

ogy. For details, see Perko (1991), Coddington and Levinson (1955), Hurewicz (1958), or Cesari (1963).

In Figure 7.3.1, we have drawn  $R$  as a ring-shaped region because any closed orbit must encircle a fixed point ( $P$  in Figure 7.3.1) and no fixed points are allowed in  $R$ .

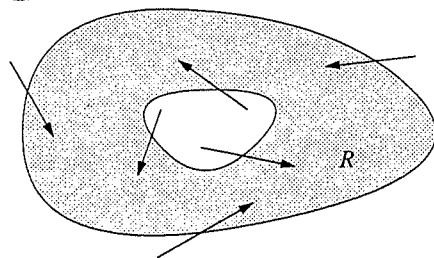


Figure 7.3.2

When applying the Poincaré-Bendixson theorem, it's easy to satisfy conditions (1)–(3); condition (4) is the tough one. How can we be sure that a confined trajectory  $C$  exists? The standard trick is to construct a trapping region  $R$ , i.e., a closed connected set such that the vector field points "inward" everywhere on the boundary of  $R$  (Figure 7.3.2). Then all trajectories in  $R$  are confined. If we can also arrange that there are no fixed points in  $R$ , then the Poincaré-Bendixson theorem ensures that  $R$  contains a closed orbit.

The Poincaré-Bendixson theorem can be difficult to apply in practice. One convenient case occurs when the system has a simple representation in polar coordinates, as in the following example.

### EXAMPLE 7.3.1:

Consider the system

$$\begin{aligned}\dot{r} &= r(1-r^2) + \mu r \cos \theta \\ \dot{\theta} &= 1.\end{aligned}\quad (1)$$

When  $\mu = 0$ , there's a stable limit cycle at  $r = 1$ , as discussed in Example 7.1.1. Show that a closed orbit still exists for  $\mu > 0$ , as long as  $\mu$  is sufficiently small.

**Solution:** We seek two concentric circles with radii  $r_{\min}$  and  $r_{\max}$ , such that  $\dot{r} < 0$  on the outer circle and  $\dot{r} > 0$  on the inner circle. Then the annulus  $0 < r_{\min} \leq r \leq r_{\max}$  will be our desired trapping region. Note that there are no fixed points in the annulus since  $\dot{\theta} > 0$ ; hence if  $r_{\min}$  and  $r_{\max}$  can be found, the Poincaré-Bendixson theorem will imply the existence of a closed orbit.

To find  $r_{\min}$ , we require  $\dot{r} = r(1-r^2) + \mu r \cos \theta > 0$  for all  $\theta$ . Since  $\cos \theta \geq -1$ , a sufficient condition for  $r_{\min}$  is  $1-r^2-\mu > 0$ . Hence any  $r_{\min} < \sqrt{1-\mu}$  will work, as long as  $\mu < 1$  so that the square root makes sense. We should choose  $r_{\min}$  as large as possible, to hem in the limit cycle as tightly as we can. For instance, we

similar argument, the flow is inward on the out

for all  $\mu < 1$ , and it lies somewhere in the annulus

The estimate can exist even for  $\mu = 1$ . In fact, for  $\mu > 1$ , and in particular, when  $\mu = 1$ , a closed orbit disappears. It's also possible for small  $\mu$  (Exercise 7.3.9).

7.3.1 are conservative. In fact, the closed orbit in Figure 7.3.3 shows a computer-generated phase portrait of the system. We're asked to explore what happens for larger  $\mu$ , and to find a critical  $\mu$  beyond which the closed orbit disappears. Some analytical insight about the closed orbit for small  $\mu$  (Exercise 7.3.9).

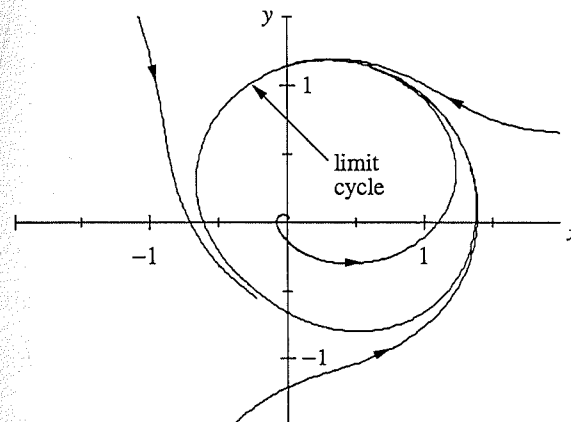


Figure 7.3.3

When polar coordinates are inconvenient, we may still be able to find an appropriate trapping region by examining the system's nullclines, as in the next example.

### EXAMPLE 7.3.2:

In the fundamental biochemical process called glycolysis, living cells obtain energy by breaking down sugar. In intact yeast cells as well as in yeast or muscle extracts, glycolysis can proceed in an oscillatory fashion, with the concentrations of various intermediates waxing and waning with a period of several minutes. For reviews, see Chance et al. (1973) or Goldbeter (1980).

A simple model of these oscillations has been proposed by Sel'kov (1968). In dimensionless form, the equations are

$$\begin{aligned}\dot{x} &= -x + ay + x^2y \\ \dot{y} &= b - ay - x^2y\end{aligned}$$

where  $x$  and  $y$  are the concentrations of ADP (adenosine diphosphate) and F6P (fructose-6-phosphate), and  $a, b > 0$  are kinetic parameters. Construct a trapping region for this system.

**Solution:** First we find the nullclines. The first equation shows that  $\dot{x} = 0$  on the curve  $y = x/(a+x^2)$  and the second equation shows that  $\dot{y} = 0$  on the curve  $y = b/(a+x^2)$ . These nullclines are sketched in Figure 7.3.4, along with some representative vectors.

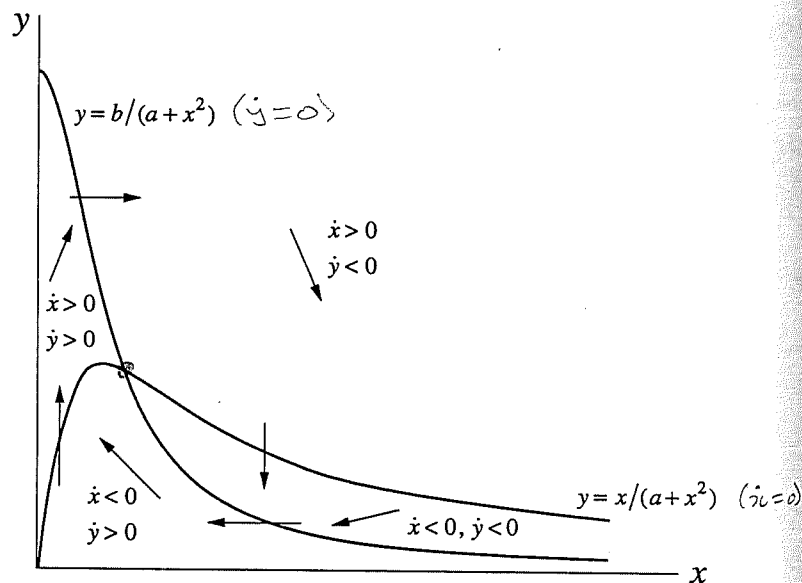


Figure 7.3.4

How did we know how to sketch these vectors? By definition, the arrows are vertical on the  $\dot{x} = 0$  nullcline, and horizontal on the  $\dot{y} = 0$  nullcline. The direction of flow is determined by the signs of  $\dot{x}$  and  $\dot{y}$ . For instance, in the region above both nullclines, the governing equations imply  $\dot{x} > 0$  and  $\dot{y} < 0$ , so the arrows point down and to the right, as shown in Figure 7.3.4.

Now consider the region bounded by the dashed line shown in Figure 7.3.5. We claim that it's a trapping region. To verify this, we have to show that all the vectors on the boundary point into the box. On the horizontal and vertical sides, there's no problem: the claim follows from Figure 7.3.4. The tricky part of the construction is the diagonal line of slope  $-1$  extending from the point  $(b, b/a)$  to the nullcline  $y = x/(a+x^2)$ . Where did this come from?

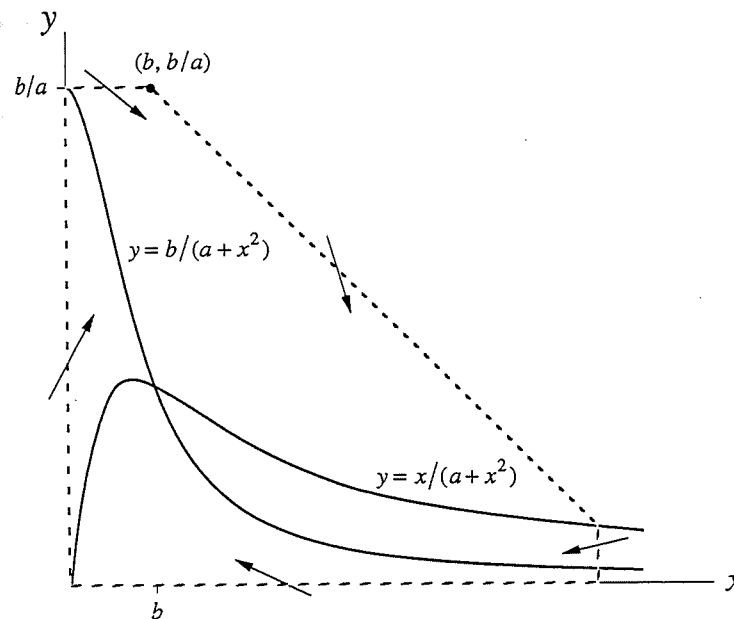


Figure 7.3.5

To get the right intuition, consider  $\dot{x}$  and  $\dot{y}$  in the limit of very large  $x$ . Then  $\dot{x} \approx x^2 y$  and  $\dot{y} \approx -x^2 y$ , so  $\dot{y}/\dot{x} = dy/dx \approx -1$  along trajectories. Hence the vector field at large  $x$  is roughly parallel to the diagonal line. This suggests that in a more precise calculation, we should compare the sizes of  $\dot{x}$  and  $-\dot{y}$ , for some sufficiently large  $x$ .

In particular, consider  $\dot{x} - (-\dot{y})$ . We find

$$\begin{aligned}\dot{x} - (-\dot{y}) &= -x + ay + x^2 y + (b - ay - x^2 y) \\ &= b - x.\end{aligned}$$

Hence

$$-\dot{y} > \dot{x} \text{ if } x > b.$$

This inequality implies that the vector field points inward on the diagonal line in Figure 7.3.5, because  $dy/dx$  is more negative than  $-1$ , and therefore the vectors are steeper than the diagonal line. Thus the region is a trapping region, as claimed. ■

Can we conclude that there is a closed orbit inside the trapping region? No! There is a fixed point in the region (at the intersection of the nullclines), and so the conditions of the Poincaré-Bendixson theorem are not satisfied. But if this fixed point is a repeller, then we can prove the existence of a closed orbit by considering

the modified "punctured" region shown in but drawn larger for clarity.)

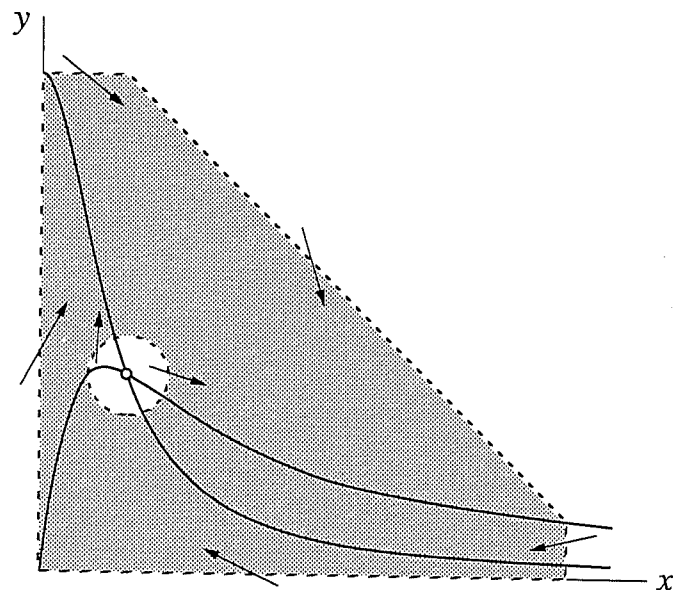


Figure 7.3.6

The repeller drives all neighboring trajectories into the shaded region, and since this region is free of fixed points, the Poincaré–Bendixson theorem applies.

Now we find conditions under which the fixed point is a repeller.

### EXAMPLE 7.3.3:

Once again, consider the glycolytic oscillator  $\dot{x} = -x + ay + x^2y$ ,  $\dot{y} = b - ay - x^2y$  of Example 7.3.2. Prove that a closed orbit exists if  $a$  and  $b$  satisfy an appropriate condition, to be determined. (As before,  $a, b > 0$ .)

*Solution:* By the argument above, it suffices to find conditions under which the fixed point is a repeller, i.e., an unstable node or spiral. (In general, the Jacobian is

$$A = \begin{pmatrix} -1 + 2xy & a + x^2 \\ -2xy & -(a + x^2) \end{pmatrix}.$$

After some algebra, we find that at the fixed point

$$x^* = b, \quad y^* = \frac{b}{a + b^2},$$

the Jacobian has determinant  $\Delta = a + b^2 > 0$  and trace

$$\tau = -\frac{b^4 + (2a - 1)b^2 + (a + a^2)}{a + b^2}.$$

Hence the fixed point is unstable for  $\tau > 0$ , and stable for  $\tau < 0$ . The dividing line  $\tau = 0$  occurs when

$$b^2 = \frac{1}{2}(1 - 2a \pm \sqrt{1 - 8a}).$$

This defines a curve in  $(a, b)$  space, as shown in Figure 7.3.7.

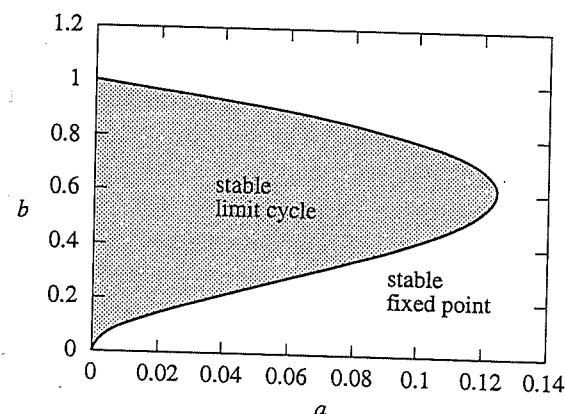


Figure 7.3.7

For parameters in the region corresponding to  $\tau > 0$ , we are guaranteed that the system has a closed orbit—numerical integration shows that it is actually a stable limit cycle. Figure 7.3.8 shows a computer-generated phase portrait for the typical case  $a = 0.08$ ,  $b = 0.6$ . ■

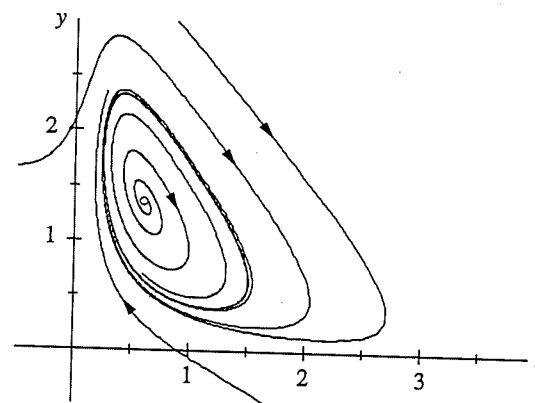


Figure 7.3.8