III. First-Order Systems of Ordinary Differential Equations
10. Application: Population Dynamics

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10. Application: Population Dynamics

Earlier in the course we studied models of population dynamics that were single first-order equations in the form

$$\frac{\mathrm{d}p}{\mathrm{d}t} = R(p)p\,,$$

where $p(t)$ is the size of the population as a function of time, and $R(p)$ models the growth rate of the population as a function of p. For a population in a closed ecosystem the growth rate is simply the birth rate minus the mortality rate. In more complicated situations it must also account for migration in to and out of the ecosystem.

The simplest such model takes $R(p) = r$ for some constant r, which has the solution $p(t) = p_I e^{rt}$ when $p(0) = p_I$. This is the so-called exponential model because when $r > 0$ its solution grows exponentially, while when $r < 0$ its solution decays exponentially. The ability of an individual to survive and reproduce depends upon the environment experienced by that individual. The assumption that $R(p)$ is constant assumes that this environment is unaffected by the number of individuals present. However once the population grows large enough there might be competition between its individuals for resources, which should reduce the growth rate. The simplest model that captures this effect takes $R(p)$ to be a linear function of p,

$$R(p) = r - ap\,, \qquad \text{for some constants } a \text{ and } r\,.$$

While this *logistic model* could be solved analytically, we found it helpful to study it with phase-line portraits. In this chapter we extend these ideas to study models of two interacting populations with phase-plane portraits.

10.1. **Models of Two Interacting Populations.** We now consider two populations that interact in a shared environment. We let the size of these populations be $p_1(t)$ and $p_2(t)$ and consider first-order autonomous models of the form

$$\frac{\mathrm{d}p_1}{\mathrm{d}t} = R_1(p_1,p_2)p_1\,, \qquad \frac{\mathrm{d}p_2}{\mathrm{d}t} = R_2(p_1,p_2)p_2\,, \tag{10.1a}$$

where $R_1(p_1,p_2)$ and $R_2(p_1,p_2)$ model the growth rates of the first and second populations as functions of p_1 and p_2. We will specialize further to the case where $R_1(p_1,p_2)$ and $R_2(p_1,p_2)$ depend linearly upon p_1 and p_2 as

$$\begin{aligned} R_1(p_1,p_2) &= r_1 - a_{11}p_1 - a_{12}p_2\,, \qquad &&\text{for some constants } a_{11},\ a_{12}, \text{ and } r_1\,,\\ R_2(p_1,p_2) &= r_2 - a_{21}p_1 - a_{22}p_2\,, \qquad &&\text{for some constants } a_{21},\ a_{22}, \text{ and } r_2\,. \end{aligned} \tag{10.1b}$$

These models assume that the growth rates for each population can depend upon the size of the two populations, but nothing else. It assumes moreover that this dependence is linear. Both of these assumptions are huge oversimplifications for any ecosystem. Still, there are instances when such models correctly capture phenomena that are observed in real populations.

Remark. When such models are used in practice, p_1 and p_2 often are not the number of individuals in the respective populations, but rather are the biomass of the populations. This makes more sense than simply counting individuals because the amount of resources an individual will consume is roughly proportional to its biomass.

The constants a_{11}, a_{12}, a_{21}, a_{22}, r_1, and r_2 are *parameters* in the family of models (10.1). In practice their values are chosen so that the model fits some observed behavior. The process of choosing what data to fit and how to fit it is often called *calibrating* a model. The process of testing the model by comparing its predictions with certain observed behavior is often called *validating* the model. We will not address how to either calibrate or validate models in this course. Rather, we will ask what behaviors are predicted by the model associated with given values of these parameters. These kinds of predictions are useful in the calibration and validation processes.

It is important to understand the role each of the six parameters plays in the family of models (10.1). There are three basic roles, which we describe below.

The parameters r_1 and r_2 are the bare growth rates for the respective populations. Namely, they are the rates at which the populations grow when both populations are small. When $r_k > 0$ the k^{th} population will thrive on the resources available in the environment. When $r_k < 0$ the k^{th} population will decline without some additional resource, usually provided by the other population either as food or through a cooperative relationship.

The parameters a_{11} and a_{22} represent how the growth rates respond to increased numbers in their respective populations. When $a_{kk} > 0$ the growth rate for the k^{th} population will reduce as that population grows. This will be the case when individuals in the population compete for the same food resource. When $a_{kk} < 0$ the growth rate for the k^{th} population will increase as that population grows. This might be the case when a greater population density increases the likelihood of individuals finding mates. However, because the models (10.1) exhibit unrealistic behavior in such regimes, we will restrict our attention to models where $a_{11} \geq 0$ and $a_{22} \geq 0$.

The parameters a_{12} and a_{21} represent how the two populations interact. If one of these is zero than that equation decouples from the other and can be studied by methods we studied earlier in the course. In order to insure that the model (10.1) is interactive, we will require that a_{12} and a_{21} are *both nonzero*. The nature of the interaction can be read off from the signs of these so-called coupling parameters.

- When a_{12} and a_{21} have opposite signs then one of the populations benefits from and harms the other. This would be the case, for example, when one population preys on the other. Such models are often called *predator-prey models*.
- When $a_{12} > 0$ and $a_{21} > 0$ then each population is effected adversely by the other. This would be the case, for example, when both populations compete for the same food resource. Such models are often called *competing species models*.
- When $a_{12} < 0$ and $a_{21} < 0$ then each population benefits from the other. This would be the case, for example, when the populations cooperate. Such models are sometimes called *cooperating species models*.

In this chapter we apply the methods presented in the previous two chapters to build an understanding of the dynamics of these models.

10.2. **Predator-Prey Models.** In this section we will study predator-prey models in the form

$$(10.2) \qquad x' = (r - ax - by)x\,, \qquad y' = (-s + cx - dy)y\,,$$

where the parameters b, c, r, and s are positive while a and d are nonnegative. It should be clear that x and y represent the populations of prey and predators respectively.

Example. Sketch the phase-plane portrait for the predator-prey model

$$x' = (12 - 2x - 3y)x\,, \qquad y' = (-15 + 5x)y\,.$$

Solution. First, we find the stationary points of the model. These satisfy

$$0 = (12 - 2x - 3y)x\,, \qquad 0 = (-15 + 5x)y\,.$$

The second equation is satisfied when either $x = 3$ or $y = 0$. When $x = 3$ the first equation can only be satisfied when $y = 2$. When $y = 0$ the first equation can be satisfied when either $x = 0$ or $x = 6$. Therefore the stationary points are

$$(0,0)\,, \qquad (6,0)\,, \qquad (3,2)\,.$$

Next, we linearize the model about each stationary point. Because

$$\mathbf{f}(x,y) = \begin{pmatrix} f(x,y) \\ g(x,y) \end{pmatrix} = \begin{pmatrix} (12 - 2x - 3y)x \\ (-15 + 5x)y \end{pmatrix} = \begin{pmatrix} 12x - 2x^2 - 3xy \\ -15y + 5xy \end{pmatrix}\,,$$

the Jacobian matrix of partial derivatives is

$$\boldsymbol{\partial}\mathbf{f}(x,y) = \begin{pmatrix} \partial_x f(x,y) & \partial_y f(x,y) \\ \partial_x g(x,y) & \partial_y g(x,y) \end{pmatrix} = \begin{pmatrix} 12 - 4x - 3y & -3x \\ 5y & -15 + 5x \end{pmatrix}\,.$$

By evaluating this at each stationary point we compute the coefficient matrix for the linearization about that point. These matrices then give the following information about what the phase-plane portrait of the nonlinear system looks like near these points.

- At $(0,0)$ the coefficient matrix of the linearization is

  $$\mathbf{A} = \boldsymbol{\partial}\mathbf{f}(0,0) = \begin{pmatrix} 12 & 0 \\ 0 & -15 \end{pmatrix}\,.$$

  Because $\mathbf{A}$ is diagonal, we can read off that its eigenvalues are 12 and -15. This implies that near $(0,0)$ the phase-plane portrait is a *saddle*, which is *unstable*. Because

  $$\mathbf{A} - 12\mathbf{I} = \begin{pmatrix} 0 & 0 \\ 0 & -27 \end{pmatrix}\,, \qquad \mathbf{A} + 15\mathbf{I} = \begin{pmatrix} 27 & 0 \\ 0 & 0 \end{pmatrix}\,,$$

  the eigenpairs of $\mathbf{A}$ are

  $$\left(12\,, \begin{pmatrix} 1 \\ 0 \end{pmatrix}\right)\,, \qquad \left(-15\,, \begin{pmatrix} 0 \\ 1 \end{pmatrix}\right)\,.$$

  There is one orbit that emerges from $(0,0)$ tangent to each half of the x-axis. There is one orbit that approaches $(0,0)$ tangent to each half of the y-axis.

- At $(6,0)$ the coefficient matrix of the linearization is
$$\mathbf{A} = \boldsymbol{\partial}\mathbf{f}(6,0) = \begin{pmatrix} -12 & -18 \\ 0 & 15 \end{pmatrix} .$$
Because $\mathbf{A}$ is upper triangular, we can read off that its eigenvalues are -12 and 15. This implies that near $(6,0)$ the phase-plane portrait is a *saddle*, which is *unstable*. Because
$$\mathbf{A} + 12\mathbf{I} = \begin{pmatrix} 0 & -18 \\ 0 & 27 \end{pmatrix} , \qquad \mathbf{A} - 15\mathbf{I} = \begin{pmatrix} -27 & -18 \\ 0 & 0 \end{pmatrix} ,$$
the eigenpairs of $\mathbf{A}$ are
$$\left(-12 \, , \, \begin{pmatrix} 1 \\ 0 \end{pmatrix} \right) , \qquad \left(15 \, , \, \begin{pmatrix} -2 \\ 3 \end{pmatrix} \right) .$$
There is one orbit that approaches $(6,0)$ tangent to each half of the x-axis. There is one orbit that emerges from $(6,0)$ tangent to each half of the line $y = -\frac{3}{2}(x-6)$.
- At $(3,2)$ the coefficient matrix of the linearization is
$$\mathbf{A} = \boldsymbol{\partial}\mathbf{f}(3,2) = \begin{pmatrix} -6 & -9 \\ 10 & 0 \end{pmatrix} .$$
The characteristic polynomial of $\mathbf{A}$ is
$$p(z) = z^2 - \mathrm{tr}(\mathbf{A})z + \det(\mathbf{A}) = z^2 + 6z + 90 = (z+3)^2 + 9^2 ,$$
from which we see that the eigenvalues of $\mathbf{A}$ are the conjugate pair $-3 \pm i9$. Because $a_{21} = 10 > 0$, this implies that near $(3,2)$ the phase-plane portrait is a *counterclockwise spiral sink*, which is *attracting*. Because its phase portrait is a spiral sink near $(3,2)$, this model cannot be conservative over the first quadrant.

Finally, like every population model in this chapter, this model has semistationary solutions that lie on the x and y-axes.

- There are semistationary solutions of the form $(0, Y(t))$ where $Y(t)$ satisfies the $y' = -15y$. A phase-line portrait shows these orbits move along the y-axis as
$$\begin{array}{c} \quad + \qquad\qquad - \\ \rightarrow\rightarrow\rightarrow\rightarrow \bullet \leftarrow\leftarrow\leftarrow\leftarrow \; y \\ 0 \end{array}$$
This shows the orbits on the y-axis move towards the stationary point $(0,0)$.
- There are semistationary solutions of the form $(X(t), 0)$ where $X(t)$ satisfies $x' = (12 - 2x)x$. A phase-line portrait of the equation $x' = 2(6-x)x$ shows that these orbits move along the x-axis as
$$\begin{array}{c} - \qquad\qquad + \qquad\qquad - \\ \leftarrow\leftarrow\leftarrow\leftarrow \bullet \rightarrow\rightarrow\rightarrow\rightarrow \bullet \leftarrow\leftarrow\leftarrow\leftarrow \; x \\ 0 \qquad\qquad\quad 6 \end{array}$$
In particular, there is an orbit that moves along the x-axis from the stationary point $(0,0)$ to the stationary point $(0,6)$. □

The above analysis suggests the following sketch of the phase-plane portrait.

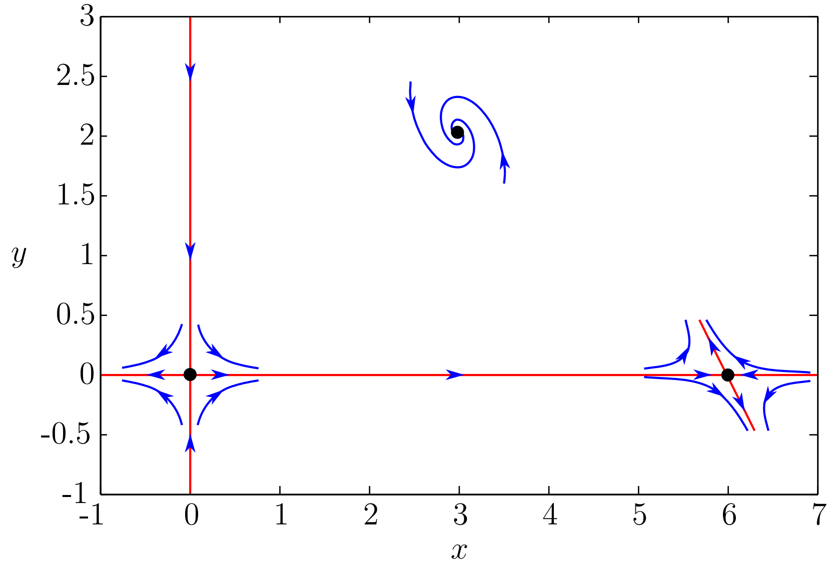

FIGURE 10.1. Sketch of the phase-plane portrait for Example 1 showing the stationary points, semistationary solutions, and the behavior near stationary points obtained by linearization.

The foregoing sketch gives a fair indication of the phase-plane portrait for Example 1. For comparison, below we give a more complete version obtained by numerical methods.

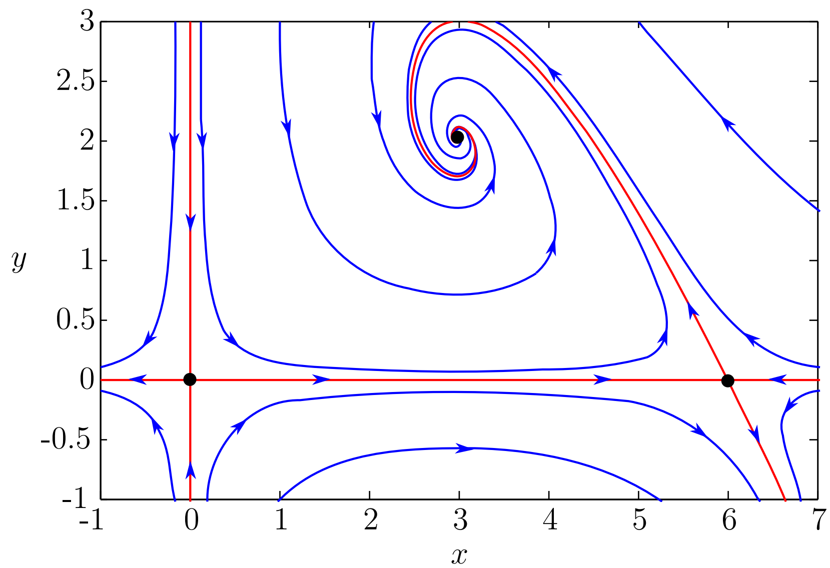

FIGURE 10.2. The phase-plane portrait for Example 1 showing the stationary points, semistationary solutions, and representative orbits obtained by numerical methods.

Remark. Elements of the more complete phase-plane portrait shown in Figure 10.2 can be figured out from the sketch in Figure 10.1. For example, the separatrix orbit that emerges from the saddle point at $(6, 0)$ into the first quadrant clearly cannot leave the first quadrant or run off to infinity, so it must spiral into the counterclockwise spiral sink at $(3, 2)$. This orbit is shown in red in Figure 10.2. It could have been added to the sketch in Figure 10.1. It then would have been clear that the remaining orbits in the first quadrant must behave as shown in Figure 10.2.

Example. Sketch the phase-plane portrait for the predator-prey model

$$x' = (6 - 3y)x\,, \qquad y' = (-15 + 5x)y\,.$$

Solution. First, we find the stationary points of the model. These satisfy

$$0 = (6 - 3y)x\,, \qquad 0 = (-15 + 5x)y\,.$$

The first equation is satisfied when either $x = 0$ or $y = 2$. When $x = 0$ the second equation can only be satisfied when $y = 0$. When $y = 2$ the second equation can only be satisfied when $x = 3$. Therefore the stationary points are $(0, 0)$ and $(3, 2)$.

Next, we linearize the model about each stationary point. Because

$$\mathbf{f}(x, y) = \begin{pmatrix} f(x, y) \\ g(x, y) \end{pmatrix} = \begin{pmatrix} (6 - 3y)x \\ (-15 + 5x)y \end{pmatrix} = \begin{pmatrix} 6x - 3xy \\ -15y + 5xy \end{pmatrix},$$

the Jacobian matrix of partial derivatives is

$$\boldsymbol{\partial}\mathbf{f}(x, y) = \begin{pmatrix} \partial_x f(x, y) & \partial_y f(x, y) \\ \partial_x g(x, y) & \partial_y g(x, y) \end{pmatrix} = \begin{pmatrix} 6 - 3y & -3x \\ 5y & -15 + 5x \end{pmatrix}.$$

By evaluating this at each stationary point we compute the coefficient matrix for the linearization about that point. These matrices then give the following information about what the phase-plane portrait of the nonlinear system looks like near these points.

- At $(0, 0)$ the coefficient matrix of the linearization is

  $$\mathbf{A} = \boldsymbol{\partial}\mathbf{f}(0, 0) = \begin{pmatrix} 6 & 0 \\ 0 & -15 \end{pmatrix}.$$

  Because $\mathbf{A}$ is diagonal, we can read off that its eigenvalues are 6 and -15. This implies that near $(0, 0)$ the phase-plane portrait is a *saddle*, which is *unstable*. Because

  $$\mathbf{A} - 6\mathbf{I} = \begin{pmatrix} 0 & 0 \\ 0 & -21 \end{pmatrix}, \qquad \mathbf{A} + 15\mathbf{I} = \begin{pmatrix} 21 & 0 \\ 0 & 0 \end{pmatrix},$$

  the eigenpairs of $\mathbf{A}$ are

  $$\left(6\,, \begin{pmatrix} 1 \\ 0 \end{pmatrix}\right), \qquad \left(-15\,, \begin{pmatrix} 0 \\ 1 \end{pmatrix}\right).$$

  There is one orbit that emerges from $(0, 0)$ tangent to each half of the x-axis. There is one orbit that approaches $(0, 0)$ tangent to each half of the y-axis.

- At $(3,2)$ the coefficient matrix of the linearization is

$$\mathbf{A} = \boldsymbol{\partial}\mathbf{f}(3,2) = \begin{pmatrix} 0 & -9 \\ 10 & 0 \end{pmatrix} .$$

  Its characteristic polynomial is $p(z) = z^2 + 90$. Its eigenvalues thereby are the conjugate pair $\pm i\sqrt{90}$ while $a_{21} = 10 > 0$. Therefore the origin is a counterclockwise center for the linearized system. However, we cannot conclude that the stationary point $(3,2)$ is a counterclockwise center in the phase-plane portrait of the nonlinear system without additional information.

  The simplest way to see that the nonlinear system is conservative without computing an integral $H(x,y)$ is to observe that its orbit equation is

$$\frac{\mathrm{d}y}{\mathrm{d}x} = \frac{(-15+5x)y}{(6-3y)x} ,$$

  which is separable. This shows the nonlinear system is conservative, which allows us to conclude that the stationary point $(3,2)$ is a *counterclockwise center* and thereby is *stable*.

Finally, like every population model in this chapter, this model has semistationary solutions that lie on the x and y-axes.

- There are semistationary solutions of the form $(0, Y(t))$ where $Y(t)$ satisfies the $y' = -15y$. A phase-line portrait shows these orbits move along the y-axis as

$$\begin{array}{ccc} + & & - \\ \rightarrow\rightarrow\rightarrow\rightarrow & \bullet & \leftarrow\leftarrow\leftarrow\leftarrow \; y \\ & 0 & \end{array}$$

  This shows that orbits on the y-axis move towards the stationary point $(0,0)$. This model predicts that without prey to sustain it, the population of predators will die off quickly.

- There are semistationary solutions of the form $(X(t), 0)$ where $X(t)$ satisfies $x' = 6x$. A phase-line portrait of the equation $x' = 6x$ shows that these orbits move along the x-axis as

$$\begin{array}{ccc} - & & + \\ \leftarrow\leftarrow\leftarrow\leftarrow & \bullet & \rightarrow\rightarrow\rightarrow\rightarrow \; x \\ & 0 & \end{array}$$

  This shows that orbits on the x-axis move away from the stationary point $(0,0)$. This model predicts that without predators to keep its population in check, the population of prey will grow without bound.

Remark. The semistationary solutions have the explicit formulas $(0, y_I e^{-15t})$ and $(x_I e^{6t}, 0)$, but these formulas are not needed to sketch the phase-plane portrait.

The above analysis suggests the following sketch of the phase-plane portrait.

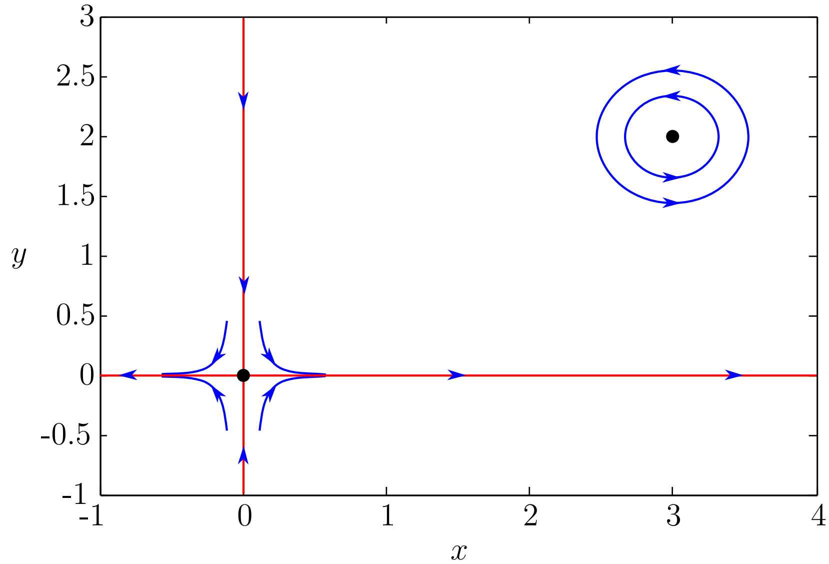

FIGURE 10.3. Sketch of the phase-plane portrait for Example 2 showing the stationary points, semistationary solutions, and the behavior near stationary points obtained by linearization.

The foregoing sketch gives a fair indication of the phase-plane portrait for Example 2. For comparison, below we give a more complete version obtained by numerical methods.

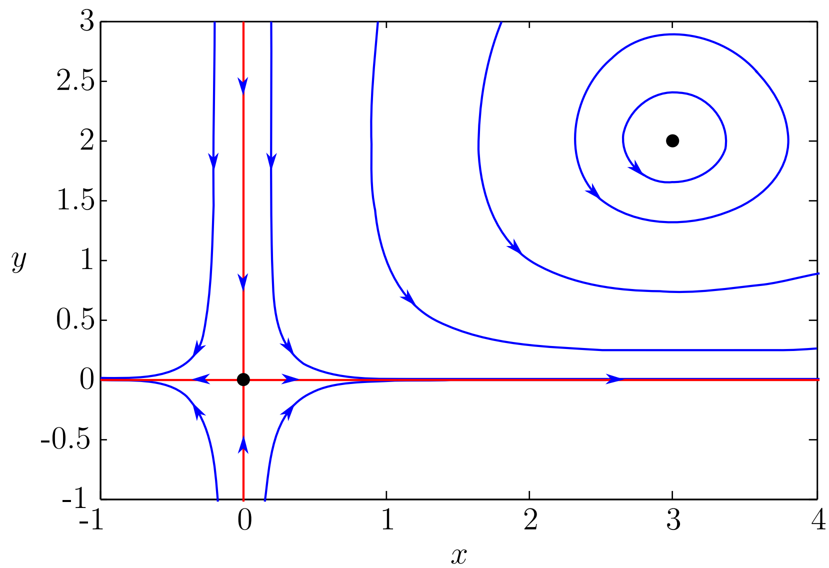

FIGURE 10.4. The phase-plane portrait for Example 2 showing the stationary points, semistationary solutions, and representative orbits obtained by numerical methods.

This more complete version of the phase-plane portrait for Example 2 could also be obtained by noticing that the orbit equation is

$$\frac{\mathrm{d}y}{\mathrm{d}x} = \frac{(-15+5x)y}{(6-3y)x}\,,$$

which is separable. Its separated form is

$$\frac{5x-15}{x}\,\mathrm{d}x + \frac{3y-6}{y}\,\mathrm{d}y = 0\,,$$

which integrates to

$$5x - 15\log(|x|) + 3y - 6\log(|y|) = c\,.$$

This cannot be solved either for y as an explicit function of x or for x as an explicit function of y. Rather, the orbits are given implicitly by $H(x,y) = c$ where the integral $H(x,y)$ is

$$H(x,y) = 5x - 15\log(|x|) + 3y - 6\log(|y|)\,.$$

This function is undefined on the x-axis and y-axis, which reflects the fact that the separated form was undefined on the x-axis and y-axis. Because this is a population model, we only care about the first quadrant of the xy-plane.

The first partial derivatives of $H(x,y)$ are

$$\partial_x H(x,y) = 5 - \frac{15}{x} = \frac{5(x-3)}{x}\,, \qquad \partial_y H(x,y) = 3 - \frac{6}{y} = \frac{3(y-2)}{y}\,.$$

Therefore the stationary point $(3,2)$ is also a critical point of the function $H(x,y)$. The Hessian matrix of $H(x,y)$ is

$$\boldsymbol{\partial}^2 H(x,y) = \begin{pmatrix} \partial_{xx}H(x,y) & \partial_{xy}H(x,y) \\ \partial_{yx}H(x,y) & \partial_{yy}H(x,y) \end{pmatrix} = \begin{pmatrix} \dfrac{15}{x^2} & 0 \\ 0 & \dfrac{6}{y^2} \end{pmatrix}.$$

Because

$$\det\bigl(\boldsymbol{\partial}^2 H(x,y)\bigr) = \frac{15}{x^2}\cdot\frac{6}{y^2}\,, \qquad \mathrm{tr}\bigl(\boldsymbol{\partial}^2 H(x,y)\bigr) = \frac{15}{x^2} + \frac{6}{y^2}\,,$$

we see that these are both positive off the x-axis and y-axis. The function $H(x,y)$ thereby is strictly convex (concave up) in each quadrant. Therefore its critical point $(3,2)$ is a global minimum of $H(x,y)$ in the first quadrant. Because the orbits of our model are the level sets of $H(x,y)$, we see that counterclockwise periodic orbits fill out the first quadrant. □

Remark. We could have generated Figure 10.4 by plotting the level sets of $H(x,y)$ in each quadrant. When doing so, care must be taken to avoid the x-axis and y-axis where $H(x,y)$ is undefined. The directions of the orbits along the level sets can be inferred from the directions of the semistationary orbits.

10.3. **Competing Species Models.** In this section we will study competing species models in the form

$$x' = (r - ax - by)x\,, \qquad y' = (s - cx - dy)y\,, \tag{10.3}$$

where the parameters a, b, c, d, r, and s are positive.

Example. Sketch the phase-plane portrait for the competing species model

$$x' = (16 - 4x - 2y)x\,, \qquad y' = (10 - x - 2y)y\,.$$

Solution. First, we find the stationary points of the model. These satisfy

$$0 = (16 - 4x - 2y)x\,, \qquad 0 = (10 - x - 2y)y\,.$$

The first equation is satisfied if $x = 0$ or $4x + 2y = 16$. The second equation is satisfied if $y = 0$ or $x + 2y = 10$. Therefore there are four possibilities.

- By setting $x = 0$ and $y = 0$ we obtain the stationary point $(0, 0)$.
- By setting $x = 0$ and $x + 2y = 10$ we obtain the stationary point $(0, 5)$.
- By setting $4x + 2y = 16$ and $y = 0$ we obtain the stationary point $(4, 0)$.
- By setting $4x + 2y = 16$ and $x + 2y = 10$ we obtain the stationary point $(2, 4)$.

Therefore the stationary points are

$$(0, 0)\,, \qquad (0, 5)\,, \qquad (4, 0)\,, \qquad (2, 4)\,.$$

Next, we linearize the model about each stationary point. Because

$$\mathbf{f}(x, y) = \begin{pmatrix} f(x, y) \\ g(x, y) \end{pmatrix} = \begin{pmatrix} (16 - 4x - 2y)x \\ (10 - x - 2y)y \end{pmatrix} = \begin{pmatrix} 16x - 4x^2 - 2xy \\ 10y - xy - 2y^2 \end{pmatrix}\,,$$

the Jacobian matrix of partial derivatives is

$$\boldsymbol{\partial}\mathbf{f}(x, y) = \begin{pmatrix} \partial_x f(x, y) & \partial_y f(x, y) \\ \partial_x g(x, y) & \partial_y g(x, y) \end{pmatrix} = \begin{pmatrix} 16 - 8x - 2y & -2x \\ -y & 10 - x - 4y \end{pmatrix}\,.$$

By evaluating this at each stationary point we compute the coefficient matrix for the linearization about that point. These matrices then give the following information about what the phase-plane portrait of the nonlinear system looks like near these points.

- At $(0, 0)$ the coefficient matrix of the linearization is

  $$\mathbf{A} = \boldsymbol{\partial}\mathbf{f}(0, 0) = \begin{pmatrix} 16 & 0 \\ 0 & 10 \end{pmatrix}\,.$$

  Because $\mathbf{A}$ is diagonal, we can read off that its eigenvalues are 16 and 10. This implies that near $(0, 0)$ the phase-plane portrait is a *nodal source*, which is *repelling*. Because

  $$\mathbf{A} - 16\mathbf{I} = \begin{pmatrix} 0 & 0 \\ 0 & -6 \end{pmatrix}\,, \qquad \mathbf{A} - 10\mathbf{I} = \begin{pmatrix} 6 & 0 \\ 0 & 0 \end{pmatrix}\,,$$

  the eigenpairs of $\mathbf{A}$ are

  $$\left(16\,, \begin{pmatrix} 1 \\ 0 \end{pmatrix}\right)\,, \qquad \left(10\,, \begin{pmatrix} 0 \\ 1 \end{pmatrix}\right)\,.$$

There is one orbit that emerges from $(0,0)$ tangent to each half of the x-axis. All other orbits emerge from $(0,0)$ tangent to one half of the y-axis.

- At $(0,5)$ the coefficient matrix of the linearization is

$$\mathbf{A} = \boldsymbol{\partial}\mathbf{f}(0,5) = \begin{pmatrix} 6 & 0 \\ -5 & -10 \end{pmatrix} .$$

Because $\mathbf{A}$ is lower triangular, we can read off that its eigenvalues are 6 and -10. This implies that near $(0,5)$ the phase-plane portrait is a *saddle*, which is *unstable*. Because

$$\mathbf{A} - 6\mathbf{I} = \begin{pmatrix} 0 & 0 \\ -5 & -16 \end{pmatrix} , \qquad \mathbf{A} + 10\mathbf{I} = \begin{pmatrix} 16 & 0 \\ -5 & 0 \end{pmatrix} ,$$

the eigenpairs of $\mathbf{A}$ are

$$\left(6 \, , \begin{pmatrix} 16 \\ -5 \end{pmatrix} \right) , \qquad \left(-10 \, , \begin{pmatrix} 0 \\ 1 \end{pmatrix} \right) .$$

There is one orbit that emerges from $(0,5)$ tangent to each half of the line $y = 5 - \frac{5}{16}x$. There is one orbit that approaches $(0,5)$ tangent to each half of the y-axis.

- At $(4,0)$ the coefficient matrix of the linearization is

$$\mathbf{A} = \boldsymbol{\partial}\mathbf{f}(4,0) = \begin{pmatrix} -16 & -8 \\ 0 & 6 \end{pmatrix} .$$

Because $\mathbf{A}$ is upper triangular, we can read off that its eigenvalues are -16 and 6. This implies that near $(4,0)$ the phase-plane portrait is a *saddle*, which is *unstable*. Because

$$\mathbf{A} + 16\mathbf{I} = \begin{pmatrix} 0 & -8 \\ 0 & 22 \end{pmatrix} , \qquad \mathbf{A} - 6\mathbf{I} = \begin{pmatrix} -22 & -8 \\ 0 & 0 \end{pmatrix} ,$$

the eigenpairs of $\mathbf{A}$ are

$$\left(-16 \, , \begin{pmatrix} 1 \\ 0 \end{pmatrix} \right) , \qquad \left(6 \, , \begin{pmatrix} -4 \\ 11 \end{pmatrix} \right) .$$

There is one orbit that approaches $(4,0)$ tangent to each half of the y-axis. There is one orbit that emerges from $(4,0)$ tangent to each half of the line $y = -\frac{11}{4}(x-4)$.

- At $(2,4)$ the coefficient matrix of the linearization is

$$\mathbf{A} = \boldsymbol{\partial}\mathbf{f}(2,4) = \begin{pmatrix} -8 & -4 \\ -4 & -8 \end{pmatrix} .$$

The characteristic polynomial of $\mathbf{A}$ is

$$p(z) = z^2 - \operatorname{tr}(\mathbf{A})z + \det(\mathbf{A}) = z^2 + 16z + 48 = (z+12)(z+4) ,$$

from which we see that its eigenvalues are -12 and -4. This implies that near $(2,4)$ the phase-plane portrait is a *nodal sink*, which is *stable*. Because

$$\mathbf{A} + 12\mathbf{I} = \begin{pmatrix} 4 & -4 \\ -4 & 4 \end{pmatrix}, \qquad \mathbf{A} + 4\mathbf{I} = \begin{pmatrix} -4 & -4 \\ -4 & -4 \end{pmatrix},$$

the eigenpairs of $\mathbf{A}$ are

$$\left(-12, \begin{pmatrix} 1 \\ 1 \end{pmatrix}\right), \qquad \left(-4, \begin{pmatrix} 1 \\ -1 \end{pmatrix}\right).$$

There is one orbit that approaches $(2,4)$ tangent to each half of the line $y = 4 + (x-2)$. All other orbits approach $(2,4)$ tangent to one half of the line $y = 4 - (x-2)$.

Finally, like every population model in this chapter, this model has semistationary solutions that lie on the x and y-axes.

- There are semistationary solutions of the form $(0, Y(t))$ where $Y(t)$ satisfies $y' = (10-2y)y$. A phase-line portrait of the equation $y' = 2(5-y)y$ shows that these orbits move along the y-axis as

$$\begin{array}{ccccc} - & & + & & - \\ \leftarrow\leftarrow\leftarrow\leftarrow & \bullet & \rightarrow\rightarrow\rightarrow\rightarrow & \bullet & \leftarrow\leftarrow\leftarrow\leftarrow \; y \\ & 0 & & 5 & \end{array}$$

  In particular, there is an orbit that moves along the y-axis from the stationary point $(0,0)$ to the stationary point $(0,5)$.

- There are semistationary solutions of the form $(X(t), 0)$ where $X(t)$ satisfies $x' = (16-4x)x$. A phase-line portrait of the equation $x' = 4(4-x)x$ shows that these orbits move along the x-axis as

$$\begin{array}{ccccc} - & & + & & - \\ \leftarrow\leftarrow\leftarrow\leftarrow & \bullet & \rightarrow\rightarrow\rightarrow\rightarrow & \bullet & \leftarrow\leftarrow\leftarrow\leftarrow \; x \\ & 0 & & 4 & \end{array}$$

  In particular, there is an orbit that moves along the x-axis from the stationary point $(0,0)$ to the stationary point $(4,0)$. □

Remark. Because the stationary points $(0,0)$ and $(2,4)$ are neither a saddle nor a center, we know that the nonlinear system in the previous example does not have an integral $H(x,y)$ over any region containing either of those points. In particular, there is no integral defined over the entire first quadrant.

The above analysis suggests the following sketch of the phase-plane portrait.

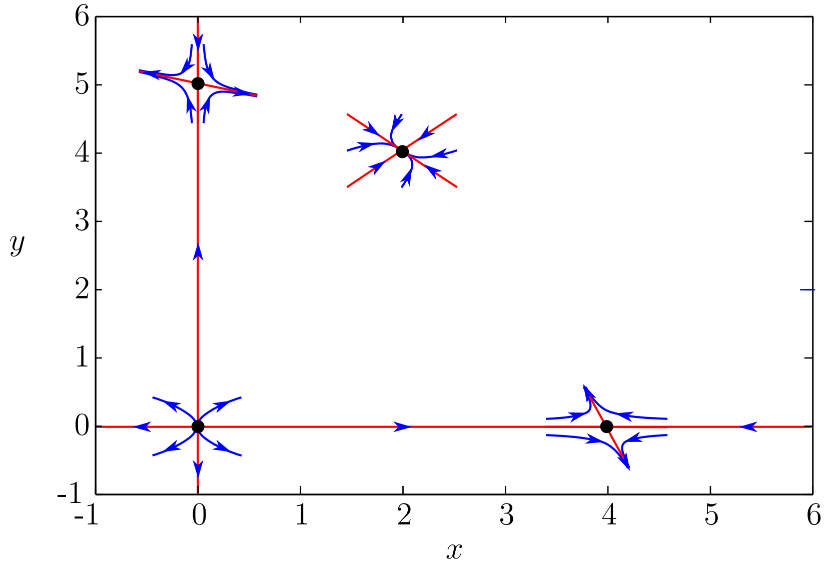

FIGURE 10.5. Sketch of the phase-plane portrait for Example 3 showing the stationary points, semistationary solutions, and the behavior near stationary points obtained by linearization.

The foregoing sketch gives a fair indication of the phase-plane portrait for Example 3. For comparison, below we give a more complete version obtained by numerical methods.

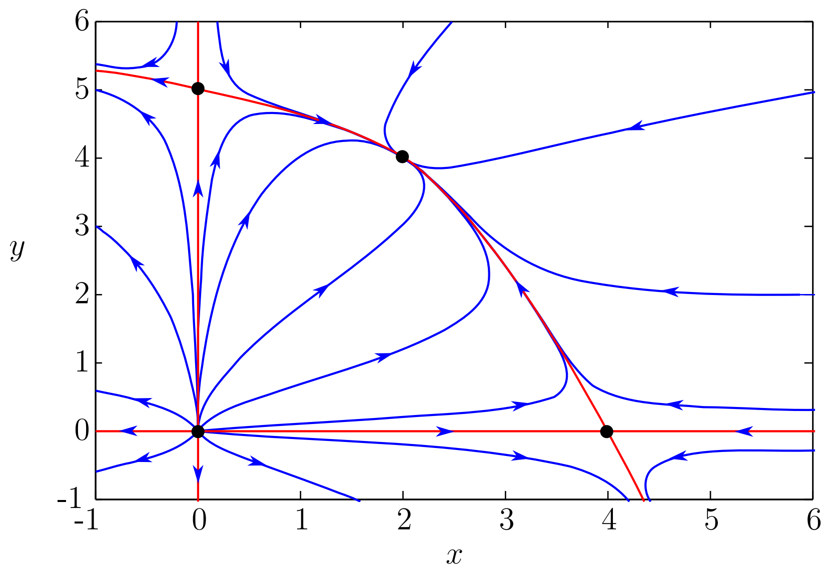

FIGURE 10.6. The phase-plane portrait for Example 3 showing the stationary points, semistationary solutions, and representative orbits obtained by numerical methods.

Remark. We see from Figure 10.6 that every orbit that starts in the first quadrant will approach the nodal sink at $(2, 4)$ as time goes to infinity. In this case the competition between the two species does not lead to the extinction of one of them. In other words, our model shows these two species will generally coexist. The next example shows a different outcome.

Example. Sketch the phase-plane portrait for the competing species model

$$x' = (16 - 4x - 3y)x\,, \qquad y' = (7 - 3x - y)y\,.$$

Solution. First, we find the stationary points of the model. These satisfy

$$0 = (16 - 4x - 3y)x\,, \qquad 0 = (7 - 3x - y)y\,.$$

The first equation is satisfied if $x = 0$ or $4x + 3y = 16$. The second equation is satisfies if $y = 0$ or $3x + y = 7$. Therefore there are four possibilities.

- By setting $x = 0$ and $y = 0$ we obtain the stationary point $(0, 0)$.
- By setting $x = 0$ and $3x + y = 7$ we obtain the stationary point $(0, 7)$.
- By setting $4x + 3y = 16$ and $y = 0$ we obtain the stationary point $(4, 0)$.
- By setting $4x + 3y = 16$ and $3x + y = 7$ we obtain the stationary point $(1, 4)$.

Therefore the stationary points are

$$(0, 0)\,, \qquad (0, 7)\,, \qquad (4, 0)\,, \qquad (1, 4)\,.$$

Next, we linearize the model about each stationary point. Because

$$\mathbf{f}(x, y) = \begin{pmatrix} f(x, y) \\ g(x, y) \end{pmatrix} = \begin{pmatrix} (16 - 4x - 3y)x \\ (7 - 3x - y)y \end{pmatrix} = \begin{pmatrix} 16x - 4x^2 - 3xy \\ 7y - 3xy - y^2 \end{pmatrix}\,,$$

the Jacobian matrix of partial derivatives is

$$\boldsymbol{\partial}\mathbf{f}(x, y) = \begin{pmatrix} \partial_x f(x, y) & \partial_y f(x, y) \\ \partial_x g(x, y) & \partial_y g(x, y) \end{pmatrix} = \begin{pmatrix} 16 - 8x - 3y & -3x \\ -3y & 7 - 3x - 2y \end{pmatrix}\,.$$

By evaluating this at each stationary point we compute the coefficient matrix for the linearization about that point. These matrices then give the following information about what the phase-plane portrait of the nonlinear system looks like near these points.

- At $(0, 0)$ the coefficient matrix of the linearization is

  $$\mathbf{A} = \boldsymbol{\partial}\mathbf{f}(0, 0) = \begin{pmatrix} 16 & 0 \\ 0 & 7 \end{pmatrix}\,.$$

  Because $\mathbf{A}$ is diagonal, we can read off that its eigenvalues are 16 and 7. This implies that near $(0, 0)$ the phase-plane portrait is a *nodal source*, which is *repelling*. Because

  $$\mathbf{A} - 16\mathbf{I} = \begin{pmatrix} 0 & 0 \\ 0 & -9 \end{pmatrix}\,, \qquad \mathbf{A} - 7\mathbf{I} = \begin{pmatrix} 9 & 0 \\ 0 & 0 \end{pmatrix}\,,$$

  the eigenpairs of $\mathbf{A}$ are

  $$\left(16\,, \begin{pmatrix} 1 \\ 0 \end{pmatrix}\right)\,, \qquad \left(7\,, \begin{pmatrix} 0 \\ 1 \end{pmatrix}\right)\,.$$

There is one orbit that emerges from $(0,0)$ tangent to each half of the x-axis. All other orbits emerge from $(0,0)$ tangent to one half of the y-axis.

- At $(0,7)$ the coefficient matrix of the linearization is

$$\mathbf{A} = \boldsymbol{\partial}\mathbf{f}(0,0) = \begin{pmatrix} -5 & 0 \\ -21 & -7 \end{pmatrix}.$$

Because $\mathbf{A}$ is lower triangular, we can read off that its eigenvalues are -5 and -7. This implies that near $(0,7)$ the phase-plane portrait is a *nodal sink*, which is *attracting*. Because

$$\mathbf{A} + 5\mathbf{I} = \begin{pmatrix} 0 & 0 \\ -21 & -2 \end{pmatrix}, \qquad \mathbf{A} + 7\mathbf{I} = \begin{pmatrix} 2 & 0 \\ -21 & 0 \end{pmatrix},$$

the eigenpairs of $\mathbf{A}$ are

$$\left(-5\,, \begin{pmatrix} 2 \\ -21 \end{pmatrix}\right), \qquad \left(-7\,, \begin{pmatrix} 0 \\ 1 \end{pmatrix}\right).$$

There is one orbit that approaches $(0,7)$ tangent to each half of the y-axis. All other orbits approach $(0,7)$ tangent to one half of the line $y = 7 - \frac{21}{2}x$.

- At $(4,0)$ the coefficient matrix of the linearization is

$$\mathbf{A} = \boldsymbol{\partial}\mathbf{f}(4,0) = \begin{pmatrix} -16 & -12 \\ 0 & -5 \end{pmatrix}.$$

Because $\mathbf{A}$ is upper triangular, we can read off that its eigenvalues are -16 and -5. This implies that near $(4,0)$ the phase-plane portrait is a *nodal sink*, which is *attracting*. Because

$$\mathbf{A} + 16\mathbf{I} = \begin{pmatrix} 0 & -12 \\ 0 & 11 \end{pmatrix}, \qquad \mathbf{A} + 5\mathbf{I} = \begin{pmatrix} -11 & -12 \\ 0 & 0 \end{pmatrix},$$

the eigenpairs of $\mathbf{A}$ are

$$\left(-16\,, \begin{pmatrix} 1 \\ 0 \end{pmatrix}\right), \qquad \left(-5\,, \begin{pmatrix} -12 \\ 11 \end{pmatrix}\right).$$

There is one orbit that approaches $(4,0)$ tangent to each half of the x-axis. All other orbits approach $(4,0)$ tangent to one half of the line $y = -\frac{11}{12}(x-4)$.

- At $(1,4)$ the coefficient matrix of the linearization is

$$\mathbf{A} = \boldsymbol{\partial}\mathbf{f}(1,4) = \begin{pmatrix} -4 & -3 \\ -12 & -4 \end{pmatrix}.$$

The characteristic polynomial of $\mathbf{A}$ is

$$p(z) = z^2 - \mathrm{tr}(\mathbf{A})z + \det(\mathbf{A}) = z^2 + 8z - 20 = (z+10)(z-2)\,,$$

from which we see that its eigenvalues are -10 and 2. This implies that near $(1,4)$ the phase-plane portrait is a *saddle*, which is *unstable*. Because

$$\mathbf{A} + 10\mathbf{I} = \begin{pmatrix} 6 & -3 \\ -12 & 6 \end{pmatrix}, \qquad \mathbf{A} - 2\mathbf{I} = \begin{pmatrix} -6 & -3 \\ -12 & -6 \end{pmatrix},$$

the eigenpairs of $\mathbf{A}$ are

$$\left(-10\,,\,\begin{pmatrix}1\\2\end{pmatrix}\right)\,,\qquad\left(2\,,\,\begin{pmatrix}1\\-2\end{pmatrix}\right)\,.$$

There is one orbit that approaches $(1,4)$ tangent to each half of the line $y = 4+2(x-1)$. There is one orbit that emerges from $(1,4)$ tangent to one half of the line $y = 4-2(x-1)$.

Finally, like every population model in this chapter, this model has semistationary solutions that lie on the x and y-axes.

- There are semistationary solutions of the form $(0, Y(t))$ where $Y(t)$ satisfies the $y' = (7-y)y$. A phase-line portrait of the equation $y' = (7-y)y$ shows that these orbits move along the y-axis as

$$\begin{array}{ccccccc} & - & & + & & - & \\ \leftarrow\leftarrow\leftarrow\leftarrow & \bullet & \rightarrow\rightarrow\rightarrow\rightarrow & \bullet & \leftarrow\leftarrow\leftarrow\leftarrow & y \\ & 0 & & 7 & & \end{array}$$

  In particular, there is an orbit that moves along the y-axis from the stationary point $(0,0)$ to the stationary point $(0,7)$.

- There are semistationary solutions of the form $(X(t), 0)$ where $X(t)$ satisfies $x' = (16-4x)x$. A phase-line portrait of the equation $x' = 4(4-x)x$ shows that these orbits move along the x-axis as

$$\begin{array}{ccccccc} & - & & + & & - & \\ \leftarrow\leftarrow\leftarrow\leftarrow & \bullet & \rightarrow\rightarrow\rightarrow\rightarrow & \bullet & \leftarrow\leftarrow\leftarrow\leftarrow & x \\ & 0 & & 4 & & \end{array}$$

  In particular, there is an orbit that moves along the x-axis from the stationary point $(0,0)$ to the stationary point $(4,0)$. □

Remark. Because the stationary points $(0,0)$, $(0,7)$, and $(4,0)$ are neither a saddle nor a center, we know that the nonlinear system in the previous example does not have an integral $H(x,y)$ over any region containing either of those points. This does not preclude the possibility that an integral $H(x,y)$ exists that is undefined on parts of the x-axis and y-axis.

The above analysis suggests the following sketch of the phase-plane portrait.

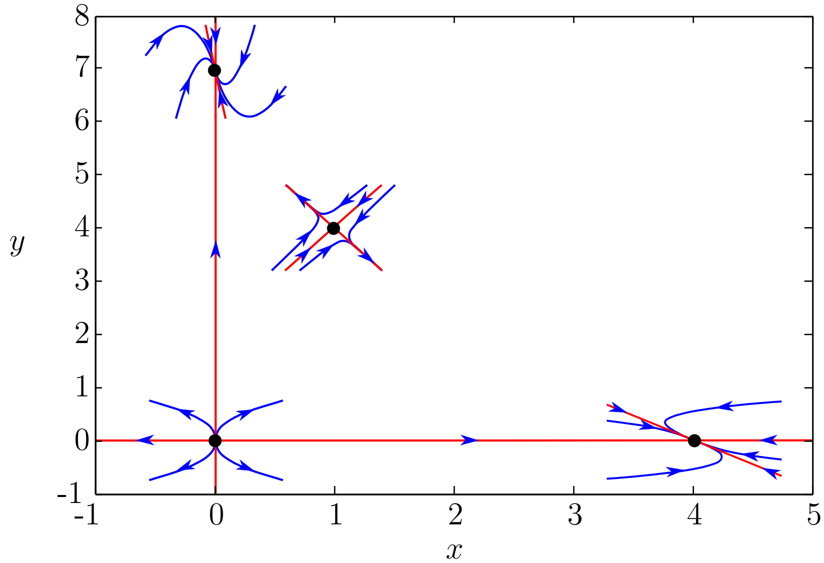

FIGURE 10.7. Sketch of the phase-plane portrait for Example 4 showing the stationary points, semistationary solutions, and the behavior near stationary points obtained by linearization.

The foregoing sketch gives a fair indication of the phase-plane portrait for Example 4. For comparison, below we give a more complete version obtained by numerical methods.

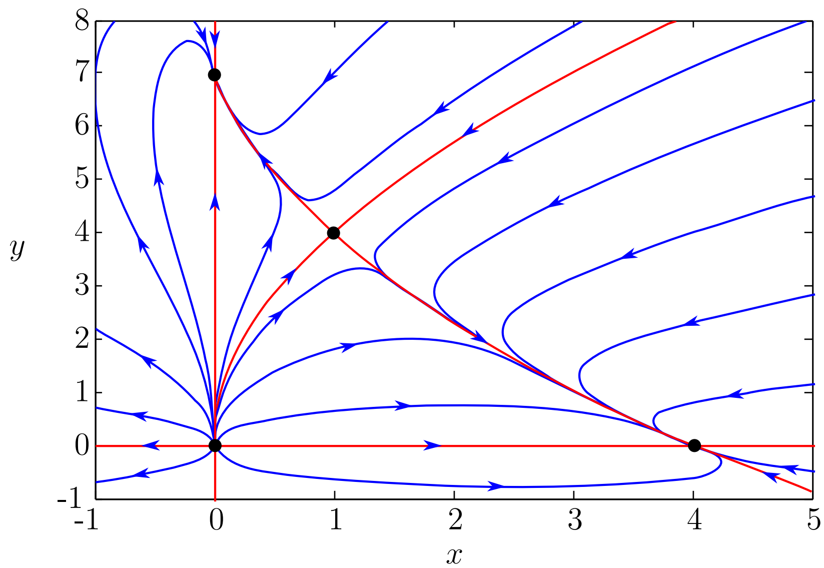

FIGURE 10.8. The phase-plane portrait for Example 4 showing the stationary points, semistationary solutions, and representative orbits obtained by numerical methods.

10.4. **Cooperating Species Models.** In this section we will study cooperating species models in the form

$$x' = (r - ax + by)x\,, \qquad y' = (s + cx - dy)y\,, \tag{10.4}$$

where the parameters a, b, c, d, r, and s are positive.

Example. Sketch the phase-plane portrait for the competing species model

$$x' = (27 - 9x + y)x\,, \qquad y' = (20 + 4x - 4y)y\,.$$

Solution. First, we find the stationary points of the model. These satisfy

$$0 = (27 - 9x + y)x\,, \qquad 0 = (20 + 4x - 4y)y\,.$$

The first equation is satisfied if $x = 0$ or $9x - y = 27$. The second equation is satisfied if $y = 0$ or $-4x + 4y = 20$. Therefore there are four possibilities.

- By setting $x = 0$ and $y = 0$ we obtain the stationary point $(0, 0)$.
- By setting $x = 0$ and $-4x + 4y = 20$ we obtain the stationary point $(0, 5)$.
- By setting $9x - y = 27$ and $y = 0$ we obtain the stationary point $(3, 0)$.
- By setting $9x - y = 27$ and $-4x + 4y = 20$ we obtain the stationary point $(4, 9)$.

Therefore the stationary points are

$$(0, 0)\,, \qquad (0, 5)\,, \qquad (3, 0)\,, \qquad (4, 9)\,.$$

Next, we linearize the model about each stationary point. Because

$$\mathbf{f}(x, y) = \begin{pmatrix} f(x, y) \\ g(x, y) \end{pmatrix} = \begin{pmatrix} (27 - 9x + y)x \\ (20 + 4x - 4y)y \end{pmatrix} = \begin{pmatrix} 27x - 9x^2 + xy \\ 20y + 4xy - 4y^2 \end{pmatrix}\,,$$

the Jacobian matrix of partial derivatives is

$$\boldsymbol{\partial}\mathbf{f}(x, y) = \begin{pmatrix} \partial_x f(x, y) & \partial_y f(x, y) \\ \partial_x g(x, y) & \partial_y g(x, y) \end{pmatrix} = \begin{pmatrix} 27 - 18x + y & x \\ 4y & 20 + 4x - 8y \end{pmatrix}\,.$$

By evaluating this at each stationary point we compute the coefficient matrix for the linearization about that point. These matrices then give the following information about what the phase-plane portrait of the nonlinear system looks like near these points.

- At $(0, 0)$ the coefficient matrix of the linearization is

  $$\mathbf{A} = \boldsymbol{\partial}\mathbf{f}(0, 0) = \begin{pmatrix} 27 & 0 \\ 0 & 20 \end{pmatrix}\,.$$

  Because $\mathbf{A}$ is diagonal, we can read off that it has eigenvalues 27 and 20. This implies that near $(0, 0)$ the phase-plane portrait is a *nodal source*, which is *repelling*. Because

  $$\mathbf{A} - 27\mathbf{I} = \begin{pmatrix} 0 & 0 \\ 0 & -7 \end{pmatrix}\,, \qquad \mathbf{A} - 20\mathbf{I} = \begin{pmatrix} 7 & 0 \\ 0 & 0 \end{pmatrix}\,,$$

  the eigenpairs of $\mathbf{A}$ are

  $$\left(27\,, \begin{pmatrix} 1 \\ 0 \end{pmatrix}\right)\,, \qquad \left(20\,, \begin{pmatrix} 0 \\ 1 \end{pmatrix}\right)\,.$$

There is one orbit that emerges from $(0,0)$ tangent to each half of the y-axis. All other orbits emerge from $(0,0)$ tangent to one half of the x-axis.

- At $(0,5)$ the coefficient matrix of the linearization is

$$\mathbf{A} = \boldsymbol{\partial}\mathbf{f}(0,5) = \begin{pmatrix} 32 & 0 \\ 20 & -20 \end{pmatrix} .$$

Because $\mathbf{A}$ is lower triangular, we can read off that its eigenvalues are 32 and -20. This implies that near $(0,5)$ the phase-plane portrait is a *saddle*, which is *unstable*. Because

$$\mathbf{A} - 32\mathbf{I} = \begin{pmatrix} 0 & 0 \\ 20 & -52 \end{pmatrix} , \qquad \mathbf{A} + 20\mathbf{I} = \begin{pmatrix} 52 & 0 \\ 20 & 0 \end{pmatrix} ,$$

the eigenpairs of $\mathbf{A}$ are

$$\left(32 \, , \begin{pmatrix} 13 \\ 5 \end{pmatrix} \right) , \qquad \left(-20 \, , \begin{pmatrix} 0 \\ 1 \end{pmatrix} \right) .$$

There is one orbit that emerges from $(0,5)$ tangent to each half of the line $y = 5 - \frac{5}{13}x$. There is one orbit that approaches $(0,5)$ tangent to each half of the y-axis.

- At $(3,0)$ the coefficient matrix of the linearization is

$$\mathbf{A} = \boldsymbol{\partial}\mathbf{f}(3,0) = \begin{pmatrix} -27 & 3 \\ 0 & 32 \end{pmatrix} .$$

Because $\mathbf{A}$ is upper triangular, we can read off that its eigenvalues are -27 and 32. This implies that near $(3,0)$ the phase-plane portrait is a *saddle*, which is *unstable*. Because

$$\mathbf{A} + 27\mathbf{I} = \begin{pmatrix} 0 & 3 \\ 0 & 59 \end{pmatrix} , \qquad \mathbf{A} - 32\mathbf{I} = \begin{pmatrix} -59 & 3 \\ 0 & 0 \end{pmatrix} ,$$

the eigenpairs of $\mathbf{A}$ are

$$\left(-27 \, , \begin{pmatrix} 1 \\ 0 \end{pmatrix} \right) , \qquad \left(32 \, , \begin{pmatrix} 3 \\ 59 \end{pmatrix} \right) .$$

There is one orbit that approaches $(3,0)$ tangent to each half of the y-axis. There is one orbit that emerges from $(3,0)$ tangent to each half of the line $y = -\frac{59}{3}(x-3)$.

- At $(4,9)$ the coefficient matrix of the linearization is

$$\mathbf{A} = \boldsymbol{\partial}\mathbf{f}(4,9) = \begin{pmatrix} -36 & 9 \\ 16 & -36 \end{pmatrix} .$$

The characteristic polynomial of $\mathbf{A}$ is

$$p(z) = z^2 - \mathrm{tr}(\mathbf{A})z + \det(\mathbf{A}) = z^2 + 72z + 36^2 - 16\cdot 9 = (z+36)^2 - 12^2 = (z+24)(z+48) ,$$

from which we see that its eigenvalues are -24 and -48. This implies that near $(2,4)$ the phase-plane portrait is a *nodal sink*, which is *stable*. Because

$$\mathbf{A} + 24\mathbf{I} = \begin{pmatrix} -12 & 9 \\ 16 & -12 \end{pmatrix}, \qquad \mathbf{A} + 48\mathbf{I} = \begin{pmatrix} 12 & 9 \\ 16 & 12 \end{pmatrix},$$

the eigenpairs of $\mathbf{A}$ are

$$\left(-24, \begin{pmatrix} 3 \\ 4 \end{pmatrix}\right), \qquad \left(-48, \begin{pmatrix} 3 \\ -4 \end{pmatrix}\right).$$

There is one orbit that approaches $(4,9)$ tangent to each half of the line $y = 9 + \frac{4}{3}(x-4)$. All other orbits approach $(4,9)$ tangent to one half of the line $y = 9 - \frac{4}{3}(x-4)$.

Finally, like every population model in this chapter, this model has semistationary solutions that lie on the x and y-axes.

- There are semistationary solutions of the form $(0, Y(t))$ where $Y(t)$ satisfies the $y' = (20-4y)y$. A phase-line portrait of the equation $y' = 4(5-y)y$ shows that these orbits move along the y-axis as

$$\begin{array}{ccccc} - & & + & & - \\ \leftarrow\leftarrow\leftarrow\leftarrow & \bullet & \rightarrow\rightarrow\rightarrow\rightarrow & \bullet & \leftarrow\leftarrow\leftarrow\leftarrow \; y \\ & 0 & & 5 & \end{array}$$

  In particular, there is an orbit that moves along the y-axis from the stationary point $(0,0)$ to the stationary point $(0,5)$.

- There are semistationary solutions of the form $(X(t), 0)$ where $X(t)$ satisfies $x' = (27-9x)x$. A phase-line portrait of the equation $x' = 9(3-x)x$ shows that these orbits move along the x-axis as

$$\begin{array}{ccccc} - & & + & & - \\ \leftarrow\leftarrow\leftarrow\leftarrow & \bullet & \rightarrow\rightarrow\rightarrow\rightarrow & \bullet & \leftarrow\leftarrow\leftarrow\leftarrow \; x \\ & 0 & & 3 & \end{array}$$

  In particular, there is an orbit that moves along the x-axis from the stationary point $(0,0)$ to the stationary point $(3,0)$. $\square$

The above analysis suggests the following sketch of the phase-plane portrait, which suggests that all solutions which have both species present will approach the attracting stationary point $(4,9)$ as $t \to \infty$. At this point each species approaches a higher population than it would in the absence of the other species. This shows the benefit of their interspecies cooperation.

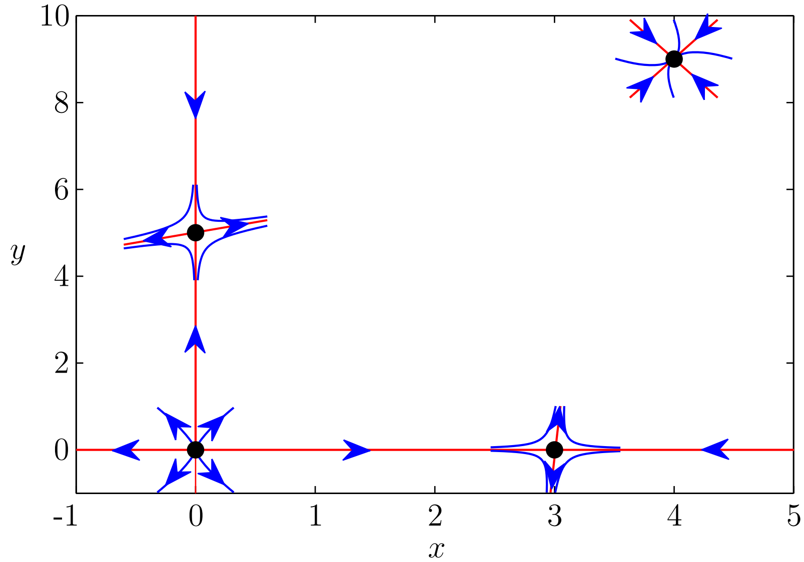

Figure 10.9. Sketch of the phase-plane portrait for Example 5 showing the stationary points, semistationary solutions, and the behavior near stationary points obtained by linearization.

The foregoing sketch gives a fair indication of the phase-plane portrait for Example 5. For comparison, below we give a more complete version obtained by numerical methods.

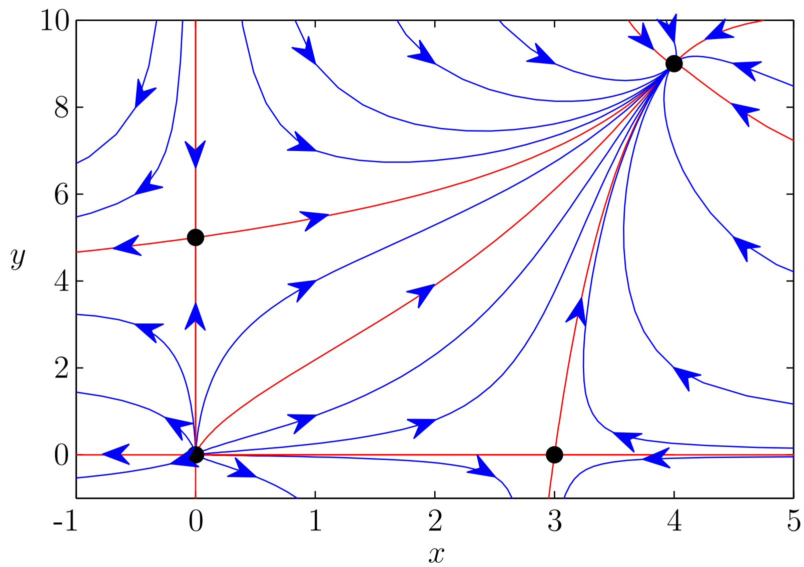

Figure 10.10. The phase-plane portrait for Example 5 showing the stationary points, semistationary solutions, and representative orbits obtained by numerical methods.

10.5. **Models with Equal Bare Growth Rates.** In this section we will study the family of models with equal bare growth rates, which has the form

$$x' = (r - ax - by)x\,, \qquad y' = (r - cx - dy)y\,, \tag{10.5}$$

where the parameters a, b, c, d, and r satisfy

$$a \geq 0\,, \qquad b \neq 0\,, \qquad c \neq 0\,, \qquad d \geq 0\,, \qquad ad - bc \neq 0\,. \tag{10.6}$$

This family includes predator-prey models when $bc < 0$, competing species models when $b > 0$ and $c > 0$, and cooperating species models when $b < 0$ and $c < 0$. However, because it assumes equal bare growth rates given by r, these models do not arise often in practice. We study them here to illustrate phase-plane portrait methods.

10.5.1. *Special Solutions Along a Line.* The condition $ad - bc \neq 0$ in (10.6) insures that there is a unique point (x_*, y_*) that satisfies

$$1 = ax_* + by_*\,, \qquad 1 = cx_* + dy_*\,. \tag{10.7}$$

This point is given by

$$x_* = \frac{d-b}{ad-bc}\,, \qquad y_* = \frac{a-c}{ad-bc}\,. \tag{10.8}$$

Because $ad - bc \neq 0$, this point will not be the origin.

Remark. If either $d = b$ or $a = c$ then this point will lie on the y-axis or the x-axis respectively — specifically, it will be

$$(x_*, y_*) = \left(0\,, \frac{1}{d}\right) \quad \text{or} \quad (x_*, y_*) = \left(\frac{1}{a}\,, 0\right)\,.$$

Otherwise this point will lie off the axes.

Remark. It is clear from (10.7) that $(x_* r, y_* r)$ is a stationary point of system (10.5). If $r = 0$ it is the origin. If $r \neq 0$ and $(a-c)(d-b) = 0$ then by the previous remark it lies on the y-axis or the x-axis. If $r \neq 0$ and $(a-c)(d-b) \neq 0$ then by the previous remark it lies off the axes.

The assumption of equal bare growth rates allows us to construct nonstationary solutions to system (10.5) along the line that passes through the origin and the point (x_*, y_*). Points on this line are given by $(x_* z, y_* z)$ for some real number z. Therefore we seek solutions $(x(t), y(t))$ of system (10.5) in the form

$$x(t) = x_* z(t)\,, \qquad y(t) = y_* z(t)\,. \tag{10.9}$$

Because (x_*, y_*) satisfies (10.7), this form implies that

$$\begin{aligned} x' &= x_* z'\,, \qquad & (r - ax - by)x &= (r - (ax_* + by_*)z)x_* z = x_*(r - z)z\,, \\ y' &= y_* z'\,, \qquad & (r - cx - dy)y &= (r - (cx_* + dy_*)z)y_* z = y_*(r - z)z\,. \end{aligned}$$

From this we see that system (10.5) is satisfied when z satisfies

$$z' = (r - z)z\,. \tag{10.10}$$

The stationary points of this equation are $z = 0$ and $z = r$, which by form (10.9) correspond to the stationary points $(0, 0)$ and $(x_* r, y_* r)$ of system (10.5). Every nonstationary solution $z(t)$ of equation (10.10) yields a nonstationary solution of system (10.5) through formula (10.9).

Remark. When $(a-c)(d-b) = 0$ these nonstationary solutions lie on either the y-axis or the x-axis. Hence, they are among the semistationary solutions that were considered earlier. Otherwise they are new solutions that can be added to a phase-plane portrait. When $(a-c)(d-b) > 0$ they lie in the first and third quadrant. When $(a-c)(d-b) < 0$ they lie in the second and fourth quadrant.

10.5.2. *Integrating the System.* Here we show how sometimes system (10.5) can be integrated. We will use the method for solving dilation invariant first-order equations that was presented in Section 9.2 of Part I. Please review that material before reading this subsection.

First we will reduce the problem of finding solutions of system (10.5) to that of finding solutions of system (10.5) with $r = 0$. This reduction is achieved in two steps. The first step is to notice that the assumption of equal bare growth rates allows us to intoduce new dependent variables u and v that are related to x and y by

$$x = e^{rt} u \,, \qquad y = e^{rt} v \,, \tag{10.11}$$

and thereby transform system (10.5) into

$$u' = -e^{rt}(au + bv)u \,, \qquad v' = -e^{rt}(cu + dv)v \,. \tag{10.12}$$

Exercise. Derive system (10.12) by substituting the expressions for x and y given by (10.11) into system (10.5).

When $r = 0$ system (10.12) reduces to the autonomous system

$$u' = -(au + bv)u \,, \qquad v' = -(cu + dv)v \,. \tag{10.13}$$

This system is just the original system (10.5) with $r = 0$ and (u, v) replacing (x, y). The second step is to notice that when $r \neq 0$ solutions of system (10.12) can be obtained from solutions of the autonomous system (10.13) by replacing t with $(e^{rt} - 1)/r$. By combining this observation with the substitution (10.11) we have reduced the solution of system (10.5) to the solution of system (10.13).

Exercise. Show that if $(u(t), v(t))$ is the solution of the autonomous system (10.13) for initial data (x_I, y_I) then the solution of the original system (10.5) for initial data (x_I, y_I) is given by

$$\left(e^{rt} u\left(\frac{e^{rt} - 1}{r}\right) , \, e^{rt} v\left(\frac{e^{rt} - 1}{r}\right)\right) . \tag{10.14}$$

Example. The solution of (10.13) for initial data $(x_I, 0)$ with $x_I \neq 0$ is a semistationary solution in the form $(u, 0)$ where $u' = -au^2$ and $u(0) = x_I$. For $u \neq 0$ this first-order equation has the separated form

$$-\frac{1}{u^2}\, \mathrm{d}u = a\, \mathrm{d}t \,.$$

This can be integrated to obtain the implicit solution

$$\frac{1}{u} = at + \frac{1}{x_I}\,.$$

This can be solved for u to find the explicit solution

$$u = \frac{x_I}{1 + a x_I t}\,.$$

Thus, system (10.13) with initial data $(x_I, 0)$ has the semistationary solution

$$\left(\frac{x_I}{1 + a x_I t}\,,\, 0 \right)$$

Therefore from (10.14) we see that for every $r \neq 0$ system (10.5) with initial data $(x_I, 0)$ has the solution

$$\left(\frac{x_I e^{rt}}{1 + a x_I \dfrac{e^{rt} - 1}{r}}\,,\, 0 \right)\,.$$

Remark. Of course, the solution of system (10.5) found in the above example could also have been found by directly seeking a semistationary solution in the form $(x, 0)$. Here we obtained it by a less direct route in order to illustrate how to use the reduction of system (10.5) to system (10.13).

Next, the point of reducing system (10.5) to system (10.13) is that the reduced system has a simpler orbit equation than the original. Specifically, the orbit equation of system (10.13) is

$$\frac{\mathrm{d}v}{\mathrm{d}u} = \frac{cu + dv}{au + bv}\,\frac{v}{u}\,,$$

which can be brought into the dilation invariant form

$$\frac{\mathrm{d}v}{\mathrm{d}u} = \frac{c + d\,\dfrac{v}{u}}{a + b\,\dfrac{v}{u}}\,\frac{v}{u}\,, \tag{10.15}$$

We saw in Section 10.2 of Part I that we can transform this equation into a separable equation by introducing the new dependent variable $w = v/u$. We thereby obtain

$$u\frac{\mathrm{d}w}{\mathrm{d}u} = \frac{c + dw}{a + bw}\,w - w = \frac{c - a + (d - b)w}{a + bw}\,w\,. \tag{10.16}$$

Exercise. Derive equation (10.16) by substituting $v = uw$ into equation (10.15).

The separable equation (10.16) has the stationary solutions

$$w = 0\,, \quad \text{and} \quad w = \frac{a - c}{d - b} \quad \text{when } (a - c)(d - b) \neq 0.$$

The stationary solution $w = 0$ leads to semistationary solutions of the original system (10.5) in the form $(x, 0)$ that were derived in the last example. When $(a - c)(d - b) \neq 0$

the stationary solution $w = \frac{a-c}{d-b}$ leads to the solutions found in the previous subsection. Specifically, setting

$$v = wu = \frac{a-c}{d-b}\,u$$

into the first equation of (10.13) yields the reduced equation

$$u' = -(au + bv)u = -(a + bw)u^2 = -\frac{ad-bc}{d-b}\,u^2\,.$$

Nonstationary solutions of the separable equation (10.16) can lead to new explicit solutions of the original system (10.5).

Exercises on Population Dynamics

(1) Answer the following questions:
   (a) Which variable will we represent as the prey and which variable will we represent as the predator in a predator-prey model?
   (b) What's the difference between a predator-prey model and a competing species model?
   (c) According to how this online text, what do a_{11} and a_{22} represent? What do a_{12} and a_{21} represent?

Solution

For 2-11, identify whether the model is a predator-prey model or a competing species model. Sketch the phase portrait.

(2) $x' = x(2-y) \qquad y' = y(-3+x)$

Solution

(3) $x' = x(3-x-y) \qquad y' = y(4-2y-\frac{3}{2}x)$

Solution

(4) $x' = x(1-2y) \qquad y' = y(-1+x)$

Solution

(5) $x' = 4x(1-x-y) \qquad y' = y(2-y-3x)$

Solution

(6) $x' = x(3-2x-y) \qquad y' = y(4-y-3x)$

Solution

(7) $x' = x(3-2x-y) \qquad y' = y(-1+2x)$

Solution

(8) $x' = x(3-x-2y) \qquad y' = y(\frac{3}{2}-2y-\frac{1}{4}x)$

Solution

(9) $x' = x(12-8x-4y) \qquad y' = y(-1+x)$

Solution

(10) $x' = x(2-x-y) \qquad y' = y(-1+2x)$

Solution

(11) $x' = x(2-2x-2y) \qquad y' = y(3-2y-2x)$

Solution

(12) Sketch the phase portrait for the following cooperating species model. How is it different from a competing species phase portrait and explain how that makes intuitive sense?

$$x' = x(4-4x+2y) \qquad y' = y(10-6y+x)$$

Solution

(13) For the following system, find the values of α and β for which there is a counterclockwise center at the critical point that is NOT the origin. (Note: $\alpha, \beta \neq 0$)

$$x' = x(\alpha - y) \qquad y' = y(x - \beta)$$

Solution

(14) For the following system of differential equations where $\alpha, \beta, \gamma, \delta > 0$:

$$\begin{aligned} \frac{\mathrm{d}x}{\mathrm{d}t} &= x(1 - \alpha x - \beta y) \\ \frac{\mathrm{d}y}{\mathrm{d}t} &= y(2 - \gamma y - \delta x) \end{aligned}$$

(a) Find ALL of the stationary points.
(b) Calculate the Jacobian, $\partial \mathbf{f}(0,0)$. (ie Only evaluate the Jacobian at the origin). What type of phase portrait is it? Where do the values on the diagonal of the evaluated Jacobian originate from (within the system of differential equations)?
(c) If $\gamma = \beta$ and $\delta = 5\alpha$, describe the behavior (just whether it's a nodal sink/source, spiral, etc.) and the eigenvalues at each of the stationary points.

Solution

Navigation to Other Chapters

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