Chapter Title: Interactions: Predator—Prey, Spraying of Pests, Carnivores in Australia

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# 9

# Interactions: Predator–Prey, Spraying of Pests, Carnivores in Australia

**Mathematics developed:**

> system of two coupled ordinary differential equations;
> equilibria; linearization about the equilibria to determine linear
> stability properties

## 9.1 Introduction

So far we have considered the equations governing the evolution of only one species. The problem becomes more interesting when there are two or more interacting species. The results are often unexpected (and counterintuitive). This is precisely the reason why having a mathematical model for the interactions is helpful.

The fish population in the upper Adriatic Sea forms an interesting ecological system. The sharks prey on the small fish, while the small fish feed on the plankton. They reach a balance with human fishing. Only small changes in populations were observed to occur from year to year prior to World War I. However, during World War I fishing was suspended, resulting, for a while, in more small fish than usual. Because of the war no observations were made. Soon thereafter, the population of sharks increased since they had more than the usual amount of food available. The increased number of sharks in turn devoured so many of the fish that when the fishermen returned after the war, they found, contrary to what they expected, that there was less than the usual catch of small fish. The growth of the small fish led to the growth of the sharks, which then led to the decline of the small fish.

The equations often used to model the above situation, and others like it—the "predator–prey" problem—are a coupled set of nonlinear ordinary differential equations. Again we study their equilibria and the stability of these equilibria.

## 9.2  The Nonlinear System and Its Linear Stability

Let $x(t)$ and $y(t)$ be the two interacting species

$$\frac{d}{dt}x = f(x, y), \tag{9.1}$$

$$\frac{d}{dt}y = g(x, y). \tag{9.2}$$

$f$ and $g$ are in general nonlinear functions of $x$ and $y$. The procedure we use to gain some information on the possible behaviors of this system is as follows:

1. Find the equilibrium solutions $x^*$ and $y^*$ of the above system by solving the simultaneous algebraic equations:

$$f(x^*, y^*) = 0 \text{ and } g(x^*, y^*) = 0. \tag{9.3}$$

2. Determine if the equilibrium is stable or unstable. This can be done easily only for small perturbations from the equilibrium. To do this, we first *linearize* the nonlinear equations about the equilibrium solution $(x^*, y^*)$. We write

$$x(t) = x^* + u(t), \tag{9.4}$$

$$y(t) = y^* + v(t), \tag{9.5}$$

$$\frac{d}{dt}x = \frac{d}{dt}(x^* + u) = \frac{d}{dt}u, \ \frac{d}{dt}y = \frac{d}{dt}v,$$

since $(x^*, y^*)$ do not depend on time (i.e., they are at equilibrium). Next we expand $f$ and $g$ about the equilibrium in a Taylor series:

$$f(x, y) = f(x^*, y^*) + \overbrace{\frac{\partial f}{\partial x}(x^*, y^*)}^{\equiv a_{11}} \cdot u + \overbrace{\frac{\partial f}{\partial y}(x^*, y^*)}^{\equiv a_{12}} \cdot v$$

$$+ \text{ terms involving } u^2, v^2, uv, u^3, v^3, \text{ etc.}$$

$$\cong a_{11}u + a_{12}v, \tag{9.6}$$

since $f(x^*, y^*) = 0$ from Eq. (9.3). The process of dropping the higher order terms (the nonlinear terms) is called *linearization*.

It is valid if we are to study only the behavior of the solution very near the equilibrium points $(x^*, y^*)$ (so that $u$ and $v$ are small in some measure, and $u^2$, $v^2$, $uv$, etc., are smaller still). Similarly

$$g(x, y) \cong a_{21}u + a_{22}v, \tag{9.7}$$

where

$$a_{21} = \frac{\partial g}{\partial x}(x^*, y^*) \text{ and } a_{22} = \frac{\partial g}{\partial y}(x^*, y^*).$$

3. We end up, after this process of linearization, with a coupled *linear* system:

$$\begin{aligned}
\frac{du}{dt} &= a_{11}u + a_{12}v, \\
\frac{dv}{dt} &= a_{21}u + a_{22}v,
\end{aligned} \tag{9.8}$$

or in matrix form:

$$\frac{d}{dt}\begin{bmatrix} u \\ v \end{bmatrix} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}\begin{bmatrix} u \\ v \end{bmatrix},$$

which is sometimes written in the following notation:

$$\frac{d}{dt}\mathbf{u} = A\mathbf{u}.$$

4. For linear equations with constant coefficients, we try exponential solutions:

$$u(t) = u_0 e^{\lambda t}, \, v(t) = v_0 e^{\lambda t}.$$

Substituting into the ordinary differential equation, we get

$$\lambda u_0 = a_{11}u_0 + a_{12}v_0,$$

$$\lambda v_0 = a_{21}u_0 + a_{22}v_0,$$

or

$$\begin{bmatrix} a_{11} - \lambda & a_{12} \\ a_{21} & a_{22} - \lambda \end{bmatrix}\begin{bmatrix} u_0 \\ v_0 \end{bmatrix} = 0.$$

To have nontrivial solutions, we must have

$$\det \begin{bmatrix} a_{11} - \lambda & a_{12} \\ a_{21} & a_{22} - \lambda \end{bmatrix} = 0. \tag{9.9}$$

Expanding out the determinant we obtain the characteristic equation

$$\lambda^2 - (a_{11} + a_{22})\lambda + (a_{11}a_{22} - a_{12}a_{21}) = 0,$$

which we rewrite as

$$\lambda^2 - p\lambda + q = 0, \tag{9.10}$$

where

$$p \equiv a_{11} + a_{22} = T_r\{A\},$$

$$q \equiv a_{11}a_{22} - a_{12}a_{21} = \det A,$$

are the trace and determinant of the matrix $A$. Solving the quadratic equation we obtain the two eigenvalues

$$\lambda_1 = \frac{p}{2} + \frac{\sqrt{p^2 - 4q}}{2}, \quad \lambda_2 = \frac{p}{2} - \frac{\sqrt{p^2 - 4q}}{2}. \tag{9.11}$$

The two parameters $p$ and $q$ determine the stability of the system under consideration. Refer to Figure 9.1 for the following cases.

a. If $q < 0$, the two eigenvalues are real, one positive and one negative. In this case, the equilibrium ($u = 0$, $v = 0$) is a *saddle point*, which is unstable. ($e^{\lambda_1 t}$ grows exponentially; $e^{\lambda_2 t}$ decays exponentially. The general solution is a linear combination of $e^{\lambda_1 t}$ and $e^{\lambda_2 t}$, and hence unstable.)

b. If $0 < q < p^2/4$, we will have two real roots of the same sign. For $p < 0$, both roots are negative and we will have a *stable node*. For $p > 0$, both roots are positive and we have an *unstable node*.

c. If $q > p^2/4$, both roots are complex and we will have oscillations. The amplitude of the oscillation will increase or decrease in $t$ depending on the sign of $p$. For $p < 0$, we have a *stable focus*. For $p > 0$, we have an *unstable focus*. Finally, if $p = 0$, we have a *center* (which is neutral: borderline stability). We will explain the meaning of these terms in a moment. The
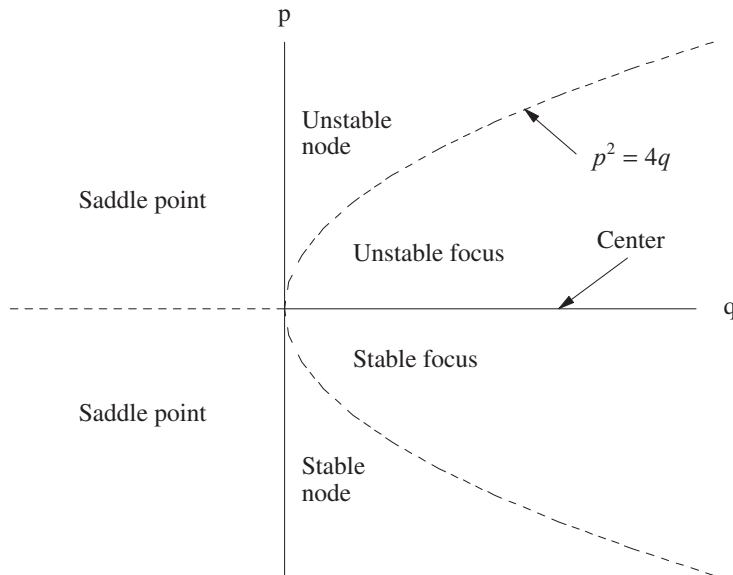
Figure 9.1. The stability of the equilibrium depends on two parameters, $p$ and $q$. (Modified from original figure in Kot [2001], by permission.)

solution to Eq. (9.8) is, in general,

$$\mathbf{u} = \mathbf{u}_0^{(1)} e^{\lambda_1 t} + \mathbf{u}_0^{(2)} e^{\lambda_2 t}. \tag{9.12}$$

$\mathbf{u}_0^{(1)}$, $\mathbf{u}_0^{(2)}$ are constant vectors. $\mathbf{u}_0^{(1)}$ is also called the *eigenvector* corresponding to the eigenvalue $\lambda_1$, etc.

The general solution (9.12) will grow in time (hence the origin $u = 0$, $v = 0$, is *unstable*) if either $\lambda_1$ or $\lambda_2$ has a positive real part. On the other hand, the origin is *stable* only if both $\lambda_1$ and $\lambda_2$ have a negative real part.

We shall use arrows to indicate the "trajectories" of the solutions as time increases.

Project any initial point $\mathbf{u}(0)$ onto $\mathbf{u}_0^{(1)}$ and $\mathbf{u}_0^{(2)}$. As time increases, the $\mathbf{u}_0^{(1)}$ part becomes $\mathbf{u}_0^{(1)} e^{\lambda_1 t}$; i.e., it contracts or expands by the factor $e^{\lambda_1 t}$. The $\mathbf{u}_0^{(2)}$ part will evolve according to $\mathbf{u}_0^{(2)} e^{\lambda_2 t}$.

## 9.3 Lotka–Volterra Predator–Prey Model

Let us now return to the problem posed in the introduction.

Fishing activity was greatly curtailed in the upper Adriatic during World War I. Umberto D'Ancona, an Italian marine biologist, showed

Figure 9.2. Vito Volterra (1840–1940).

that this period coincided with an increase in the number of sharks relative to their prey, the small fish, which eat algae. When the fishermen returned to the sea at the end of the war, they found that the fish stock had diminished severely, even though there had not been much fishing in the preceding years. At the time, Umberto was engaged to Luisa Volterra. He brought this problem to the attention of Vito Volterra, his future father-in-law and a famous mathematician (Figure 9.2).

The equations Vito wrote down to describe this situation are now known as the Lotka–Volterra equations:

$$\frac{d}{dt}x = rx - axy, \tag{9.13}$$

$$\frac{d}{dt}y = bxy - ky. \tag{9.14}$$

Here $x(t)$ denotes the population density of the prey, which are the small fish in this case. $y(t)$ is the population density of the predator, the sharks. The fish eat algae, which is abundant, and grow at a per

capita rate $\left(\frac{1}{x}\frac{d}{dt}x\right)$ of $r$. The small fish are eaten by the sharks, and so their population density decreases at a per capita rate that is proportional to $y$, the population density of the predator, with proportionality $a$. The predators, on the other hand, will die off without food. So if $x = 0$, $\frac{1}{y}\frac{d}{dt}y$ decreases at the rate $k$, which is inversely proportional to the time it takes for the predators to die of starvation. In the presence of prey, the population of the predator grows at a per capita rate of $bx$, proportional to the amount of food available.

Linear Analysis

To analyze this system, we first look for the equilibria $(x^*, y^*)$ by setting the time derivatives in Eqs. (9.13) and (9.14) to zero:

$$rx^* - ax^*y^* = 0, \quad bx^*y^* - ky^* = 0. \tag{9.15}$$

The first algebraic equation has two roots:

$$x^* = 0 \quad \text{and} \quad y^* = r/a.$$

Substituting $x^* = 0$ into the second algebraic equation, we find that we must have $y^* = 0$. Similarly, substituting $y^* = r/a$ into the second equation (or, for that matter, any nonzero value of $y^*$) implies that $x^* = k/b$. Thus we have found two equilibria. They are

$$(x_1^*, y_1^*) = (0, 0)$$

and

$$(x_2^*, y_2^*) = (k/b, r/a).$$

Each of these two pairs of values solves Eq. (9.15) simultaneously.

We now consider the stability of each of the two equilibria by perturbing them slightly by the amount $(u, v)$:

$$x(t) = x^* + u(t), \quad y(t) = y^* + v(t). \tag{9.16}$$

The perturbations satisfy Eq. (9.8) and we can solve them using the method outlined in section 9.2. Alternatively the same result can be obtained in the following more intuitive way. For $(x^*, y^*) = (x_1^*, y_1^*) = (0, 0)$, the equations governing the evolution of the perturbations

$(u, v)$ are obtainable by substituting (9.16) into Eqs. (9.13) and (9.14), yielding

$$\frac{d}{dt}u = ru - auv,$$

$$\frac{d}{dt}v = buv - kv.$$

For small perturbations, we drop the quadratic terms in favor of linear terms, giving

$$\frac{d}{dt}u \simeq ru,$$

$$\frac{d}{dt}v \simeq -kv. \tag{9.17}$$

The same two equations can also be arrived at using the formal procedure in (9.6) and (9.7) (In that notation we have $a_{11} = r$, $a_{12} = 0$, $a_{21} = 0$, and $a_{22} = -k$.) The solution to Eq. (9.17) is unstable (and we say the equilibrium $(x_1^*, y_1^*) = (0, 0)$ is an unstable saddle; check by evaluating $p$ and $q$).

It turns out that the two equations in (9.18) are decoupled and can be solved easily to yield

$$u(t) = u(0)e^{rt}, \quad v(t) = v(0)e^{-kt}.$$

A small increase from $(0, 0)$ will lead to an exponential growth in the prey (because the predators are so few in number and algae are plentiful). A small increase in predators, on the other hand, will not lead to a growth of the predator population. Instead the predators will die of starvation because there are so few fish to prey upon for food. Nevertheless, the equilibrium $(0, 0)$ is still unstable because one of the populations does not stay low when perturbed.

Near the second equilibrium, we substitute

$$x(t) = x_2^* + u(t) = k/b + u(t),$$

$$y(t) = y_2^* + v(t) = r/a + v(t),$$

into Eqs. (9.13) and (9.14) and find

$$\frac{d}{dt}u = r\left(\frac{k}{b} + u\right) - a\left(\frac{k}{b} + u\right)\left(\frac{r}{a} + v\right)$$

$$= ru - ru - a\left(\frac{k}{b}\right) \cdot v - auv$$

$$\cong -a\left(\frac{k}{b}\right)v, \tag{9.18}$$

after ignoring the quadratic term ($uv$).

Similarly,

$$\frac{d}{dt}v = b\left(\frac{k}{b} + u\right)\left(\frac{r}{a} + v\right) - k\left(\frac{r}{a} + v\right)$$

$$= b\left(\frac{r}{a}\right)u + kv + buv - kv$$

$$\cong b\left(\frac{r}{a}\right)u. \tag{9.19}$$

(You can verify that the same two equations can be obtained by using the $a_{ij}$'s. In this case $a_{11} = 0$, $a_{12} = -a(k/b)$, $a_{21} = b(r/a)$, $a_{22} = 0$. Since $p \equiv a_{11} + a_{22} = 0$, $q \equiv a_{11}a_{22} - a_{12}a_{21} = rk > 0$, the equilibrium $(x_2^*, y_2^*) = (k/b, r/a)$ is of borderline stability, and is in fact a *center*.)

Equations (9.18) and (9.19) can in fact be solved by differentiating one of the equations and substituting the second equation to eliminate one of the unknowns:

$$\frac{d^2}{dt^2}u = -a(k/b)\frac{d}{dt}v = -kru.$$

This equation, when written in the form

$$\frac{d^2}{dt^2}u + kru = 0,$$

is recognized as the equation for a harmonic oscillator. The solution is

$$u(t) = A\cos(\sqrt{kr}t) + B\sin(\sqrt{kr}t). \tag{9.20}$$

From (9.18), $v = -b/(ka)\frac{d}{dt}u$, and we have

$$v(t) = (b/a)\sqrt{r/k}[A\sin\sqrt{kr}t - B\cos\sqrt{kr}t]. \tag{9.21}$$

It is therefore seen that the solution is oscillatory and is periodic with period $2\pi/\sqrt{kr}$. It can be shown that the prey perturbation leads the predator perturbation by a quarter cycle (or, equivalently, lags behind it by three quarter cycles). (Solution (9.20) can be rewritten, without loss of generality, as

$$u(t) = C\cos(\sqrt{kr}t + \delta),$$

where $C$ and $\delta$ are arbitrary constants. Solution (9.21) can then be rewritten as

$$v(t) = (b/a)\sqrt{r/k} \cdot C\sin(\sqrt{kr}t + \delta)$$
$$= (b/a)\sqrt{r/k} \cdot C\cos(\sqrt{kr}t + \delta - \pi/2).)$$

Nonlinear Analysis

From the above analysis, we conclude that the nonlinear system, (9.13) and (9.14), does not possess any equilibria that are stable. So we don't expect that the solution to the system will approach equilibrium as a steady state. We further showed that the solution in the neighborhood of $(x^*, y^*) = (k/b, r/a)$ is periodic. The question remains as to the behavior of the solution at finite distances from this "equilibrium." We will next show that the solution remains periodic.

Figure 9.3 displays the direction field of the solution at each point $(x, y)$ of the phase plane. The slope of the direction field is obtained when one divides (9.14) by (9.13):

$$\frac{dy}{dx} = \frac{dy/dt}{dx/dt} = \frac{y(bx - k)}{x(r - ay)}. \tag{9.22}$$

At each point $(x, y)$, the slope $dy/dx$ can be found by evaluating the right-hand side and plotted as a short line. The result is plotted in Figure 9.3. The direction of the arrows in the figure indicates the direction of increase as $t$ increases. This can be inferred from (9.13) and (9.14) for any value of $(x, y)$. In particular, the arrows should point towards the right for $y < r/a$ and towards the left for $y > r/a$. They should point up for $x > k/b$ and down for $x < k/b$. Figure 9.3 shows that the nonlinear solution cycles around the point $(x_2^*, y_2^*)$. A cyclic solution, as indicated by closed loops in the phase plane, is a periodic solution.
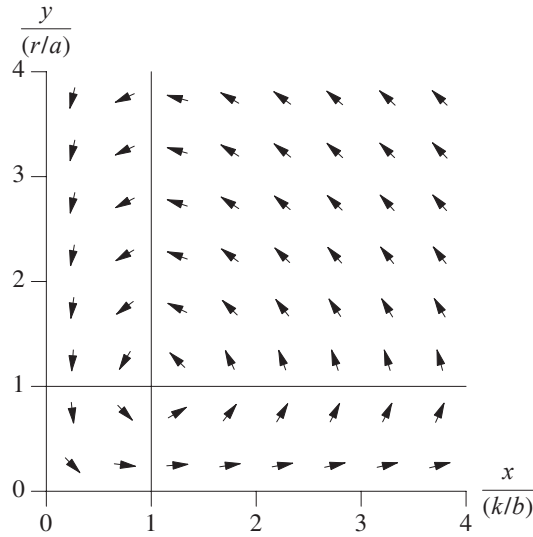
Figure 9.3. The direction field of Lotka–Volterra equations. (Modified from original figure in Kot [2001], by permission.)

Since the solution is periodic, one can define

$$x_{\text{average}} = \frac{1}{T} \int_{t_0}^{t_0+T} x(t)\, dt,$$

$$y_{\text{average}} = \frac{1}{T} \int_{t_0}^{t_0+T} y(t)\, dt,$$

as the value averaged over a period, where $T$ is the period of the oscillation, and $t_0$ is any time. Volterra showed that these averaged values can be found exactly by integrating the original equations (9.13) and (9.14): from (9.13) one has

$$\frac{1}{x}\frac{d}{dt}x = r - ay.$$

Integrating both sides with respect to $t$ yields, for the left-hand side:

$$\int_{t_0}^{t_0+T} \frac{1}{x}\frac{dx}{dt}\, dt = \ln\left[\frac{x(t_0 + T)}{x(t_0)}\right] = \ln\left[\frac{x(t_0)}{x(t_0)}\right] = 0,$$

and for the right-hand side:

$$\int_{t_0}^{t_0+T} (r - ay)dt = rT - aTy_{\text{average}}.$$

Thus, we have

$$0 = rT - aTy_{\text{average}},$$

yielding

$$\boxed{y_{\text{average}} = r/a.} \tag{9.23a}$$

A similar consideration for (9.14) will yield

$$\boxed{x_{\text{average}} = k/b.} \tag{9.23b}$$

Note that these are the same as the "equilibrium" $(x_2^*, y_2^*)$, about which the solution is cycling.

Some rather counterintuitive results now follow. If the growth rate $r$ of the prey is somehow increased, we don't get a corresponding increase in the average prey population (because $x_{\text{average}}$ is independent of $r$). Instead, the predator population increases. If the death rate of the predator is increased, the prey's average population is increased, while the average population of the predator is unaffected.

## 9.4  Harvesting of Predator and Prey

Let us now return to modeling the problem that concerned D'Ancona originally, and add a harvesting term to both the prey and predator equations (i.e., the harvesting is indiscriminate with respect to fish and shark):

$$\frac{dx}{dt} = rx - axy - qEx,$$

$$\frac{dy}{dt} = bxy - ky - qEy.$$

These can be rewritten as

$$\frac{dx}{dt} = (r - qE)x - axy, \tag{9.24}$$

$$\frac{dy}{dt} = bxy - (k + qE)y. \tag{9.25}$$

Equation (9.24) is the same as (9.13) (without harvesting), except with the prey growth rate $r$ reduced to $r - qE$. Equation (9.25) is the same as (9.14) except with the predator death rate $k$ increased to $k + qE$. The average prey and predator population densities then become, by modifying (9.23):

$$x_{\text{average}} = (k + qE)/b, \tag{9.26}$$

$$y_{\text{average}} = (r - qE)/a. \tag{9.27}$$

During the war, when the fishing effort ($E$) is reduced, it actually increases the average shark population while reducing the average fish population, as (9.26) and (9.27) show.

What happens after the war, when fishing is increased?

Indiscriminate Spraying of Insects

The cottony cushion scale insect (*Icerya purchasi*) was accidentally introduced into America in 1868 from Australia and threatened to destroy the American citrus industry. To control this insect, its natural Australian predator, a ladybird beetle (*Novius cardinalis*), was introduced, and the beetles reduced the scale insects to a low level. When DDT was discovered and found to kill the scale insects, it was applied by the orchardists in the hope of further reducing the scale insects. The spraying of DDT killed insects and beetles indiscriminately at the same per capita rate. Discuss the effect of spraying. Is it beneficial to the citrus industry?

## 9.5 The Case of the Missing Large Mammalian Carnivores

Meganesia, which comprises Australia, Tasmania, and New Guinea, is unusual in its extraordinary lack of large mammalian carnivores throughout its history. One possible cause may be the notoriously infertile soil of this old continent with a stable geological history. It takes an area of grassland with billions of individual grasses to sustain a few thousand large herbivores. These, in turn, may be able to support fewer than one hundred large carnivores. If the environment is poor,

large herbivores will be rare and thinly spread. The density of the prey is so low that a population of large mammalian meat-eaters cannot be sustained. Cold-blooded reptiles, on the other hand, eat far less than mammals do, having no need to create inner body heat. This scenario may explain what happened in Meganesia, home to a remarkable array of carnivorous reptiles (Flannery, 1993).

Consider the predator–prey equations:

$$\frac{dx}{dt} = rx(1 - x/K) - axy, \tag{9.28}$$

$$\frac{dy}{dt} = -ky + bxy, \tag{9.29}$$

where $y$ is the population of meat-eating predator. If the prey $x$ are the herbivores, whose population growth follows the logistic equation (resource limited), with $K$ being the carrying capacity of the herbivores that the vegetation can support in the absence of the predator. The parameter $k/b$ measures how efficiently the predator utilizes food to make babies. The more efficient predators, such as large reptilian carnivores, have smaller values of $k/b$.

    a. When the vegetation is poor, the carrying capacity $K$ for the herbivore prey is low. If the predator is a large mammalian carnivore with high $k/b$, specifically,

$$K < k/b,$$

show that the predator will become extinct. (Find the equilibria and determine their stability.)

    b. Replace the predator by large reptilian carnivores with

$$k/b < K.$$

Show that there exists a stable equilibrium with a positive predator population.

**Solution**

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

$$f(x, y) = x[r(1 - x/K) - ay],$$

$$g(x, y) = y[-k + bx].$$

The equilibria are given by either

$$\text{(i) } x^* = 0, \ y^* = 0,$$

$$\text{(ii) } x^* = K, \ y^* = 0, \ \text{or}$$

$$\text{(iii) } x^* = k/b, \ y^* = (r/a)(1 - k/(bK)).$$

   a. For the case of large mammalian predators,

$$k/(bK) > 1,$$

(iii) is not feasible because it would have required a negative predator population. Of the remaining two equilibria, (i) is unstable and (ii) is stable. Thus the only stable long-term solution is a population of herbivores at its carrying capacity, $K$, with no predator population ($y^* = 0$). This population of herbivores is unable to sustain any large carnivores.

   b. For the case of reptilian predators,

$$k/(bK) < 1,$$

(iii) is a possibility (with $y^* > 0$). For this case (ii) becomes unstable and (iii) is stable. Thus it is possible for predator and prey to coexist.

*Stability analysis*

For both cases (a) and (b), the equations linearized about (i) are

$$\frac{du}{dt} = ru, \quad \frac{dv}{dt} = -kv,$$

where

$$u = x - x^*, \ v = y - y^*, \quad \text{with } x^* = 0, \ y^* = 0.$$

Thus (i) is an unstable saddle because $u(t) = u(0)e^{rt}$ and grows exponentially, although $v(t) = v(0)e^{-kt}$ decays.

For case (a), the linearized equations about (ii) are

$$\frac{du}{dt} = -ru - aKv, \quad \frac{dv}{dt} = -(k - bK)v,$$

where $u = x - x^*, v = y - y^*$, with $x^* = K, y^* = 0$. So

$$v(t) = v(0)e^{-(k-bK)t} \ \text{decays because} \ k - bK > 0,$$

and

$$u(t) = -\frac{aK v(0)}{(r - k + bK)}e^{-(k-bK)t} - Ce^{-rt}$$

also decays for $k - bK > 0$. Thus the equilibrium (ii) is stable for case (a).

For case (b), $k - bK < 0$, $u(t)$, and $v(t)$ grow exponentially, and so (ii) is unstable.

The stability of (iii) is to be determined by linearizing the equations about (iii):

$$\frac{du}{dt} = -\frac{kr}{bK}u - \frac{ka}{b}v, \quad \frac{dv}{dt} = (r/a)(1 - k/bK) \cdot bu.$$

Combining, we get

$$\frac{d^2u}{dt^2} + \frac{kr}{bK}\frac{du}{dt} + kr(1 - k/bK)u = 0.$$

Assume an exponential solution

$$u(t) = u(0)e^{\lambda t}$$

yields

$$\lambda^2 + \frac{kr}{bK}\lambda + kr(1 - k/bK) = 0;$$

then

$$\lambda = -\frac{kr}{2bK} \pm \left\{\frac{1}{4}\left(\frac{kr}{bK}\right)^2 - kr(1 - k/bK)\right\}^{1/2}.$$

Since the real part of $\lambda$ is always negative, the equilibirum (iii) is stable for case (b).

## 9.6 Comment

The mathematical model appears to have confirmed the conjecture by Flannery (1993) and neatly explained why Australia lacks large meat-eating mammals. However, reality might not be as tidy.

Figure 9.4.  Skeleton of *Thylacoleo carnifex*.

Flannery mentioned that there were approximately 60 species of mammals that weighed more than 20 lbs. before the arrival of humans in Australia some 50,000 years ago, but he thought all except three were herbivores and there were no large meat-eaters among them.

The Tasmanian devil, weighing less than 20 lbs., is best described as a miniature marsupial hyena. The spotted-tail quall is the marsupial version of the weasel. Both still survive. When the extinct marsupial lion (*Thylacoleo carnifex*) was first described from fossils in the 1850s, it was thought to have been among the "fellest and most destructive of predatory beasts," the ecological equivalent of a lion. Since then its size has been revised steadily downward. Flannery thought it was the marsupial equivalent of a medium-sized cat on other continents. Using the only known complete skeleton of *Thylacoleo carnifex* (Figure 9.4), a specimen from Moree, a team of paleontologists headed by Stephen Wroe from the University of New South Wales just recently revised its weight dramatically upward, to as much as 164 kg, with an average of between 100 kg and 130 kg. "That would be a good-size female lion or tiger," Wroe said. "It has been suggested that big mammalian predators could not exist in Australia because there wasn't enough food for them," he explained. "But these new measurements show that *Thylacoleo* was

a big kick-arse carnivore by any standard, blowing the old theory right out of the water" (*News in Science*, April 6, 1999).

## 9.7  More Examples of Interactions

**Example 1.** *Romantic Romeo, Fickle Juliet* (Strogatz, 1988)
*R*: Romeo's love for Juliet.

$$\frac{dR}{dt} = aJ, \ \ a > 0:$$

Romeo's love grows in response to Juliet's love.
*J*: Juliet's love for Romeo.

$$\frac{dJ}{dt} = -bR, \ \ b > 0:$$

Juliet's love decreases in response to Romeo's love for her. Can they be simultaneously in love with each other?

This system of linear equations has only one equilibrium, at the origin ($R = 0, J = 0$). The stability of this equilibrium can be determined by the eigenvalue method outlined earlier. However, since this system is linear, we can actually obtain an exact solution, not just information about the stability of the point ($R = 0, J = 0$). We divide the two equations:

$$\frac{dR}{dJ} = \frac{dR/dt}{dJ/dt} = \frac{aJ}{-bR},$$

$$bR\,dR + aJ\,dJ = 0,$$

$$bR^2(t) + aJ^2(t) = \text{ constant}, \quad C = bR(0)^2 + aJ^2(0).$$

The orbits are ellipses in the *R*–*J* plane. Romeo and Juliet can be simultaneously in love with each other only one quarter of the time.

The detailed time evolution of the solution can also be found:

$$\frac{d^2R}{dt^2} = \frac{d}{dt}\frac{d}{dt}R = \frac{d}{dt}(aJ) = a\frac{dJ}{dt} = a(-bR),$$
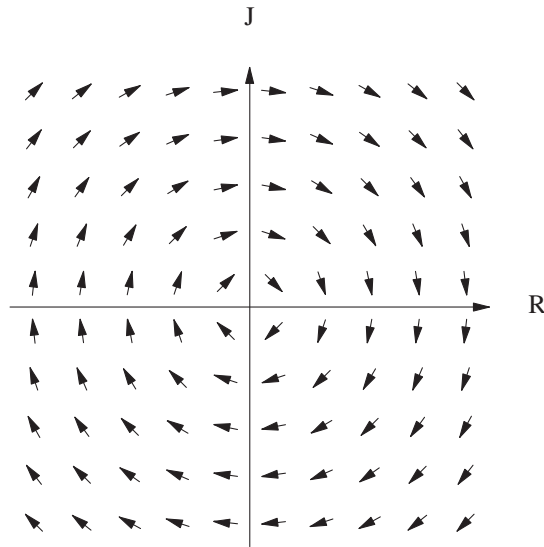
so

$$\frac{d^2R}{dt^2} + abR = 0.$$

Figure 9.5. The direction field of the Romeo–Juliet system.

If we try an exponential solution of the form

$$R(t) = ce^{\lambda t},$$

we will find that $\lambda^2 = -ab$. So $\lambda_1 = \sqrt{ab}i$, $\lambda_2 = -\sqrt{ab}i$.

The general solution is

$$R(t) = c_1 e^{i\sqrt{ab}t} + c_2 e^{-i\sqrt{ab}t},$$

$$\left( J = \frac{dR}{dt} / a = \frac{i\sqrt{ab}}{a} c_1 e^{i\sqrt{ab}t} - \frac{i\sqrt{ab}}{a} c_2 e^{-i\sqrt{ab}t} \right).$$

Alternatively, since $e^{i\theta} = \cos\theta + i\sin\theta$ (Euler's formula), we can rewrite the solution as

$$R(t) = c_3 \cos(\sqrt{ab}t) + c_4 \sin(\sqrt{ab}t),$$

where the $c$'s are arbitrary constants:

$$J = -\sqrt{\frac{b}{a}} c_3 \sin(\sqrt{ab}t) + \sqrt{\frac{b}{a}} c_4 \cos(\sqrt{ab}t).$$

To see the phase relationship between $R$ and $J$, consider the initial special condition $R(0) = 0$. Then $c_3 = 0$. In this case

$$R(t) = c_4 \sin(\sqrt{ab}t),$$

$$J(t) = \sqrt{\frac{b}{a}}c_4 \cos(\sqrt{ab}t) = \sqrt{\frac{b}{a}}c_4 \sin\left(\sqrt{ab}t + \frac{\pi}{2}\right)$$

$$= \sqrt{\frac{b}{a}}R\left(t + \frac{\pi}{2}/\sqrt{ab}\right).$$

Juliet's feeling lags Romeo's by a quarter cycle. (See Figure 9.5.)

**Example 2.** *The CONCOM Model*
*The CONCOM Model*, the conventional combat model, is one special type of Lanchester Models for Combat or Attrition (Lanchester, 1914).

In a Lanchester model, an $x$-force and a $y$-force are engaged in a battle of attrition. The variables $x(t)$ and $y(t)$ denote the strength of the forces at time $t$. A Lanchester model assumes that, for force $x$:

$$\frac{dx}{dt} = -(OLR + CLR) + RR,$$

where $OLR$ is the operational loss rate, the loss rate due to diseases, desertions, and other noncombat mishaps. $CLR$ is the combat loss rate, and $RR$ is the reinforcement rate. A similar equation applies to $y$. The CONCOM model is

$$\frac{dx}{dt} = -ax - by + P(t),$$

$$\frac{dy}{dt} = -cx - dy + Q(t).$$

The operational loss rates are assumed to be proportional to the number of one's own troops. The combat loss rate is modeled differently depending on the type of warfare being conducted. For conventional warfare, every member of a conventional force is within range of the enemy and that conventional force $x$ has a loss rate $by$; that is, proportional to the enemy strength but independent of $x$, its own number. $x$'s loss rate is the same whether $x = 10,000$ or $1,000$. The limiting factor is how many shots $y$ can fire per minute (think U.S. Civil War).

$P(t)$ is the rate of reinforcement for $x$.

(The situation is different for ancient warfare, where $CLR$ for $x$ should be proportional to the amount of $x$-force in one-on-one combat with $y$.

For this case, one should model the per capita loss rate $(-\frac{1}{x}\frac{d}{dt}x)$ due to combat loss as $by$, so $CLR = bxy$. The same reasoning should apply to the loss rate of fish eaten by sharks. It is similar to that of one-on-one combat. So one should model the per capita loss rate of the fish as proportional to the number of sharks.)

A simplified CONCOM model is one without operational loss and replacement:

$$\frac{dx}{dt} = -by,$$

$$\frac{dy}{dt} = -cx.$$

The attrition rate of each belligerent is proportional to the size of the adversary. As before, we divide the two equations:

$$\frac{dy}{dx} = \frac{dy/dt}{dx/dt} = \frac{cx}{by},$$

$$bydy = cxdx.$$

Integrating,

$$b[y(t)^2 - y_0^2] = c[x(t)^2 - x_0^2].$$

Another way of expressing the solution is as

$$by(t)^2 - cx(t)^2 = by_0^2 - cx_0^2 \equiv K \text{ a constant.}$$

The orbits are hyperbolas in the $x$–$y$ plane. See Figure 9.6. We consider that $x$ wins the war of attrition if $y$ vanishes first. Thus $x$ wins if $K < 0$ and $y$ wins if $K > 0$. A stalemate occurs if $K = 0$, which is

$$by_0^2 = cx_0^2$$

or

$$y_0 = \sqrt{\frac{c}{b}}x_0, \quad \frac{c}{b} = \left(\frac{y_0}{x_0}\right)^2.$$

It says that to stalemate an adversary three times as numerous, it does not suffice to be three times as effective; you must be nine times as effective! This is referred to as the square law.
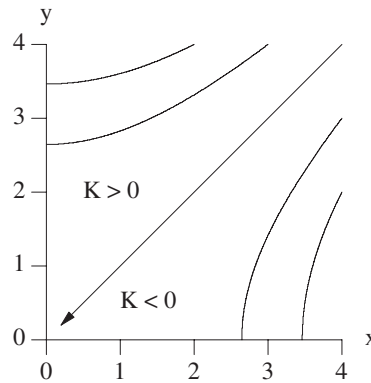
Figure 9.6. The square law of the CONCOM combat model.

## 9.8 Exercises

### 1. *Arms races*

Let $x(t)$ and $y(t)$ be the "war potential" of nations A and B. We can measure the potential in terms of the level of armaments of each country. The following system of equations models $x(t)$ and $y(t)$:

$$\frac{dx}{dt} = r(x_0 - x) + ay,$$

$$\frac{dy}{dt} = r(y_0 - y) + bx,$$

where $r = 1/(5 \text{ years})$ gives the rate at which a country is capable of change and is measured by the lifetime of a parliament. $a$ and $b$ measure how quickly a nation can arm itself in response to external threats. $a = b = 1/(1 \text{ years})$.

a. In the absence of foreign threats ($a = 0, b = 0$), each nation has an underlying equilibrium war potential. Find that equilibrium and determine its stability.

b. In the presence of interactions between the two nations, there is a buildup of war potential in response to the enemy's armament. Find the new equilibrium and determine the condition for stability (peace). The condition should be in terms of $r$, $a$, and $b$.

c. For the European arms race of 1909–1914, France was allied with Russia (A), and Germany with Austria-Hungary (B). Would the arms

race lead to war? Use the numerical values given earlier for $r$, $a$, and $b$.

## 2. *Romeo and Juliet*

Let $R(t)$ be the love of Romeo for Juliet and let $J(t)$ be the love of Juliet for Romeo. (Let's not worry about how we measure "love".) Romeo's love for Juliet grows in response to Juliet's love (with rate $b$) for him and vice versa. The lovers, however, are rather cautious; they tried to rein in their love for each other (with rate $a$). Thus the governing equations are

$$\frac{d}{dt}R = -aR + bJ,$$

$$\frac{d}{dt}J = -aJ + bR.$$

Discuss what happens to their love if their caution $a$ is larger than their responsiveness $b$, and if $a$ is smaller than $b$. You can either use the method of equilibrium and its stability to support your conclusion, or you can solve these linear equations exactly.

## 3. *Guerilla combat (GUERCOM)*

Two guerilla forces, with troop strengths $x(t)$ and $y(t)$, are in combat with each other without reinforcement. Suppose the territory is rather large and full of places to hide. The $y$-force needs to find the $x$-force first before it can inflict combat losses, and the higher the $x$, the easier it is for them to be found. Therefore, the combat loss rate for the $x$-force should be proportional $x \cdot y$. (This is unlike conventional warfare, where the full force of $x$ is open to be shot at by $y$, and so the combat loss rate for $x$ shouldn't depend on the total number of the $x$-force.) Thus

$$\frac{dx}{dt} = -axy,$$

$$\frac{dy}{dt} = -bxy,$$

where $a$ is the combat effectiveness of the $y$-force and $b$ is that of the $x$-force. Suppose initially that $x_0$, $y_0$ are the troop strengths for the $x$- and $y$-forces, and that $x_0$ is three times as numerous as $y_0$. How much more effective must the $y$-force be to stalemate its enemy?

### 4. Guerilla–conventional combat (VIETNAM)

In Vietnam, a conventional force (the United States) opposed a guerilla force (the Vietcong). This conventional force $y(t)$ is out in the open to be shot at; its combat loss rate is limited only by the number of the $x$-force that can shoot. So the model for VIETNAM is

$$\frac{dx}{dt} = -axy,$$

$$\frac{dy}{dt} = -bx.$$

The combat effectiveness of $y$ against $x$ can be measured by the constant $a$ in $x$'s combat loss rate. $a$ is proportional to the ratio between the exposed area of the body of a single guerilla combatant, $A_g$ ($\sim 2$ sq. ft.), and the area $A_x$ occupied by the guerilla force. So

$$a = c_1 \frac{A_g}{A_x}.$$

If each guerilla combatant ranges over 1,000 sq. ft. and the force is spread out, then $A_x = (1{,}000 \text{ sq. ft.}) \times x_0$. The constant $b$, which measures the combat effectiveness of the $x$-force against the conventional $y$-force, is

$$b = c_2 p_x,$$

where $p_x \cong 0.1$ is the probability that a shot by a guerilla kills an opponent. $c_1$ and $c_2$ are firing rates, and we assume that they are comparable (i.e., $c_1 \sim c_2$).

a. Derive the condition for stalemate (parabolic law).

b. Estimate the ratio of the initial forces, $y_0/x_0$, for the $y$-force to prevail.

In Vietnam, the U.S. force never exceeded its opponent by a ratio of 6. Could the United States have prevailed?

### 5. Extinction of Neanderthals

Neanderthals were the original inhabitants of Europe and their species was very stable for more than 60,000 years. Forty thousand years ago the Neanderthals were replaced by our ancestors, the early humans (Cro-Magnon), who came to Europe from Africa much later. There is evidence that the two species coexisted in some parts of Europe. The mass extinction of the Neanderthals was rapid, in 5,000 to 10,000 years.

Theories for the demise of the Neanderthals include genocide by the early humans and competition for resources with the humans. We shall investigate the latter possibility.

Let $N(t)$ be the total population of humanoids, which consists of a population of Neanderthals, $x(t)$, and early men, $y(t)$:

$$N(t) = x(t) + y(t).$$

Suppose that they lived in the same resource-limited environment and therefore the total population satisfies the logistic equation:

$$\frac{dN}{dt} = r N(1 - N/K) - \beta N, \tag{9.30}$$

where $K$ is the total carrying capacity for all the humanoids combined, and $\beta$ is their mortality rate. (We could have included $\beta$ in the definition of $r$ (and $K$), but we chose not to do so for convenience.) We assume $r > \beta > 0$ because the net growth rate should be positive for small population densities.

a. Suppose there is no difference in their survival skills. Write down two coupled equations for $x(t)$ and $y(t)$ ... the form

$$\frac{1}{x}\frac{d}{dt}x = F(x, y) - \beta, \tag{9.31}$$

$$\frac{1}{y}\frac{d}{dt}y = F(x, y) - \beta, \tag{9.32}$$

where $F(x, y)$ is the same for $x$ and for $y$. What is $F(x, y)$? You should be guided by the requirement that the sum of (9.31) and (9.32) should give you (9.30), and that if you switch $x$ and $y$ in (9.31) you will get (9.32).

b. Suppose the early humans are slightly better adapted to survival than Neanderthals, but the difference is tiny. Replace the human equation (9.32) by

$$\frac{1}{y}\frac{d}{dt}y = F(x, y) - (1 - \epsilon)\beta, \tag{9.33}$$

where $0 < \epsilon \ll 1$ is the mortality difference. The Neanderthal equation remains as (9.31). Find the equilibria of (9.31) and (9.33).

    c. Determine the stability of the equilibria.

    d. Discuss the implications of the results on equilibria and their stability. Is the extinction of the Neanderthals inevitable?

    e. By forming an equation for

$$\frac{d}{dt}(x/y) = \frac{1}{y}\frac{dx}{dt} - \left(\frac{x}{y}\right)\frac{1}{y}\frac{d}{dt}y = \cdots,$$

show that $x(t)/y(t) = A_0 e^{-\epsilon \beta t}$. Suppose we measure $\beta$ by the reciprocal of the lifetime of an individual, 30 years. We know from paleontological data that it took 5,000 to 10,000 years (take it to be 10,000 years) for the Neanderthals to become extinct. Take this as the time for $x/y$ to decrease by a factor $e$. Estimate the mortality difference.

6. **Open-access fishery**

    In an open-access fishery, fishermen are free to come and go as they please. The fishing effort $E$ is determined by the opportunity to make a profit. Let $c$ be the cost of operation, and $p$ the price the fishermen get for their catch $H$. Profit is given by

$$P = pH - cE,$$

where

$$H = qEN$$

is the harvest rate, which is proportional to the amount of fish $N$ there are in the fishery and the effort $E$ expended to catch them. When there is profit to be made, the fishermen would increase their effort in the hope of making even more profit. Thus

$$\frac{d}{dt}E = aP(t), \tag{9.34}$$

where $a$ is a proportionality constant.

    The equation governing the fish population is

$$\frac{d}{dt}N = rN\left(1 - \frac{N}{K}\right) - H. \tag{9.35}$$

Determine the equilibria $(N^*, E^*)$ and their stability of the coupled system (9.34) and (9.35). (Note that the only two unknowns are $N(t)$ and $E(t)$.) Assume $c/(pqK) < 1$.

### 7. *Epidemiology, SIR model*

A small group of infected individuals is introduced into a large (fixed) population *N*, who are susceptible to this contagious disease (e.g., smallpox). The number of infected, $I(t)$, increases at a rate $\frac{dI}{dt}$ that is proportional to the product of the number of infected and the number of susceptibles $S(t)$. Some of the infected recover from the disease, and this confers immunity, while some die from the disease and are therefore no longer infectious. We count both of these as $R(t)$: the recovered, who are immune, and the dead, who can no longer transmit the disease. Write down the three coupled differential equations for $\frac{dI}{dt}$, $\frac{dS}{dt}$, and $\frac{dR}{dt}$.

There should only be two independent proportionality constants you can use in modeling this situation.

### 8.

For the SIR model in exercise 7, draw the direction field with arrows indicating the direction of increase with time, in a plot of $I(t)$ vs. $S(t)$. Discuss what happens in time to the introduction of some infected individuals to a large population of susceptibles, and infer the condition under which an epidemic would develop.

### 9. *Two-sex models*

A process of modeling is to critically reexamine any model you have come up with, discover its deficiencies, and continually improve it.

It is obvious that the common Malthusian model on population growth is deficient:

$$\frac{dN}{dt} = BN - DN, \tag{9.36}$$

where $N(t)$ is the population density, *B* the per capita birthrate, and *D* the per capita death rate. It is deficient because it seems to imply that it is not only females that bear offspring.

A simple modification would have been:

$$\frac{dN}{dt} = Bf - DN, \tag{9.37}$$

in recognition of the fact that only the females can give birth. We can then develop a two-sex model for the male population ($m(t)$) and the female population ($f(t)$), which comprise the total population ($N(t) = m(t) + f(t)$). That model, however, also has a deficiency. The model (9.37) has the problem that there are births even if there are no males in

the population! Obviously, (9.37) is appropriate only if the females are the limiting species (i.e., $f \ll m$). If the males are the limiting species ($m \ll f$), the births should be proportional to $m$:

$$\frac{dN}{dt} = Bm - DN. \tag{9.38}$$

It is desirable to have a model that works for any $m$, $f$ densities and reduces to (9.37) if $f \ll m$ and to (9.38) if $m \ll f$. One such model is

$$\frac{dN}{dt} = B\frac{mf}{m+f} - DN. \tag{9.39}$$

This model is symmetric with respect to the two sexes.

If $m \ll f$, (9.39) reduces to (9.38). If $f \ll m$, (9.39) reduces to (9.37). Since there are two unknowns, we need to split (9.39) up into two equations:

$$\frac{df}{dt} = B_f\frac{mf}{m+f} - D_f f,$$
$$\frac{dm}{dt} = B_m\frac{mf}{m+f} - D_m m, \tag{9.40}$$

where $D_f$ is the female per capita death rate and $D_m$ is the male per capita death rate; $B_f$ is proportional to the female birthrate and $B_m$ is proportional to the male birthrate. The birth ratio, $r \equiv \frac{\text{male births}}{\text{female births}}$, is given by

$$r = \frac{B_m\frac{mf}{m+f}}{B_f\frac{mf}{m+f}} = \frac{B_m}{B_f}.$$

This quantity is assumed constant in this model.

Use (9.40) to answer the following questions:

a. Try to find the nontrivial equilibrium male and female populations ($m^*$, $f^*$). It turns out that in general there is no nontrivial equilibrium unless certain conditions involving the parameters are met. Find that condition.

b. Even if $m^*$ and $f^*$ cannot reach equilibrium individually (if the condition in (a) is not satisfied), there is a well-defined equilibrium for the sex ratio. Calculate the equilibrium sex ratio $(m/f)^*$. Assume that the death rates, $D_m$ and $D_f$, are the same.

c. For $D_f = D_m = D$, show that

$$\left[\frac{1}{B_f} f(t) - \frac{1}{B_m} m(t)\right] = \left[\frac{1}{B_f} f(0) - \frac{1}{B_m} m(0)\right] e^{-Dt}.$$

d. From (c) it is seen that after a few generations (with a generation defined by $D\Delta t \sim 1$), we practically have

$$m(t) \cong (B_m/B_f) f(t).$$

Substitute this into the female equation in (9.40) and solve for $f(t)$.

**10.** Another two-sex model that has been proposed is

$$\frac{df}{dt} = Bmf - Df,$$

$$\frac{dm}{dt} = Bmf - Dm. \tag{9.41}$$

This model, however, is problematic because it blows up in finite time.

a. Show, again, that the sex difference ($f(t) - m(t)$) becomes small in one or two generations.

b. So after a couple of generations, we can replace $m(t)$ by $f(t)$ approximately in the female equation in (9.41). This leads to

$$\frac{df}{dt} = -Df\left(1 - \frac{B}{D} f\right). \tag{9.42}$$

Show that for some $t_0$, if $f(t_0) < D/B$, the population will become extinct for $t$ much larger than $t_0$.

c. Show that if $f(t_0) > D/B$, the solution will blow up in finite ($t - t_0$). (Use separation of variables to solve (9.42).)

**11.** *Volterra equations*

Solve the Volterra equations in the form of (9.22):

$$\frac{dy}{dx} = \frac{y(bx - k)}{x(r - ay)},$$

subject to the condition that $y = y_0$ when $x = x_0$ (i.e., the trajectory at some time passes through the point $(x_0, y_0)$). Show that the solution (in the form of a relation between $x$, $y$, $x_0$, and $y_0$) implies that the trajectories $x = x(t)$, $y = y(t)$ are periodic if they do not pass through the equilibrium points. (*Hint*: Show that $y = y(t)$ is a simple closed curve.)