_1-nullclines are blue, N_2-nullclines are red, and equilibria are black dots.

Figure 3(a)

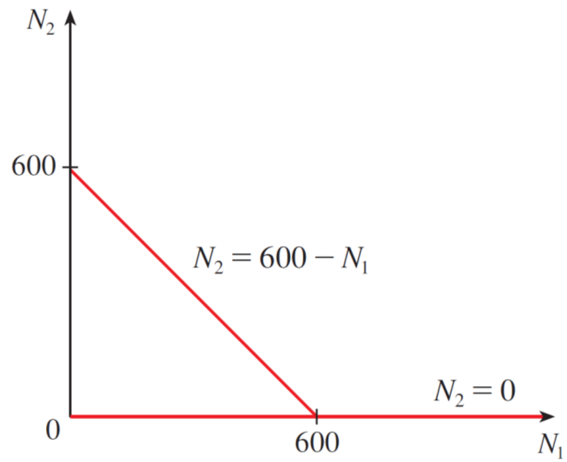
Example 1(a) – *Solution*

cont'd

The N_2-nullclines satisfy $dN_2/dt = 0$ or

$$\left(1 - \frac{N_2 + N_1}{600}\right)N_2 = 0$$

The N_2-nullclines are therefore $N_2 = 0$ and $N_1 + N_2 = 600$. The second equation can be rewritten as $N_2 = 600 - N_1$ and is plotted in Figure 3(b).

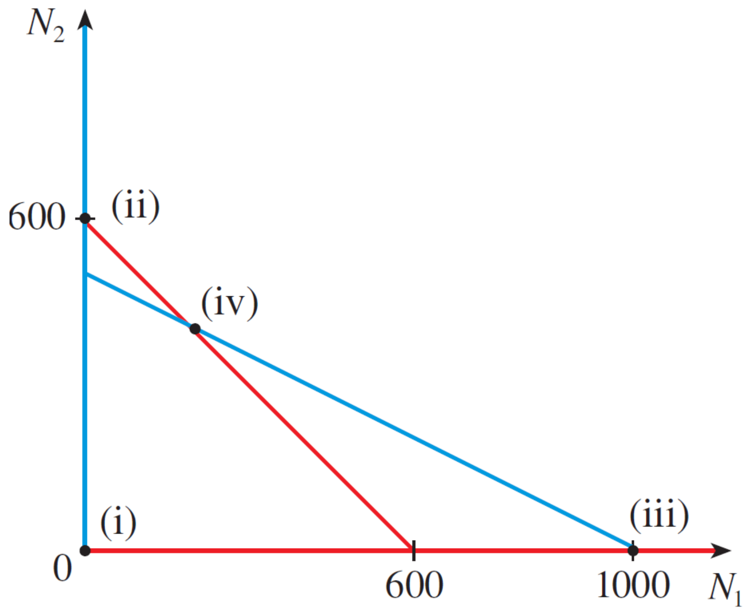


N_1-nullclines are blue, N_2-nullclines are red, and equilibria are black dots.

Figure 3(b)

Example 1(a) – *Solution*

The nullclines are plotted together, along with the equilibria, in Figure 3(c).



N_1-nullclines are blue, N_2-nullclines are red, and equilibria are black dots.

Figure 3(c)

Example 1(b) – *Solution*

cont'd

Equilibria are pairs of values $(\hat{N}_1, \hat{N}_2)$ that simultaneously satisfy the pair of equations

$$\left(1 - \frac{\hat{N}_1 + 2\hat{N}_2}{1000}\right)\hat{N}_1 = 0 \qquad \text{and} \qquad \left(1 - \frac{\hat{N}_2 + \hat{N}_1}{600}\right)\hat{N}_2 = 0$$

We can calculate the equilibria by solving the first equation for $\hat{N}_1$, substituting the result into the second equation, and then solving it for $\hat{N}_2$. There are two solutions to the first equation: $\hat{N}_1 = 0$ and $\hat{N}_1 = 1000 - 2\hat{N}_2$.

We consider each of these in turn.

Example 1(b) – *Solution*

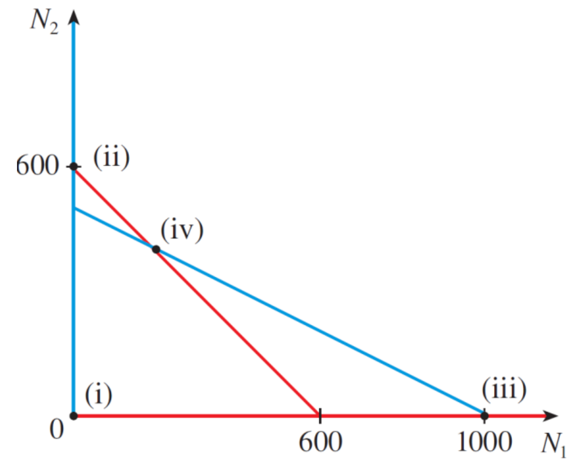
cont'd

Substituting $\hat{N}_1 = 0$ into the second equation gives

$$\left(1 - \frac{\hat{N}_2}{600}\right)\hat{N}_2 = 0$$

Solving for $\hat{N}_2$ gives $\hat{N}_2 = 0$ and $\hat{N}_2 = 600.$

Therefore two equilibria are
(i) $\hat{N}_1 = 0$, $\hat{N}_2 = 0$ and
(ii) $\hat{N}_1 = 0$, $\hat{N}_2 = 600$
[see Figure 3(c)].



N_1-nullclines are blue, N_2-nullclines are red, and equilibria are black dots.

Figure 3(c)

Example 1(b) – *Solution*

cont'd

Substituting $\hat{N}_1 = 1000 - 2\hat{N}_2$ into the second equation gives

$$\left(1 - \frac{\hat{N}_2 + (1000 - 2\hat{N}_2)}{600}\right)\hat{N}_2 = 0$$

Solving for $\hat{N}_2$ gives $\hat{N}_2 = 0$ and $\hat{N}_2 = 400$. In the first case we then have an $\hat{N}_1$ value of $\hat{N}_1 = 1000 - 2 \cdot 0 = 1000$, and in the second case we have an $\hat{N}_1$ value of $\hat{N}_1 = 1000 - 2 \cdot 400 = 200$.

Therefore a third equilibrium is (iii) $\hat{N}_1 = 1000, \hat{N}_2 = 0$ and a fourth is (iv) $\hat{N}_1 = 200, \hat{N}_2 = 400$ as shown in Figure 3(c).

Example 1(c) – *Solution*

cont'd

With $\beta = 0$, the equilibria are now pairs of values,$(\hat{N}_1, \hat{N}_2)$ that simultaneously satisfy the equations

$$\left(1 - \frac{\hat{N}_1 + 2\hat{N}_2}{1000}\right)\hat{N}_1 = 0 \qquad \text{and} \qquad \left(1 - \frac{\hat{N}_2}{600}\right)\hat{N}_2 = 0$$

The second equation no longer involves $\hat{N}_1$ and therefore we can solve it immediately for $\hat{N}_2$. We obtain $\hat{N}_2 = 0$ and $\hat{N}_2 = 600$.

Substituting $\hat{N}_2 = 0$ into the first equation gives $[1 - \hat{N}_1/1000]\hat{N}_1 = 0$. Solving this for $\hat{N}_1$ gives $\hat{N}_1 = 0$ and $\hat{N}_1 = 1000$. Therefore two equilibria are (i) $\hat{N}_1 = 0, \hat{N}_2 = 0$ and (ii) $\hat{N}_1 = 1000, \hat{N}_2 = 0$.

Example 1(c) – *Solution*

cont'd

If instead we substitute $\hat{N}_2 = 600$ into the first equation, we get

$$\left(1 - \frac{\hat{N}_1 + 1200}{1000}\right)\hat{N}_1 = 0$$

Solving this for $\hat{N}_1$ gives $\hat{N}_1 = 0$ and $\hat{N}_1 = -200$. Therefore two additional equilibria are (iii) $\hat{N}_1 = 0, \hat{N}_2 = 600$ and (iv) $\hat{N}_1 = -200, \hat{N}_2 = 600.$

Notice that equilibrium (iv) involves a negative value of $\hat{N}_1$.

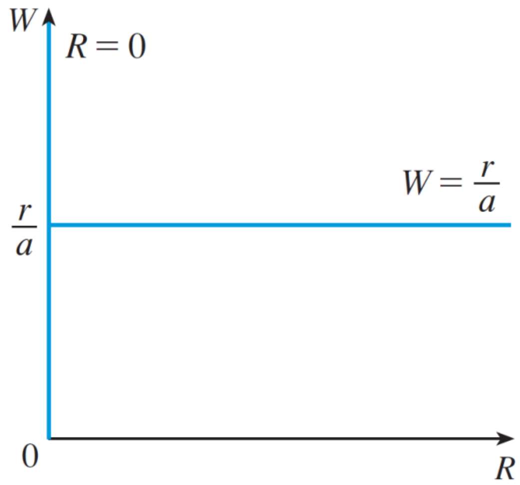
Example 1(c) – *Solution*

From a mathematical standpoint this is a perfectly fine equilibrium, but from a biological standpoint it is not of interest because it would correspond to a negative population size.

Equilibria that are biologically relevant [(i), (ii), and (iii) in this example] are referred to as **biologically feasible**.

Qualitative Dynamics in the Phase Plane

Let's return to the figure plotting the *R*-nullclines from the predator-prey model of Equations 1 .



R-nullclines are blue, *W*-nullclines are red, and equilibria are black dots.

These are curves in the plane along which $dR/dt = 0$.

Qualitative Dynamics in the Phase Plane

Therefore these curves separate the plane into regions within which either $dR/dt > 0$ or $dR/dt < 0$. We can determine which of these two situations applies in each region.

Consider the region above the line W = r/a in Figure 2(a). This corresponds to large values of W, in which case Equations 1 give

$$\frac{dR}{dt} = rR - aRW \approx -aRW < 0$$

for large enough values of W

Qualitative Dynamics in the Phase Plane

Therefore *dR*/*dt* < 0 in this region. Conversely, if *W* is close to zero, we have

$$\frac{dR}{dt} = rR - aRW \approx rR > 0$$

We can therefore indicate whether *R* is increasing or decreasing in each of these regions of the phase plane with a single arrow as in Figure 4(a).

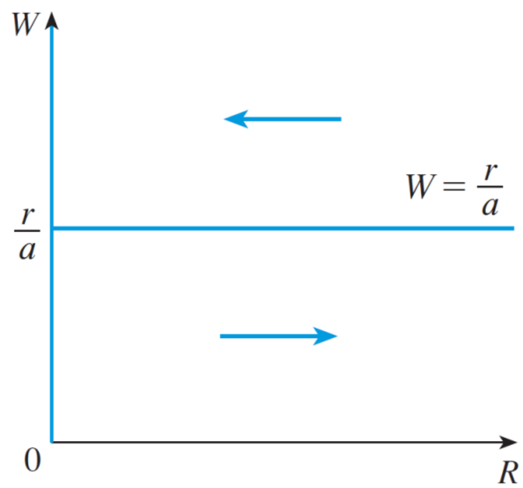
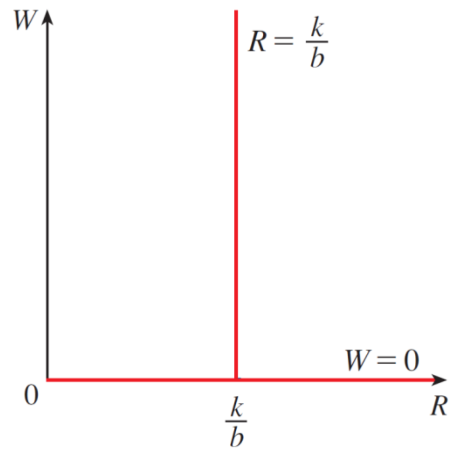


Figure 4(a)

Qualitative Dynamics in the Phase Plane

We can follow the same procedure for the *W*-nullclines in Figure 2(b).



R-nullclines are blue, *W*-nullclines are red, and equilibria are black dots.

Figure 2(b)

To the right of the line $R = k/b$ the value of R will be very large.

Qualitative Dynamics in the Phase Plane

From Equations 1 we have

$$dW/dt = -kW + bRW \approx bRW > 0$$

Conversely, if *R* is close to zero then

$$dW/dt = -kW + bRW \approx -kW < 0$$

This gives the direction arrows for *W* in Figure 4(b).

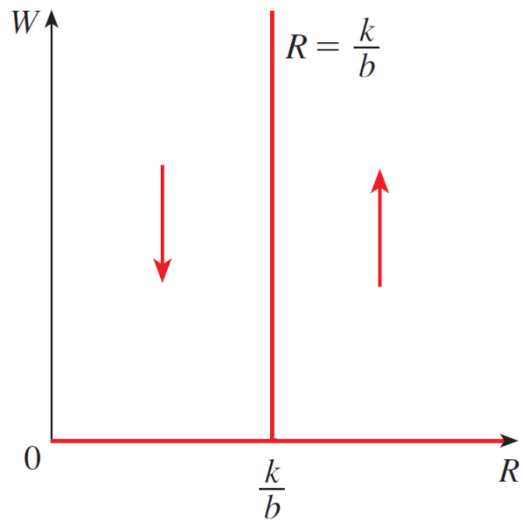
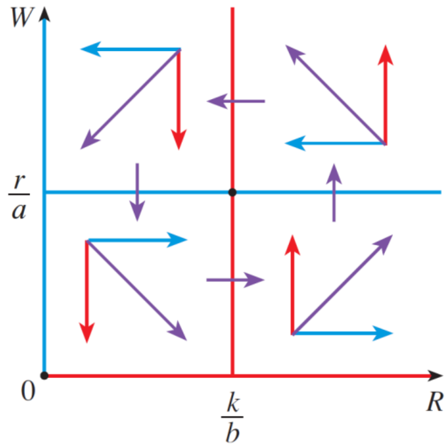


Figure 4(b)

Qualitative Dynamics in the Phase Plane

Putting these two plots together then gives the overall direction of movement by the purple arrows in the phase plane shown in Figure 4(c).



Purple arrows indicate direction of motion.

Figure 4(c)

This provides a very general, qualitative picture of the dynamics without having to plot a large number of direction arrows. In this case we see that spiraling trajectories in the phase plane are expected.

Example 2 – *Lotka-Volterra competition equations (continued)*

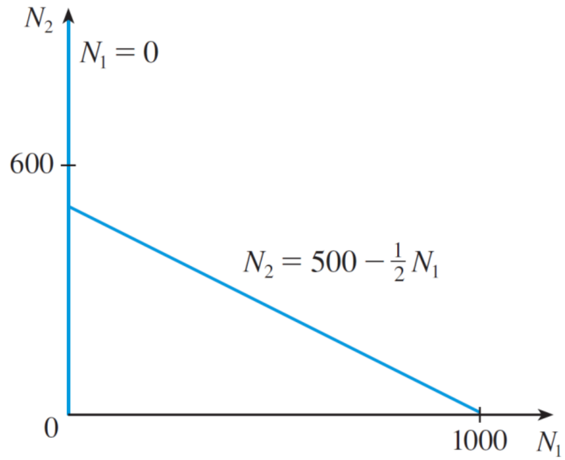
(a) Determine the qualitative dynamics in the phase plane for the Lotka-Volterra competition equations of Example 1.

(b) Plot the variables as a function of time.

Solution:

(a) We begin by first considering the N_1-nullclines shown in Figure 3(a).

Above the nullcline the value of N_2 will be very large.



N_1-nullclines are blue, N_2-nullclines are red, and equilibria are black dots.

Figure 3(a)

Example 2(a) – *Solution*

cont'd

From Equations 3 we have

$$\frac{dN_1}{dt} = \left(1 - \frac{N_1 + 2N_2}{1000}\right)N_1 \approx -\frac{2N_2}{1000}N_1 < 0$$

for large enough N_2.

But as we move closer to the origin, N_1 and N_2 will be very small. From Equations 3 we have

$$\frac{dN_1}{dt} = \left(1 - \frac{N_1 + 2N_2}{1000}\right)N_1 \approx N_1 > 0$$

[See Figure 5(a).]

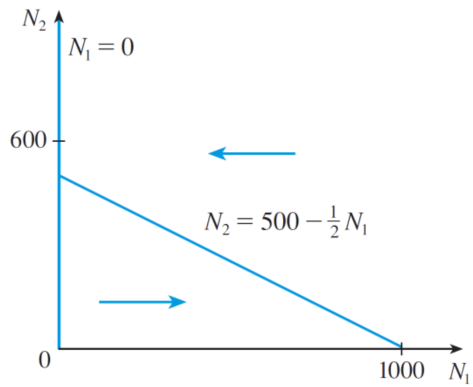


Figure 5(a)

Example 2(a) – *Solution*

cont'd

For the N_2-nullclines, a similar argument shows that to the right of the N_2-nullcline, $dN_2/dt < 0$.

Likewise, as we move close to the origin, $dN_2/dt > 0$ [see Figure 5(b)].

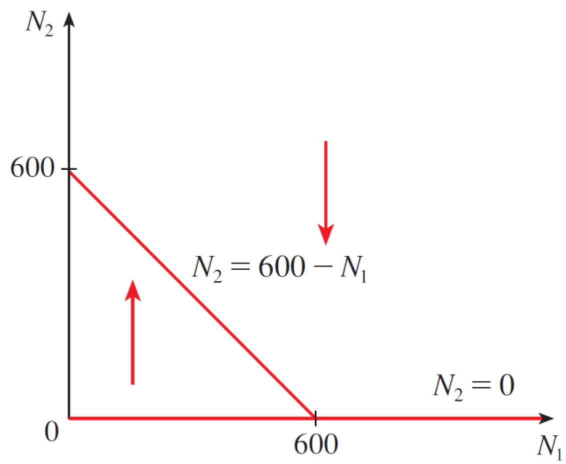
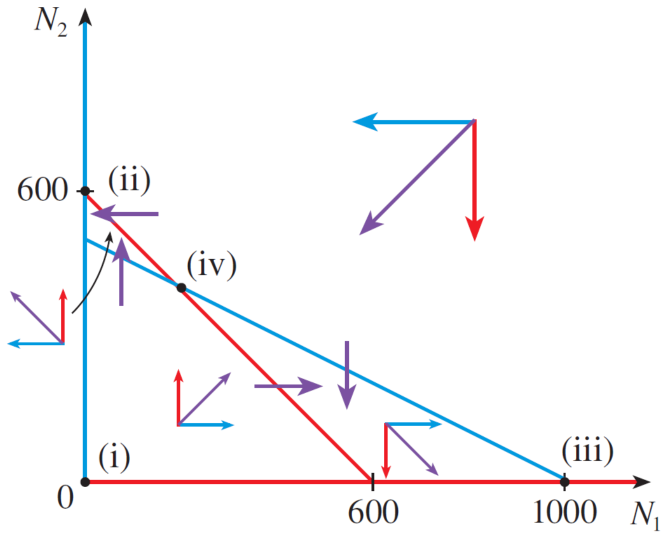


Figure 5(b)

Example 2(a) – *Solution*

Putting together these two plots gives the qualitative dynamics shown in Figure 5(c).



Purple arrows indicate direction of motion

Figure 5(c)

This reveals that equilibria (ii) and (iii) are both locally stable (if we start near either of these equilibria, we will move toward the equilibrium).

Example 2(a) – *Solution*

And we can see that equilibria (i) and (iv) are unstable (if we start near either of these, we will move away). Thus, the two species do not coexist.

One will competitively exclude the other, and the initial conditions determine which species "wins."

Example 2(b) – *Solution*

cont'd

In Figure 6 we have used a CAS to plot the variables against time for two sets of initial conditions.

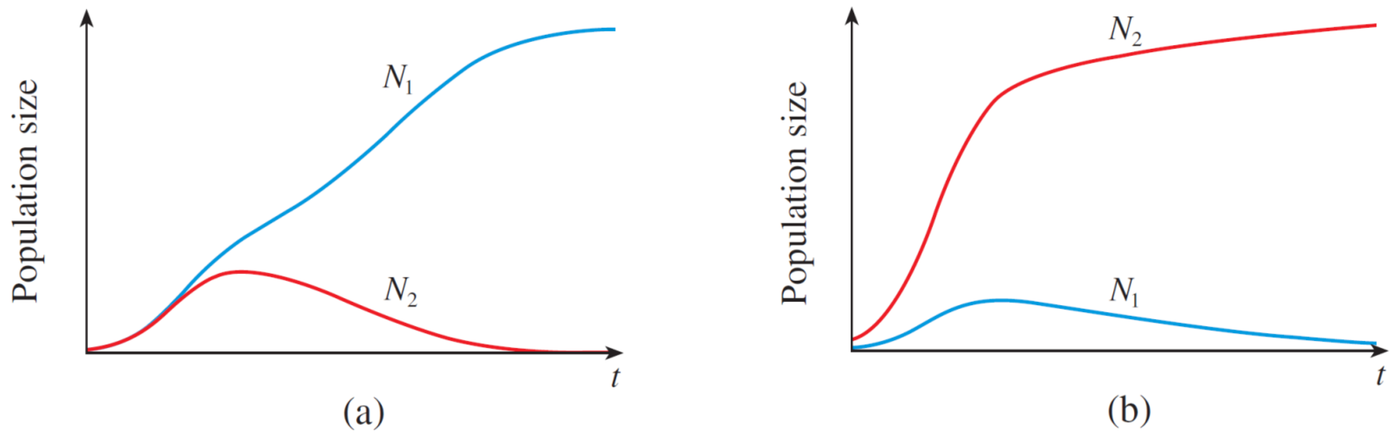


Figure 6

In part (a) N_2 initially increases but then decays to zero while N_1 continually increases. In part (b) the opposite occurs. These correspond to the variables moving toward equilibria (iii) and (ii) in Figure 5(c), respectively.