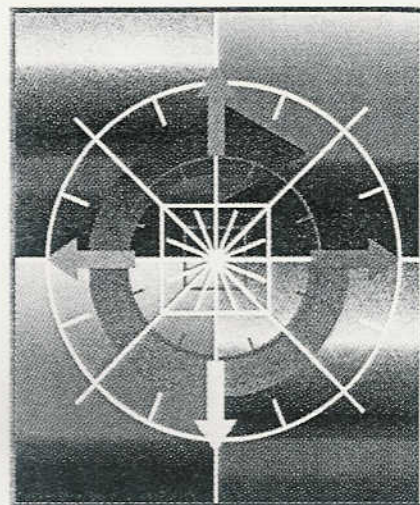


NONLINEAR SYSTEMS IN APPLICATIONS



This chapter is a survey of a few nonlinear systems that arise in biology, chemistry, and mechanics. Our intent is to describe to some extent both the modeling process and the qualitative analysis of these systems.

10.1 Lotka-Volterra Systems in Ecology

One of the most interesting contexts in which nonlinear systems of differential equations arise is the modeling of interacting populations. Such *ecological* models first appeared in the independent work of Lotka and Volterra in the 1920s and comprise a cornerstone of *mathematical biology*, or *biomathematics*. In this section, we will investigate in detail two of the most fundamental types of interaction: competition and predation.

Competition Suppose that two species P and Q compete for resources that each requires in order to live, such as food or territory. Let $p(t)$ and $q(t)$ denote the respective sizes of the two populations at time t . We will assume the following.

- i. In the absence of its competitor, each of the species is governed by a simple logistic equation with intrinsic growth rate k_i and environmental carrying capacity c_i for $i = 1, 2$. (See Section 3.4.)
- ii. The per capita growth rates, p'/p and q'/q , decrease proportionally with increasing competitor population.

These assumptions lead to

$$\frac{p'}{p} = k_1 \left(1 - \frac{p}{c_1} \right) - \alpha_1 \frac{q}{c_1} \quad \text{and} \quad \frac{q'}{q} = k_2 \left(1 - \frac{q}{c_2} \right) - \alpha_2 \frac{p}{c_2}, \quad (1)$$

in which $k_1, k_2, c_1, c_2, \alpha_1$, and α_2 are positive constants. By substituting the *dimensionless* quantities

$$x(t) = \frac{1}{c_1} p(t), \quad y = \frac{1}{c_2} q(t), \quad a = \frac{\alpha_1}{k_1} c_2, \quad \text{and} \quad b = \frac{\alpha_2}{k_2} c_1,$$

we arrive at the tidier system

$$x' = k_1 x(1 - x - ay), \quad y' = k_2 y(1 - y - bx). \tag{2}$$

Note that x and y represent the population sizes as proportions of the respective environmental carrying capacities of P and Q . Also, we view the coefficients a and b as measures of the *competitive strengths* of Q and P , respectively. Assuming that $a \neq b$, we begin our analysis of (2) by determining the equilibrium points and the nullclines of the system. The nullclines are the lines given by

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

along which the direction field is vertical, and

$$y = 0, \quad bx + y = 1,$$

along which the direction field is horizontal. There are three equilibrium points on the coordinate axes:

$$(0, 0), \quad (0, 1), \quad \text{and} \quad (1, 0),$$

and another, (x^*, y^*) , at the intersection of the lines $x + ay = 1$ and $bx + y = 1$, which is of interest only if x^* and y^* are both positive. An easy calculation gives

$$(x^*, y^*) = \left(\frac{1-a}{1-ab}, \frac{1-b}{1-ab} \right),$$

and so we observe that x^* and y^* are both positive if and only if

$$\text{either } a < 1 \text{ and } b < 1 \text{ or } a > 1 \text{ and } b > 1.$$

There are four main cases determined by the signs of $1 - a$ and $1 - b$. Figures 1a-d depict the equilibrium points and nullclines in each of these four cases.

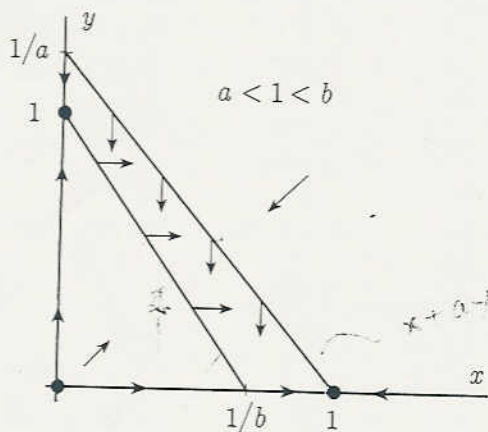


Figure 1a

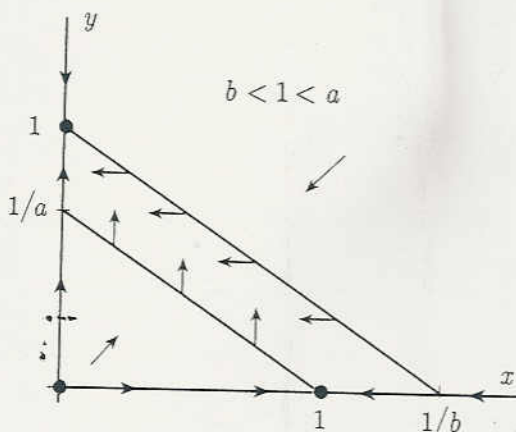


Figure 1b

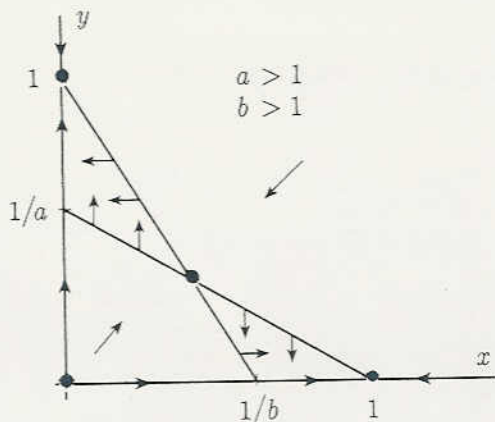


Figure 1c

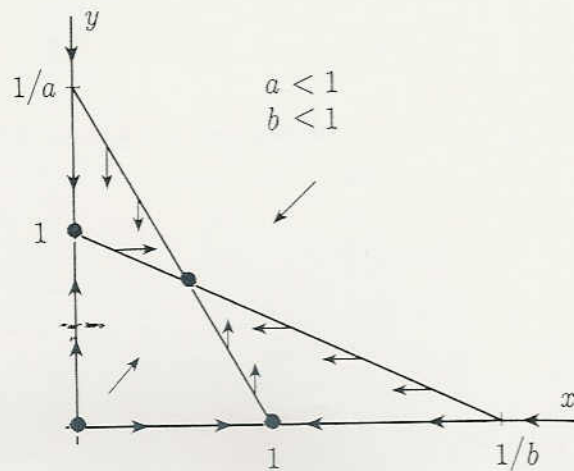


Figure 1d

The Jacobian matrix for the system (2) at (x, y) is

$$\mathcal{J}(x, y) = \begin{pmatrix} k_1(2x - 1 + ay) & -ak_1x \\ -bk_2y & k_2(2y - 1 + bx) \end{pmatrix},$$

and common to every case is the fact that the Jacobian matrix at the origin is

$$\mathcal{J}(0, 0) = \begin{pmatrix} k_1 & 0 \\ 0 & k_2 \end{pmatrix},$$

which implies that *the origin is unstable*, since k_1 and k_2 are each positive. If $k_1 \neq k_2$, the origin will be an unstable node; if $k_1 = k_2$, the origin will behave similarly, since orbits cannot spiral away from $(0, 0)$. (Why?) Also in every case, the Jacobian matrices at $(1, 0)$ and $(0, 1)$ are

$$\mathcal{J}(1, 0) = \begin{pmatrix} -k_1 & -k_1a \\ 0 & k_2(1 - b) \end{pmatrix},$$

whose eigenvalues are $-k_1$ and $k_2(1 - b)$, and

$$\mathcal{J}(0, 1) = \begin{pmatrix} k_1(1 - a) & 0 \\ -k_2b & -k_2 \end{pmatrix},$$

whose eigenvalues are $k_1(1 - a)$ and $-k_2$. So we can conclude that

- $(1, 0)$ is a stable node when $b > 1$ and a saddle point when $b < 1$;
- $(0, 1)$ is a stable node when $a > 1$ and a saddle point when $a < 1$.

We can now complete the phase portraits corresponding to Figures 1a and 1b. If $a < 1 < b$, then all orbits of (2) with $x(0) > 0$ and $y(0) \geq 0$ approach $(1, 0)$ as $t \rightarrow \infty$. If $b < 1 < a$, then all orbits of (2) with $x(0) \geq 0$ and $y(0) > 0$ approach $(0, 1)$ as $t \rightarrow \infty$. In each of these cases, the competitive strength of one species is greater than 1, while the other's is less than 1. Not surprisingly, the "stronger" species survives and the "weaker" species is driven toward extinction. Figure 2a illustrates the case where $a < 1 < b$, and Figure 2b illustrates the case where $b < 1 < a$.

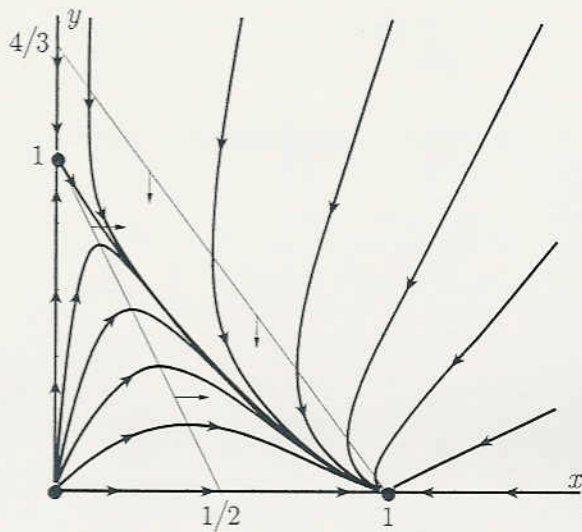


Figure 2a

$$a < 1 < b$$

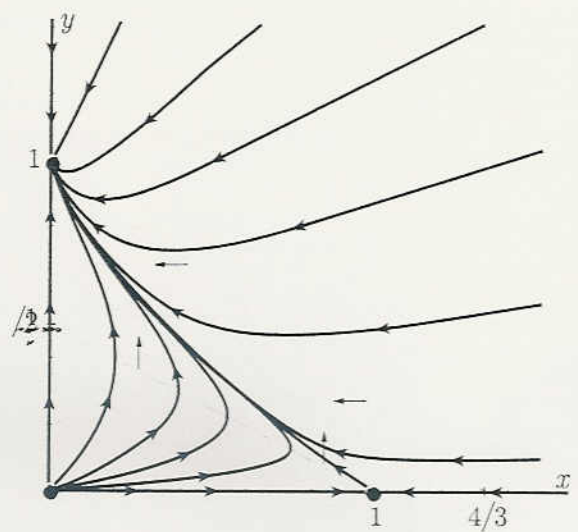


Figure 2b

$$b < 1 < a$$

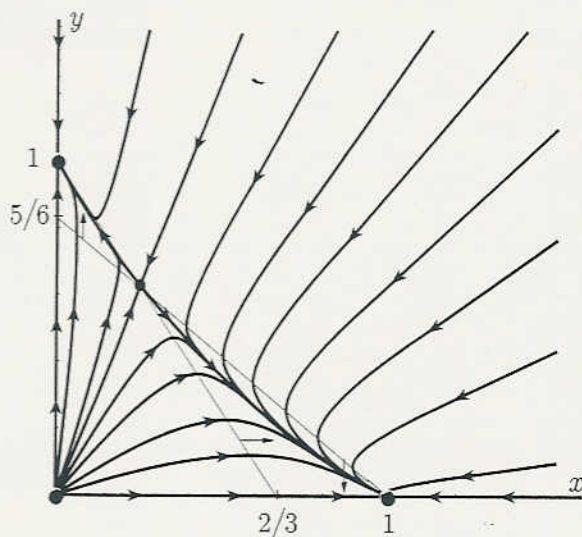


Figure 2c

$$a > 1 \quad b > 1$$

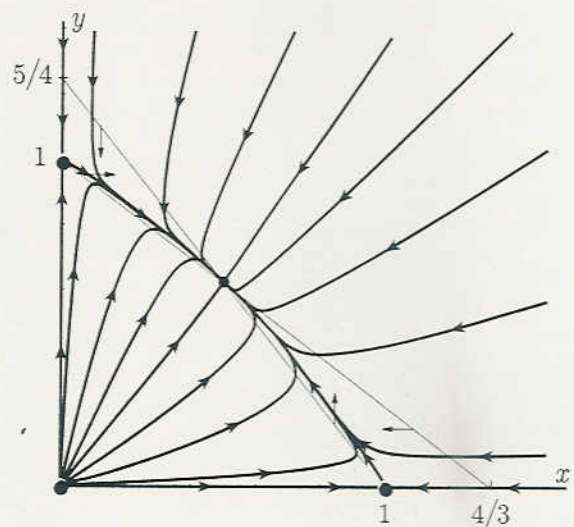


Figure 2d

$$a < 1 \quad b < 1$$

We now look to the cases in which x^* and y^* are both positive. So we assume that one or the other of the inequalities in (2) holds. In these cases, (x^*, y^*) is an equilibrium that represents *steady, long-term coexistence* of the two species. The Jacobian matrix at (x^*, y^*) is

$$\mathcal{J}(x^*, y^*) = \mathcal{J}\left(\frac{1-a}{1-ab}, \frac{1-b}{1-ab}\right) = -\frac{1}{1-ab} \begin{pmatrix} k_1(1-a) & k_1a(1-a) \\ k_2b(1-b) & k_2(1-b) \end{pmatrix}.$$

Some CAS-aided computation shows that the eigenvalues of $\mathcal{J}(x^*, y^*)$ are

$$\frac{1}{2(1-ab)} \left(r_1 + r_2 \pm \sqrt{4r_1r_2(1-ab) + (r_1 + r_2)^2} \right).$$

where

$$r_1 = -k_1(1-a) \quad \text{and} \quad r_2 = -k_2(1-b).$$

The quantity under the radical is clearly positive if $a > 1$ and $b > 1$. (Why?) If $a < 1$ and $b < 1$, then the quantity under the radical is positive as well, because

$$\begin{aligned} -4r_1r_2(1-ab) + (r_1 + r_2)^2 &\geq -4r_1r_2 + (r_1 + r_2)^2 \\ &= (r_1 - r_2)^2. \end{aligned}$$

Therefore, the eigenvalues of $\mathcal{J}(x^*, y^*)$ are real in each of the cases now under consideration. If $a < 1$ and $b < 1$, then $1 - ab \geq 0$, r_1 and r_2 are both negative, and

$$\sqrt{-4r_1r_2(1-ab) + (r_1 + r_2)^2} < \sqrt{(r_1 + r_2)^2} = |r_1 + r_2|.$$

From this we conclude that the eigenvalues of $\mathcal{J}(x^*, y^*)$ are negative and distinct. If $a > 1$ and $b > 1$, then $1 - ab < 0$, r_1 and r_2 are both positive, and

$$\sqrt{-4r_1r_2(1-ab) + (r_1 + r_2)^2} > \sqrt{(r_1 + r_2)^2} = |r_1 + r_2|.$$

From this we conclude that the eigenvalues of $\mathcal{J}(x^*, y^*)$ have opposite signs. So finally we conclude that

- if $a > 1$ and $b > 1$, then (x^*, y^*) is a saddle point;
- if $a < 1$ and $b < 1$, then (x^*, y^*) is a stable node.

If we discount the extremely unlikely event that when $a > 1$ and $b > 1$ the initial point will lie on an orbit that converges to the saddle point, then we can say that the populations tend toward stable, long-term coexistence if and only if $a < 1$ and $b < 1$. Figure 2c illustrates the case where $a > 1$ and $b > 1$. Figure 2d illustrates the case where $a < 1$ and $b < 1$.

In conclusion, suppose that we describe a species as *weak* if its competitive strength is less than 1 and *strong* if its competitive strength is greater than 1. Then the main result of this analysis can be stated as follows: *Whether it is weak or strong, a species survives in the long run if its competitor is weak. If both species are strong, then the surviving species is determined by initial conditions.*

Predation Suppose that two species live within the same environment. One species, the *prey*, is the food source for the other species, the *predator*. The prey's food source is an abundant third organism. Let $p(t)$ and $q(t)$ denote the respective sizes of the prey and predator populations at time t . We will assume the following:

- i. In the absence of predators, the prey population is governed by a simple logistic equation with intrinsic growth rate k_1 and environmental carrying capacity c_1 .
- ii. In the absence of prey, per capita growth rate of the predator population, q'/q , is a negative constant (i.e., the predator population declines exponentially).

- iii. The per capita growth rate of the prey population, p'/p , decreases proportionally with increasing predator population.
- iv. The per capita growth rate of the predator population, q'/q , increases proportionally with increasing prey population.

These assumptions lead to

$$\frac{p'}{p} = k_1 \left(1 - \frac{p}{c_1}\right) - \alpha_1 q \quad \text{and} \quad \frac{q'}{q} = -k_2 + \alpha_2 p. \quad (3)$$

With the dimensionless quantities

$$x = \frac{\alpha_2 p}{k_2}, \quad y = \frac{\alpha_1 q}{k_1}, \quad \text{and} \quad \varepsilon = \frac{c_1 \alpha_2}{k_2} = \frac{c_1}{k_2 \alpha_1}$$

we arrive at the tidier system

$$x' = k_1 x \left(1 - \frac{x}{\varepsilon} - y\right), \quad y' = -k_2 y(1 - x). \quad (4)$$

Here, x and y are just conveniently scaled population sizes. Note that if $p = c_1$ (the prey's stable equilibrium with no predators), then $q'/q = k_2(\varepsilon - 1)$. So we can think of ε as a measure of *predatory efficiency*—the efficiency with which consumption of prey results in predator reproduction. If $0 < \varepsilon < 1$, then $q'/q < 0$ when $p = c_1$, indicating that the predator is inefficient. If $\varepsilon > 1$, then $q'/q > 0$ when $p = c_1$, indicating that the predator is efficient.

We begin our analysis of (4) by determining the equilibrium points and the nature of the nullclines of the system. The nullclines are the lines given by

$$x = 0, \quad \frac{x}{\varepsilon} + y = 1,$$

along which the direction field is vertical, and

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

along which the direction field is horizontal. There are two equilibrium points on the coordinate axes:

$$(0, 0), \quad \text{and} \quad (\varepsilon, 0),$$

and another equilibrium point (x^*, y^*) at the intersection of the lines

$$\frac{x}{\varepsilon} + y = 1 \quad \text{and} \quad x = 1,$$

which is of interest only if x^* and y^* are both positive. An easy calculation gives

$$(x^*, y^*) = \left(1, \frac{\varepsilon - 1}{\varepsilon}\right),$$

and so we observe that x^* and y^* are both positive if and only if $\varepsilon > 1$. Figures 3a and b show the arrangement of equilibrium points and nullclines in each of the cases $0 < \varepsilon < 1$ and $\varepsilon > 1$, respectively.

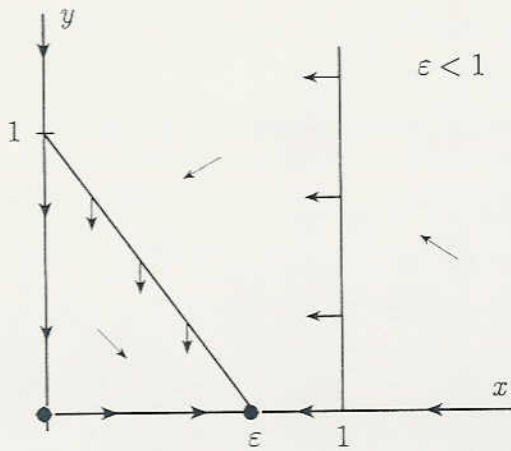


Figure 3a

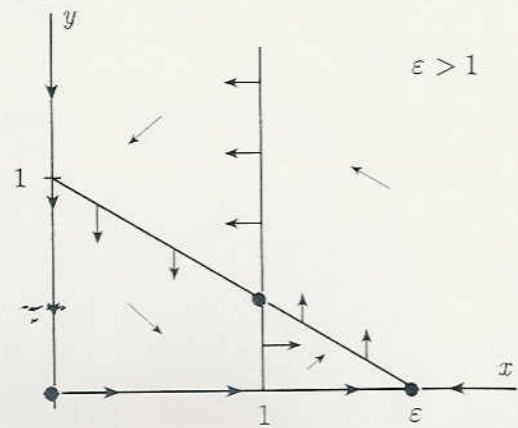


Figure 3b

In all cases the Jacobian matrix at (x, y) is

$$\mathcal{J}(x, y) = \begin{pmatrix} k_1 \left(1 - y - \frac{2x}{\varepsilon}\right) & -k_1 x \\ k_2 y & -k_2(1 - x) \end{pmatrix},$$

and so the Jacobian matrix at the origin is

$$\mathcal{J}(0, 0) = \begin{pmatrix} k_1 & 0 \\ 0 & -k_2 \end{pmatrix},$$

which implies that *the origin is a saddle point*. The Jacobian matrix at $(\varepsilon, 0)$ is

$$\mathcal{J}(\varepsilon, 0) = \begin{pmatrix} -k_1 & -k_1 \varepsilon \\ 0 & -k_2(1 - \varepsilon) \end{pmatrix},$$

whose eigenvalues are $-k_1$ and $-k_2(1 - \varepsilon)$. So we can conclude that

- $(\varepsilon, 0)$ is a stable node if $0 < \varepsilon < 1$ and a saddle point if $\varepsilon > 1$.

The Jacobian matrix at $(x^*, y^*) = (1, (\varepsilon - 1)/\varepsilon)$ is

$$\mathcal{J}\left(1, \frac{\varepsilon - 1}{\varepsilon}\right) = \begin{pmatrix} -k_1/\varepsilon & -k_1 \\ k_2(\varepsilon - 1)/\varepsilon & 0 \end{pmatrix},$$

whose eigenvalues are the roots of $\varepsilon\lambda^2 + k_1\lambda + k_1k_2(\varepsilon - 1)$, which turn out to be

$$\frac{k_1}{2\varepsilon} \left(-1 \pm \sqrt{\frac{k_1 - 4k_2\varepsilon(\varepsilon - 1)}{k_1}} \right).$$

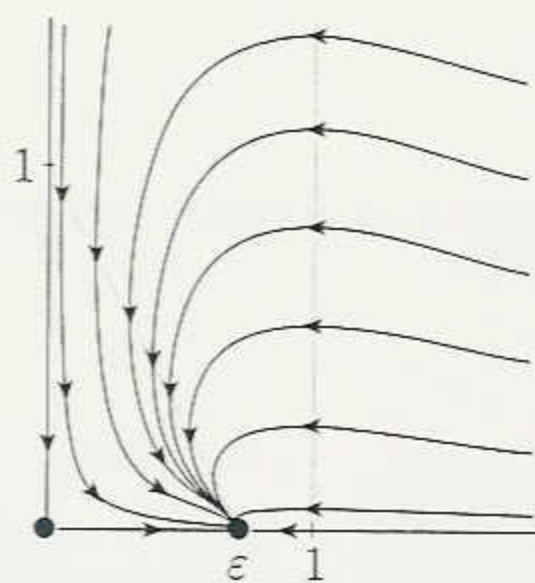


Figure 4a

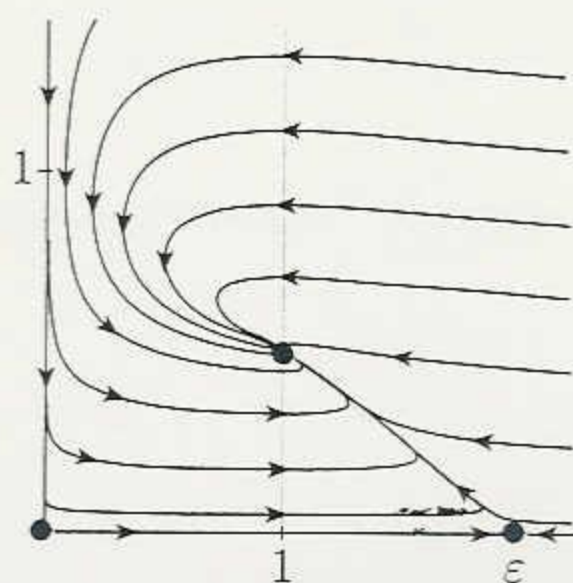


Figure 4b

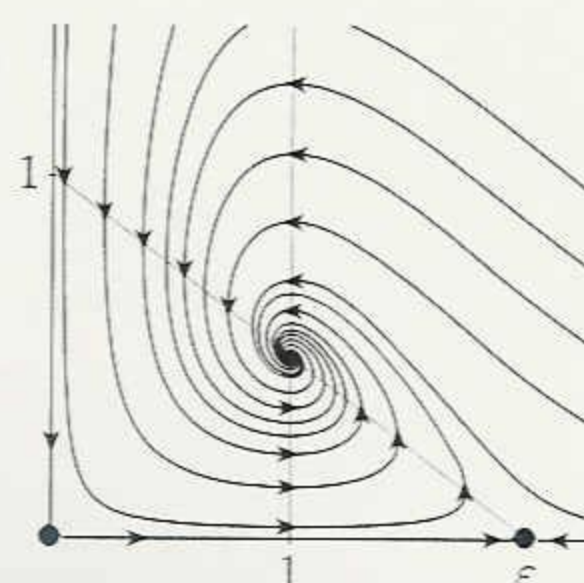


Figure 4c

From this we conclude that

- $\left(1, \frac{\varepsilon - 1}{\varepsilon}\right)$ is a stable node if $\varepsilon > 1$ and $4k_2\varepsilon(\varepsilon - 1) < k_1$;
- $\left(1, \frac{\varepsilon - 1}{\varepsilon}\right)$ is a stable spiral point if $\varepsilon > 1$ and $4k_2\varepsilon(\varepsilon - 1) > k_1$.

We can now complete the phase portraits corresponding to Figures 3a and 3b. Figure 4a is typical of the case where $0 < \varepsilon < 1$. Here, all orbits of (4) with $x(0) > 0$ and $y(0) > 0$ approach $(\varepsilon, 0)$ as $t \rightarrow \infty$, indicating that the predator tends toward extinction in the long run, while the prey survives. In the case where $\varepsilon > 1$, (x^*, y^*) may be either a stable node or a stable spiral point approached as $t \rightarrow \infty$ by all orbits of (4) with $x(0) > 0$ and $y(0) \geq 0$, indicating that the predator and prey coexist in the long run. These situations are illustrated in Figures 4b and 4c.

If ε is very large, then $(x^*, y^*) \approx (1, 1)$; the nullcline given by $x/\varepsilon + y = 1$ is nearly horizontal; and orbits with $x(0) > 0$ and $y(0) > 0$ are nearly closed—that is, there is a time T such that $(x(t), y(t)) \approx (x(0), y(0))$. In fact, in the limit as $\varepsilon \rightarrow \infty$ (a “perfectly efficient” predator), orbits with $x(0) > 0$ and $y(0) > 0$ are indeed closed, corresponding therefore to periodic solutions. This is the subject of Problem 7 at the end of this section.

We end with a simple ecological conclusion: *If the predator is efficient—as indicated by $\varepsilon > 1$ —then the predator population survives in the long run. Otherwise the predator drives itself toward extinction by consuming too much and reproducing too little.*