

Mathematical Biology

Lecture notes for MATH 4333
(formerly MATH 365)

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Chapter 1

Population Dynamics

Populations grow in size when the birth rate exceeds the death rate. Thomas Malthus, in *An Essay on the Principle of Population* (1798), used unchecked population growth to famously predict a global famine unless governments regulated family size—an idea later echoed by Mainland China’s one-child policy. The reading of Malthus is said by Charles Darwin in his autobiography to have inspired his discovery of what is now the cornerstone of modern biology: the principle of evolution by natural selection.

The Malthusian growth model is the granddaddy of all population models, and we begin this chapter with a simple derivation of the famous exponential growth law. Unchecked exponential growth obviously does not occur in nature, and population growth rates may be regulated by limited food or other environmental resources, and by competition among individuals within a species or across species. We will develop models for three types of regulation. The first model is the well-known logistic equation, a model that will also make an appearance in subsequent chapters. The second model is an extension of the logistic model to species competition. And the third model is the famous Lotka-Volterra predator-prey equations. Because all these mathematical models are nonlinear differential equations, mathematical methods to analyze such equations will be developed.

1.1 The Malthusian growth model

Let $N(t)$ be the number of individuals in a population at time t , and let b and d be the average per capita birth rate and death rate, respectively. In a short time Δt , the number of births in the population is $b\Delta tN$, and the number of deaths is $d\Delta tN$. An equation for N at time $t + \Delta t$ is then determined to be

$$N(t + \Delta t) = N(t) + b\Delta tN(t) - d\Delta tN(t),$$

which can be rearranged to

$$\frac{N(t + \Delta t) - N(t)}{\Delta t} = (b - d)N(t);$$

and as $\Delta t \rightarrow 0$,

$$\frac{dN}{dt} = (b - d)N.$$

With an initial population size of N_0 , and with $r = b - d$ positive, the solution for $N = N(t)$ grows exponentially:

$$N(t) = N_0 e^{rt}.$$

With population size replaced by the amount of money in a bank, the exponential growth law also describes the growth of an account under continuous compounding with interest rate r .

1.2 The Logistic equation

The exponential growth law for population size is unrealistic over long times. Eventually, growth will be checked by the over-consumption of resources. We assume that the environment has an intrinsic carrying capacity K , and populations larger than this size experience heightened death rates.

To model population growth with an environmental carrying capacity K , we look for a nonlinear equation of the form

$$\frac{dN}{dt} = rNF(N),$$

where $F(N)$ provides a model for environmental regulation. This function should satisfy $F(0) = 1$ (the population grows exponentially with growth rate r when N is small), $F(K) = 0$ (the population stops growing at the carrying capacity), and $F(N) < 0$ when $N > K$ (the population decays when it is larger than the carrying capacity). The simplest function $F(N)$ satisfying these conditions is linear and given by $F(N) = 1 - N/K$. The resulting model is the well-known logistic equation,

$$\frac{dN}{dt} = rN(1 - N/K), \quad (1.1)$$

an important model for many processes besides bounded population growth.

Although (1.1) is a nonlinear equation, an analytical solution can be found by separating the variables. Before we embark on this algebra, we first illustrate some basic concepts used in analyzing nonlinear differential equations.

Fixed points, also called equilibria, of a differential equation such as (1.1) are defined as the values of N where $dN/dt = 0$. Here, we see that the fixed points of (1.1) are $N = 0$ and $N = K$. If the initial value of N is at one of these fixed points, then N will remain fixed there for all time. Fixed points, however, can be stable or unstable. A fixed point is stable if a small perturbation from the fixed point decays to zero so that the solution returns to the fixed point. Likewise, a fixed point is unstable if a small perturbation grows exponentially so that the solution moves away from the fixed point. Calculation of stability by means of small perturbations is called *linear stability analysis*. For example, consider the general one-dimensional differential equation (using the notation $\dot{x} = dx/dt$)

$$\dot{x} = f(x), \quad (1.2)$$

with x_* a fixed point of the equation, that is $f(x_*) = 0$. To determine analytically if x_* is a stable or unstable fixed point, we perturb the solution. Let us write our solution $x = x(t)$ in the form

$$x(t) = x_* + \epsilon(t), \quad (1.3)$$

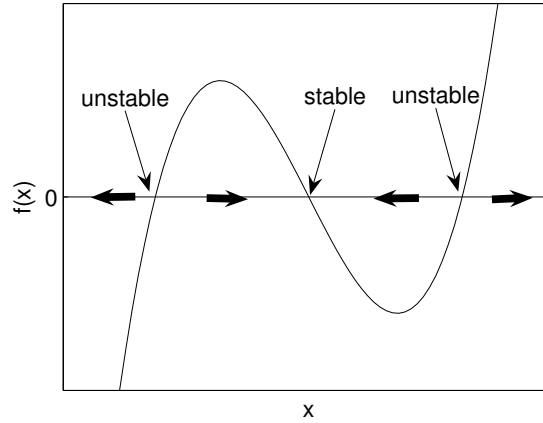


Figure 1.1: *Determining one-dimensional stability using a graphical approach.*

where initially $\epsilon(0)$ is small but different from zero. Substituting (1.3) into (1.2), we obtain

$$\begin{aligned}\dot{\epsilon} &= f(x_* + \epsilon) \\ &= f(x_*) + \epsilon f'(x_*) + \dots \\ &= \epsilon f'(x_*) + \dots,\end{aligned}$$

where the second equality uses a Taylor series expansion of $f(x)$ about x_* and the third equality uses $f(x_*) = 0$. If $f'(x_*) \neq 0$, we can neglect higher-order terms in ϵ for small times, and integrating we have

$$\epsilon(t) = \epsilon(0)e^{f'(x_*)t}.$$

The perturbation $\epsilon(t)$ to the fixed point x_* goes to zero as $t \rightarrow \infty$ provided $f'(x_*) < 0$. Therefore, the stability condition on x_* is

$$x_* \text{ is } \begin{cases} \text{a stable fixed point if} & f'(x_*) < 0, \\ \text{an unstable fixed point if} & f'(x_*) > 0. \end{cases}$$

Another equivalent but sometimes simpler approach to analyzing the stability of the fixed points of a one-dimensional nonlinear equation such as (1.2) is to plot $f(x)$ versus x . We show a generic example in Fig. 1.1. The fixed points are the x -intercepts of the graph. Directional arrows on the x -axis can be drawn based on the sign of $f(x)$. If $f(x) < 0$, then the arrow points to the left; if $f(x) > 0$, then the arrow points to the right. The arrows show the direction of motion for a particle at position x satisfying $\dot{x} = f(x)$. As illustrated in Fig. 1.1, fixed points with arrows on both sides pointing in are stable, and fixed points with arrows on both sides pointing out are unstable.

In the logistic equation (1.1), the fixed points are $N_* = 0, K$. A sketch of $F(N) = rN(1 - N/K)$ versus N , with $r, K > 0$ in Fig. 1.2 immediately shows that $N_* = 0$ is an unstable fixed point and $N_* = K$ is a stable fixed point. The

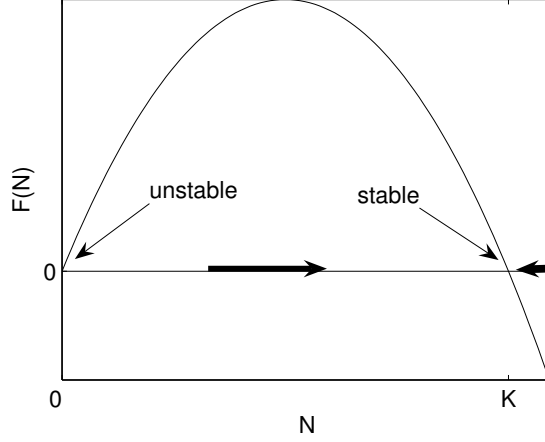


Figure 1.2: *Determining stability of the fixed points of the logistic equation.*

analytical approach computes $F'(N) = r(1 - 2N/K)$, so that $F'(0) = r > 0$ and $F'(K) = -r < 0$. Again we conclude that $N_* = 0$ is unstable and $N_* = K$ is stable.

We now solve the logistic equation analytically. Although this relatively simple equation can be solved as is, we first nondimensionalize to illustrate this very important technique that will later prove to be most useful. Perhaps here one can guess the appropriate unit of time to be $1/r$ and the appropriate unit of population size to be K . However, we prefer to demonstrate a more general technique that may be usefully applied to equations for which the appropriate dimensionless variables are difficult to guess. We begin by nondimensionalizing time and population size:

$$\tau = t/t_*, \quad \eta = N/N_*,$$

where t_* and N_* are unknown dimensional units. The derivative \dot{N} is computed as

$$\frac{dN}{dt} = \frac{d(N_*\eta)}{d\tau} \frac{d\tau}{dt} = \frac{N_*}{t_*} \frac{d\eta}{d\tau}.$$

Therefore, the logistic equation (1.1) becomes

$$\frac{d\eta}{d\tau} = rt_*\eta \left(1 - \frac{N_*\eta}{K}\right),$$

which assumes the simplest form with the choices $t_* = 1/r$ and $N_* = K$. Therefore, our dimensionless variables are

$$\tau = rt, \quad \eta = N/K,$$

and the logistic equation, in dimensionless form, becomes

$$\frac{d\eta}{d\tau} = \eta(1 - \eta), \tag{1.4}$$

with the dimensionless initial condition $\eta(0) = \eta_0 = N_0/K$, where N_0 is the initial population size. Note that the dimensionless logistic equation (1.4) has no free parameters, while the dimensional form of the equation (1.1) contains r and K . Reduction in the number of free parameters (here, two: r and K) by the number of independent units (here, also two: time and population size) is a general feature of nondimensionalization. The theoretical result is known as the *Buckingham Pi Theorem*. Reducing the number of free parameters in a problem to the absolute minimum is especially important before proceeding to a numerical solution. The parameter space that must be explored may be substantially reduced.

Solving the dimensionless logistic equation (1.4) can proceed by separating the variables. Separating and integrating from $\tau = 0$ to τ and η_0 to η yields

$$\int_{\eta_0}^{\eta} \frac{d\eta}{\eta(1-\eta)} = \int_0^{\tau} d\tau.$$

The integral on the left-hand-side can be performed using the method of partial fractions:

$$\begin{aligned} \frac{1}{\eta(1-\eta)} &= \frac{A}{\eta} + \frac{B}{1-\eta} \\ &= \frac{A + (B-A)\eta}{\eta(1-\eta)}, \end{aligned}$$

and by equating the coefficients of the numerators proportional to η^0 and η^1 , we find that $A = 1$ and $B = 1$. Therefore,

$$\begin{aligned} \int_{\eta_0}^{\eta} \frac{d\eta}{\eta(1-\eta)} &= \int_{\eta_0}^{\eta} \frac{d\eta}{\eta} + \int_{\eta_0}^{\eta} \frac{d\eta}{(1-\eta)} \\ &= \ln \frac{\eta}{\eta_0} - \ln \frac{1-\eta}{1-\eta_0} \\ &= \ln \frac{\eta(1-\eta_0)}{\eta_0(1-\eta)} \\ &= \tau. \end{aligned}$$

Solving for η , we first exponentiate both sides and then isolate η :

$$\begin{aligned} \frac{\eta(1-\eta_0)}{\eta_0(1-\eta)} &= e^{\tau}, \text{ or } \eta(1-\eta_0) = \eta_0 e^{\tau} - \eta\eta_0 e^{\tau}, \\ \text{or } \eta(1-\eta_0 + \eta_0 e^{\tau}) &= \eta_0 e^{\tau}, \text{ or } \eta = \frac{\eta_0}{\eta_0 + (1-\eta_0)e^{-\tau}}. \end{aligned}$$

Returning to the dimensional variables, we finally have

$$N(t) = \frac{N_0}{N_0/K + (1 - N_0/K)e^{-rt}}. \quad (1.5)$$

There are several ways to write the final result given by (1.5). The presentation of a mathematical result requires a good aesthetic sense and is an important element of mathematical technique. When deciding how to write (1.5), I considered if it was easy to observe the following limiting results: (1) $N(0) = N_0$; (2) $\lim_{t \rightarrow \infty} N(t) = K$; and (3) $\lim_{K \rightarrow \infty} N(t) = N_0 \exp(rt)$.

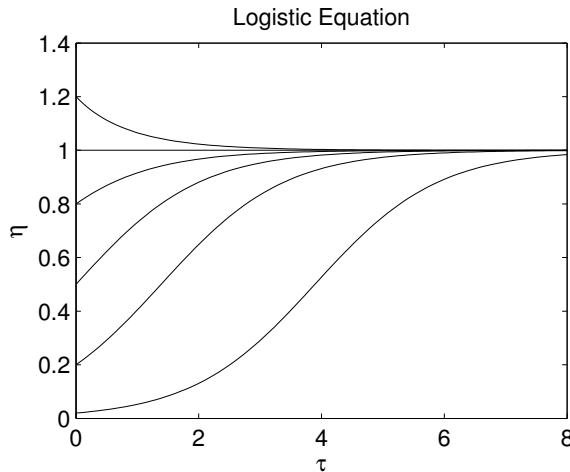


Figure 1.3: *Solutions of the dimensionless logistic equation.*

In Fig. 1.3, we plot the solution to the dimensionless logistic equation for initial conditions $\eta_0 = 0.02, 0.2, 0.5, 0.8, 1.0$, and 1.2 . The lowest curve is the characteristic ‘S-shape’ usually associated with the solution of the logistic equation. This sigmoidal curve appears in many other types of models. The MATLAB script to produce Fig. 1.3 is shown below.

```
eta0=[0.02 .2 .5 .8 1 1.2];
tau=linspace(0,8);
for i=1:length(eta0)
    eta=eta0(i)./(eta0(i)+(1-eta0(i)).*exp(-tau));
    plot(tau,eta);hold on
end
axis([0 8 0 1.25]);
xlabel('\tau'); ylabel('\eta'); title('Logistic Equation');
```

1.3 A model of species competition

Suppose that two species compete for the same resources. To build a model, we can start with logistic equations for both species. Different species would have different growth rates and different carrying capacities. If we let N_1 and N_2 be the number of individuals of species one and species two, then

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1 (1 - N_1/K_1), \\ \frac{dN_2}{dt} &= r_2 N_2 (1 - N_2/K_2).\end{aligned}$$

These are uncoupled equations so that asymptotically, $N_1 \rightarrow K_1$ and $N_2 \rightarrow K_2$. How do we model the competition between species? If N_1 is much smaller than K_1 , and N_2 much smaller than K_2 , then resources are plentiful and populations

grow exponentially with growth rates r_1 and r_2 . If species one and two compete, then the growth of species one reduces resources available to species two, and vice-versa. Since we do not know the impact species one and two have on each other, we introduce two additional parameters to model the competition. A reasonable modification that couples the two logistic equations is

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \alpha_{12} N_2}{K_1} \right), \quad (1.6a)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{\alpha_{21} N_1 + N_2}{K_2} \right), \quad (1.6b)$$

where α_{12} and α_{21} are dimensionless parameters that model the consumption of species one's resources by species two, and vice-versa. For example, suppose that both species eat exactly the same food, but species two consumes twice as much as species one. Since one individual of species two consumes the equivalent of two individuals of species one, the correct model is $\alpha_{12} = 2$ and $\alpha_{21} = 1/2$.

Another example supposes that species one and two occupy the same niche, consume resources at the same rate, but may have different growth rates and carrying capacities. Can the species coexist, or does one species eventually drive the other to extinction? It is possible to answer this question without actually solving the differential equations. With $\alpha_{12} = \alpha_{21} = 1$ as appropriate for this example, the coupled logistic equations (1.6) become

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + N_2}{K_1} \right), \quad \frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_1 + N_2}{K_2} \right). \quad (1.7)$$

For sake of argument, we assume that $K_1 > K_2$. The only fixed points other than the trivial one $(N_1, N_2) = (0, 0)$ are $(N_1, N_2) = (K_1, 0)$ and $(N_1, N_2) = (0, K_2)$. Stability can be computed analytically by a two-dimensional Taylor-series expansion, but here a simpler argument can suffice. We first consider $(N_1, N_2) = (K_1, \epsilon)$, with ϵ small. Since $K_1 > K_2$, observe from (1.7) that $\dot{N}_2 < 0$ so that species two goes extinct. Therefore $(N_1, N_2) = (K_1, 0)$ is a stable fixed point. Now consider $(N_1, N_2) = (\epsilon, K_2)$, with ϵ small. Again, since $K_1 > K_2$, observe from (1.7) that $\dot{N}_1 > 0$ and species one increases in number. Therefore, $(N_1, N_2) = (0, K_2)$ is an unstable fixed point. We have thus found that, within our coupled logistic model, species that occupy the same niche and consume resources at the same rate cannot coexist and that the species with the largest carrying capacity will survive and drive the other species to extinction. This is the so-called principle of *competitive exclusion*, also called *K-selection* since the species with the largest carrying capacity wins. In fact, ecologists also talk about *r-selection*; that is, the species with the largest growth rate wins. Our coupled logistic model does not model *r-selection*, demonstrating the potential limitations of a too simple mathematical model.

For some values of α_{12} and α_{21} , our model admits a stable equilibrium solution where two species coexist. The calculation of the fixed points and their stability is more complicated than the calculation just done, and I present only the results. The stable coexistence of two species within our model is possible only if $\alpha_{12} K_2 < K_1$ and $\alpha_{21} K_1 < K_2$.

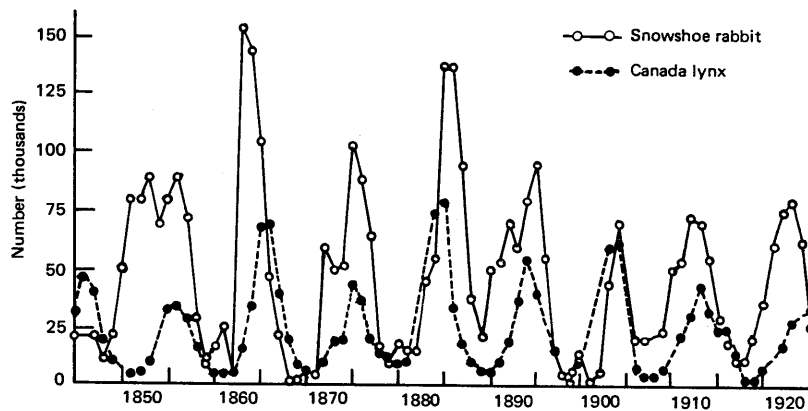


Figure 1.4: *Pelt-trading records of the Hudson Bay Company for the snowshoe hare and its predator the lynx. [From E.P. Odum, *Fundamentals of Ecology*, 1953.]*

1.4 The Lotka-Volterra predator-prey model

Pelt-trading records (Fig. 1.4) of the Hudson Bay company from over almost a century display a near-periodic oscillation in the number of trapped snowshoe hares and lynxes. With the reasonable assumption that the recorded number of trapped animals is proportional to the animal population, these records suggest that predator-prey populations—as typified by the hare and the lynx—can oscillate over time. Lotka and Volterra independently proposed in the 1920s a mathematical model for the population dynamics of a predator and prey, and these Lotka-Volterra predator-prey equations have since become an iconic model of mathematical biology.

To develop these equations, suppose that a predator population feeds on a prey population. We assume that the number of prey grow exponentially in the absence of predators (there is unlimited food available to the prey), and that the number of predators decay exponentially in the absence of prey (predators must eat prey or starve). Contact between predators and prey increases the number of predators and decreases the number of prey.

Let $U(t)$ and $V(t)$ be the number of prey and predators at time t . To develop a coupled differential equation model, we consider population sizes at time $t + \Delta t$. Exponential growth of prey in the absence of predators and exponential decay of predators in the absence of prey can be modeled by the usual linear terms. The coupling between prey and predator must be modeled with two additional parameters. We write the population sizes at time $t + \Delta t$ as

$$\begin{aligned} U(t + \Delta t) &= U(t) + \alpha \Delta t U(t) - \gamma \Delta t U(t)V(t), \\ V(t + \Delta t) &= V(t) + e\gamma \Delta t U(t)V(t) - \beta \Delta t V(t). \end{aligned}$$

The parameters α and β are the average per capita birthrate of the prey and the deathrate of the predators, in the absence of the other species. The coupling

terms model contact between predators and prey. The parameter γ is the fraction of prey caught per predator per unit time; the total number of prey caught by predators during time Δt is $\gamma \Delta t UV$. The prey eaten is then converted into newborn predators (view this as a conversion of biomass), with conversion factor e , so that the number of predators during time Δt increases by $e\gamma \Delta t UV$.

Converting these equations into differential equations by letting $\Delta t \rightarrow 0$, we obtain the well-known Lotka-Volterra predator-prey equations

$$\frac{dU}{dt} = \alpha U - \gamma UV, \quad \frac{dV}{dt} = e\gamma UV - \beta V. \quad (1.8)$$

Before analyzing the Lotka-Volterra equations, we first review fixed point and linear stability analysis applied to what is called an autonomous system of differential equations. For simplicity, we consider a system of only two differential equations of the form

$$\dot{x} = f(x, y), \quad \dot{y} = g(x, y), \quad (1.9)$$

though our results can be generalized to larger systems. The system given by (1.9) is said to be autonomous since f and g do not depend explicitly on the independent variable t . Fixed points of this system are determined by setting $\dot{x} = \dot{y} = 0$ and solving for x and y . Suppose that one fixed point is (x_*, y_*) . To determine its linear stability, we consider initial conditions for (x, y) near the fixed point with small independent perturbations in both directions, i.e., $x(0) = x_* + \epsilon(0)$, $y(0) = y_* + \delta(0)$. If the initial perturbation grows in time, we say that the fixed point is unstable; if it decays, we say that the fixed point is stable. Accordingly, we let

$$x(t) = x_* + \epsilon(t), \quad y(t) = y_* + \delta(t), \quad (1.10)$$

and substitute (1.10) into (1.9) to determine the time-dependence of ϵ and δ . Since x_* and y_* are constants, we have

$$\dot{\epsilon} = f(x_* + \epsilon, y_* + \delta), \quad \dot{\delta} = g(x_* + \epsilon, y_* + \delta).$$

The linear stability analysis proceeds by assuming that the initial perturbations $\epsilon(0)$ and $\delta(0)$ are small enough to truncate the two-dimensional Taylor-series expansion of f and g about $\epsilon = \delta = 0$ to first-order in ϵ and δ . Note that in general, the two-dimensional Taylor series of a function $F(x, y)$ about the origin is given by

$$\begin{aligned} F(x, y) &= F(0, 0) + xF_x(0, 0) + yF_y(0, 0) \\ &\quad + \frac{1}{2} [x^2 F_{xx}(0, 0) + 2xy F_{xy}(0, 0) + y^2 F_{yy}(0, 0)] + \dots, \end{aligned}$$

where the terms in the expansion can be remembered by requiring that all of the partial derivatives of the series agree with that of $F(x, y)$ at the origin. We now Taylor-series expand $f(x_* + \epsilon, y_* + \delta)$ and $g(x_* + \epsilon, y_* + \delta)$ about $(\epsilon, \delta) = (0, 0)$. The constant terms vanish since (x_*, y_*) is a fixed point, and we neglect all terms with higher orders than ϵ and δ . Therefore,

$$\dot{\epsilon} = \epsilon f_x(x_*, y_*) + \delta f_y(x_*, y_*), \quad \dot{\delta} = \epsilon g_x(x_*, y_*) + \delta g_y(x_*, y_*),$$

which may be written in matrix form as

$$\frac{d}{dt} \begin{pmatrix} \epsilon \\ \delta \end{pmatrix} = \begin{pmatrix} f_x^* & f_y^* \\ g_x^* & g_y^* \end{pmatrix} \begin{pmatrix} \epsilon \\ \delta \end{pmatrix}, \quad (1.11)$$

where $f_x^* = f_x(x_*, y_*)$, etc. Equation (1.11) is a system of linear ode's, and its solution proceeds by assuming the form

$$\begin{pmatrix} \epsilon \\ \delta \end{pmatrix} = e^{\lambda t} \mathbf{v}. \quad (1.12)$$

Upon substitution of (1.12) into (1.11), and canceling $e^{\lambda t}$, we obtain the linear algebra eigenvalue problem

$$\mathbf{J}^* \mathbf{v} = \lambda \mathbf{v}, \text{ with } \mathbf{J}^* = \begin{pmatrix} f_x^* & f_y^* \\ g_x^* & g_y^* \end{pmatrix},$$

where λ is the eigenvalue, \mathbf{v} the corresponding eigenvector, and \mathbf{J}^* the Jacobian matrix evaluated at the fixed point. The eigenvalue is determined from the characteristic equation

$$\det(\mathbf{J}^* - \lambda \mathbf{I}) = 0,$$

which for a two-by-two Jacobian matrix results in a quadratic equation for λ . From the form of the solution (1.12), the fixed point is stable if for all eigenvalues λ , $\text{Re}\{\lambda\} < 0$, and unstable if for at least one λ , $\text{Re}\{\lambda\} > 0$. Here $\text{Re}\{\lambda\}$ means the real part of the (possibly) complex eigenvalue λ .

We now reconsider the Lotka-Volterra equations (1.8). Fixed point solutions are found by solving $\dot{U} = \dot{V} = 0$, and the two solutions are

$$(U_*, V_*) = (0, 0) \text{ or } \left(\frac{\beta}{e\gamma}, \frac{\alpha}{\gamma}\right).$$

The trivial fixed point $(0, 0)$ is unstable since the prey population grows exponentially if it is initially small. To determine the stability of the second fixed point, we write the Lotka-Volterra equation in the form

$$\frac{dU}{dt} = F(U, V), \quad \frac{dV}{dt} = G(U, V),$$

with

$$F(U, V) = \alpha U - \gamma UV, \quad G(U, V) = e\gamma UV - \beta V.$$

The partial derivatives are then computed to be

$$\begin{aligned} F_U &= \alpha - \gamma V, & F_V &= -\gamma U \\ G_U &= e\gamma V, & G_V &= e\gamma U - \beta. \end{aligned}$$

The Jacobian at the fixed point $(U_*, V_*) = (\beta/e\gamma, \alpha/\gamma)$ is

$$\mathbf{J}^* = \begin{pmatrix} 0 & -\beta/e \\ e\alpha & 0 \end{pmatrix};$$

and

$$\begin{aligned} \det(\mathbf{J}^* - \lambda \mathbf{I}) &= \begin{vmatrix} -\lambda & -\beta/e \\ e\alpha & -\lambda \end{vmatrix} \\ &= \lambda^2 + \alpha\beta \\ &= 0 \end{aligned}$$

has the solutions $\lambda_{\pm} = \pm i\sqrt{\alpha\beta}$, which are pure imaginary. When the eigenvalues of the two-by-two Jacobian are pure imaginary, the fixed point is called a center and the perturbation neither grows nor decays, but oscillates. Here, the angular frequency of oscillation is $\omega = \sqrt{\alpha\beta}$, and the period of the oscillation is $2\pi/\omega$.

We plot U and V versus t (time series plot), and V versus U (phase space diagram) to see how the solutions behave. For a nonlinear system of equations such as (1.8), a numerical solution is required. The Lotka-Volterra system has four free parameters α , β , γ and e . The relevant units here are time, the number of prey, and the number of predators. The Buckingham Pi Theorem predicts that nondimensionalizing the equations can reduce the number of free parameters by three to a manageable single dimensionless grouping of parameters. We choose to nondimensionalize time using the angular frequency of oscillation and the number of prey and predators using their fixed point values. With carets denoting the dimensionless variables, we let

$$\hat{t} = \sqrt{\alpha\beta}t, \quad \hat{U} = U/U_* = \frac{e\gamma}{\beta}U, \quad \hat{V} = V/V_* = \frac{\gamma}{\alpha}V. \quad (1.13)$$

Substitution of (1.13) into the Lotka-Volterra equations (1.8) results in the dimensionless equations

$$\frac{d\hat{U}}{d\hat{t}} = r(\hat{U} - \hat{U}\hat{V}), \quad \frac{d\hat{V}}{d\hat{t}} = \frac{1}{r}(\hat{U}\hat{V} - \hat{V}),$$

with single dimensionless grouping $r = \sqrt{\alpha/\beta}$. A numerical solution uses MATLAB's `ode45.m` built-in function to integrate the differential equations. The code below produces Fig. 1.5. Notice how the predator population lags the prey population: an increase in prey numbers results in a delayed increase in predator numbers as the predators eat more prey. The phase space diagrams clearly show the periodicity of the oscillation. Note that the curves move counterclockwise: prey numbers increase when predator numbers are minimal, and prey numbers decrease when predator numbers are maximal.

```

function lotka_volterra
% plots time series and phase space diagrams
clear all; close all;
t0=0; tf=6*pi; eps=0.1; delta=0;
r=[1/2, 1, 2];
options = odeset('RelTol',1e-6,'AbsTol',[1e-6 1e-6]);
%time series plots
for i=1:length(r);
    [t,UV]=ode45(@lv_eq,[t0,tf],[1+eps 1+delta],options,r(i));
    U=UV(:,1); V=UV(:,2);
    subplot(3,1,i); plot(t,U,t,V,'--');
    axis([0 6*pi,0.8 1.25]); ylabel('predator,prey');
    text(3,1.15,['r=',num2str(r(i))]);
end
xlabel('t');
subplot(3,1,1); legend('prey', 'predator');
%phase space plot
xpos=[2.5 2.5 2.5]; ypos=[3.5 3.5 3.5];%for annotating graph
for i=1:length(r);
    for eps=0.1:0.1:1.0;
        [t,UV]=ode45(@lv_eq,[t0,tf],[1+eps 1+eps],options,r(i));
        U=UV(:,1); V=UV(:,2);
        figure(2);subplot(1,3,i); plot(U,V); hold on;
    end
    axis equal; axis([0 4 0 4]);
    text(xpos(i),ypos(i),['r=',num2str(r(i))]);
    if i==1; ylabel('predator'); end;
    xlabel('prey');
end

function dUV=lv_eq(t,UV,r)
dUV=zeros(2,1);
dUV(1) = r*(UV(1)-UV(1)*UV(2));
dUV(2) = (1/r)*(UV(1)*UV(2)-UV(2));

```

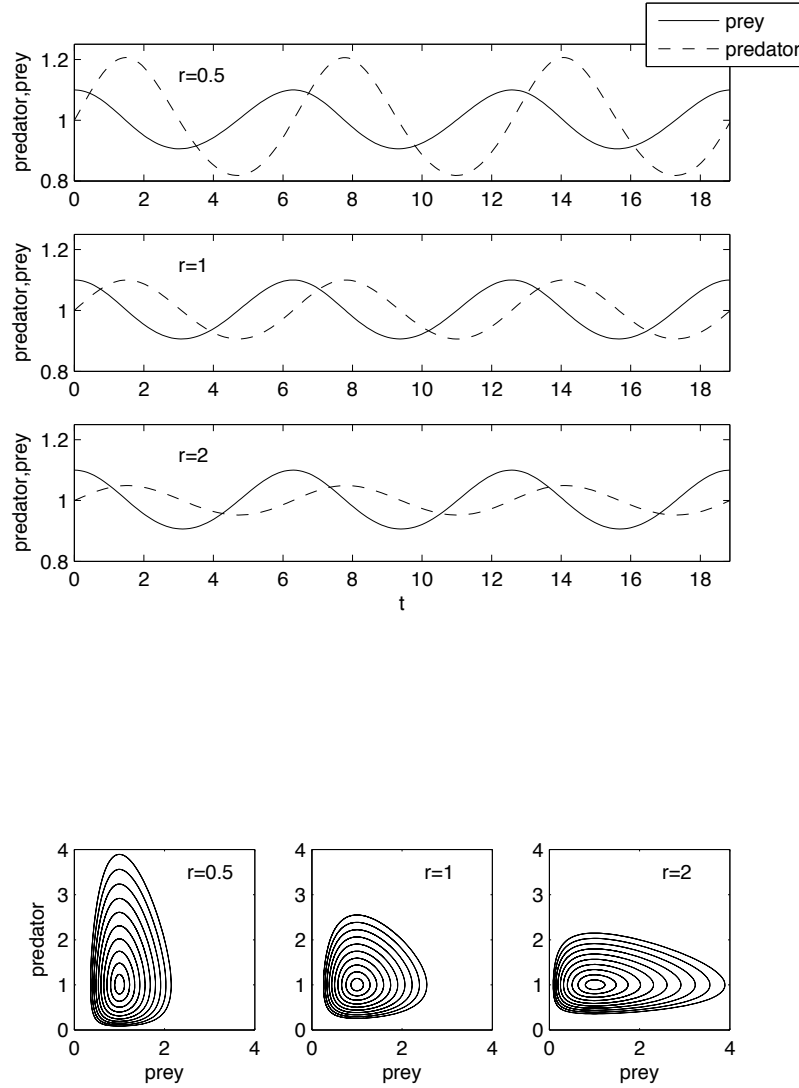


Figure 1.5: *Solutions of the dimensionless Lotka-Volterra equations. Upper plots: time-series solutions; lower plots: phase space diagrams.*

