# Part I Unstructured population models

# Section A
# SINGLE-SPECIES MODELS

## 1 Exponential, logistic, and Gompertz growth

Tradition dictates that we begin with a simple homogeneous population. This population is that 'homogeneous green gunk' that I referred to in the preface. I will represent the number (or sometimes the density) of individuals in this population by $N(t)$. I will also make frequent reference to the rate of change, $dN/dt$, and to the per capita rate of change, $(1/N)\,dN/dt$, of this population.

Let us assume that all changes in this population result from births and deaths and that the per capita birth rate $b$ and per capita death rate $d$ are constant:

$$\frac{1}{N}\frac{dN}{dt} = b - d. \tag{1.1}$$

The difference between the per capita birth and death rates, $r \equiv b - d$, plays a particularly important role and is known as the *intrinsic rate of growth*. Equation (1.1) is commonly rewritten, in terms of $r$, as

$$\frac{dN}{dt} = rN. \tag{1.2}$$

One must also add an initial condition, such as

$$N(0) = N_0, \tag{1.3}$$

that specifies the number of individuals at the start of the process.

Equation (1.2) is a linear, first-order differential equation. It is easily integrated, either as a separable equation or with an integrating factor, and it possesses the solution

$$N(t) = N_0 e^{rt}. \tag{1.4}$$

This solution grows exponentially for positive intrinsic rates of growth and

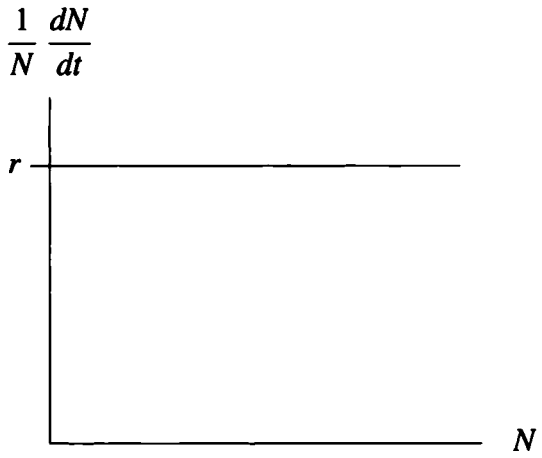


Fig. 1.1. Per capita growth rate.

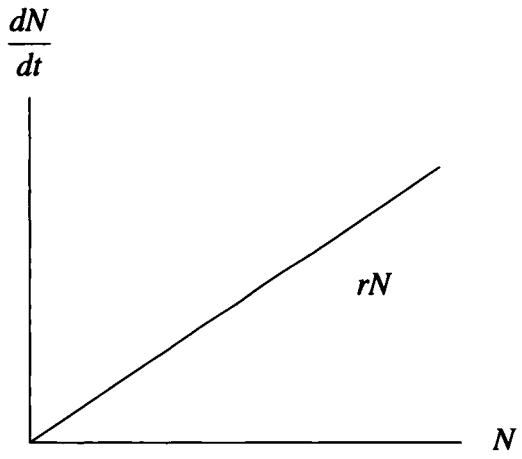


Fig. 1.2. Population growth rate.

decays exponentially for negative intrinsic rates of growth. It remains constant when births balance deaths.

Three different graphs capture the behavior of this system. In Figure 1.1, I have plotted the per capita growth rate as a function of the population size. The per capita growth rate remains constant for all population sizes: crowding has no effect on individuals. However, the growth rate for the entire population (Figure 1.2) increases with number as each new individual adds its own undiminished contribution to the total growth rate. The result (Figure 1.3) is a population that grows at ever-increasing rates.

The population size $N^* = 0$ is an *equilibrium point*. Since there is no

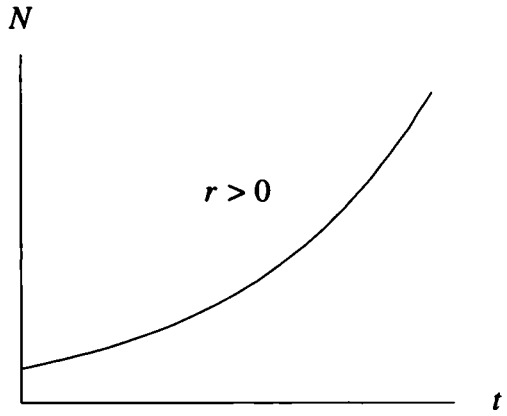


Fig. 1.3. Population trajectory.

immigration or emigration in this model, populations that start at zero stay at zero. For positive $r$, this equilibrium is *unstable*. After small perturbations, the population moves away from zero. For negative $r$, this equilibrium is *asymptotically stable*. Small perturbations now decay back to zero. I will say more about equilibria and stability later.

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**Problem 1.1** ***Monod's† nightmare***

*Escherichia coli* is a bacterium that has been used extensively in microbiological studies. *Escherichia coli* cells are rod shaped; they are 0.75 $\mu$m wide and 2 $\mu$m long. Under ideal conditions, a population of *E. coli* doubles in just over 20 minutes.

(1) What is $r$ for *E. coli?*

(2) If $N_0 = 1$, how long would it take for an exponentially growing population of *E. coli* experiencing ideal conditions to fill your classroom?

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There are several defects with this simple exponential model:

(1) The model has constant per capita birth and death rates and generates limitless growth. This is patently unrealistic.

(2) The model is deterministic; we have ignored chance or stochastic effects. Stochastic effects are particularly important at small population sizes.

† Jacques Monod (1910–1976) was the recipient of a 1965 Nobel Prize for Medicine for his work on gene regulation. He also conducted innovative experimental studies on the kinetics and stoichiometry of microbial growth (Panikov, 1995).

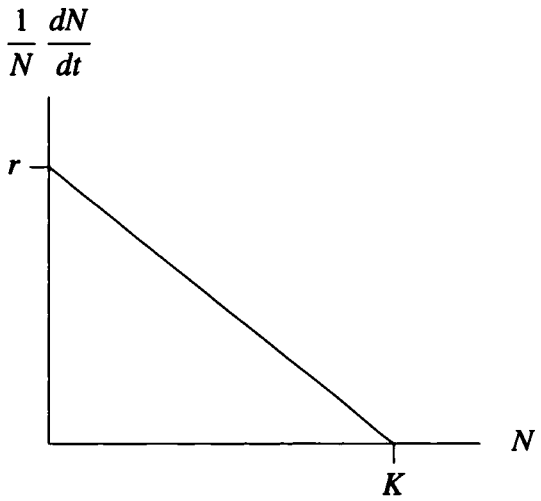


Fig. 1.4. Decreasing per capita growth rate.

(3) The model ignores lags. The growth rate does not depend on the past. Moreover, the population responds *instantaneously* to changes in the current population size.

(4) We have ignored temporal and spatial variability.

Let us start with the first defect.

What are the factors that regulate the growth of populations? There have been two schools of thought. In 1933, A. J. Nicholson, an Australian entomologist, published a seminal paper in which he stressed the importance of density-dependent population regulation. Nicholson (1933), the British ornithologist David Lack (1954), and others argued that populations are regulated by biotic factors such as competition and disease that have a disproportionately large effect on high-density populations. The opposing view, promulgated by the Australian entomologists H. G. Andrewartha and L. C. Birch (1954), is that populations are kept in check by abiotic, density-independent factors, such as vagaries in the weather, that have as adverse an effect on low-density populations as they do on high-density populations.

The dispute between these two schools occupied ecology for most of the 1950s (Tamarin, 1978; Kingsland, 1985; Sinclair, 1989). Density-dependent and density-independent factors may both be important in regulating populations. From a modeling perspective, however, it is easier to start with density-dependent regulation.

Consider a per capita growth rate that decreases linearly with population

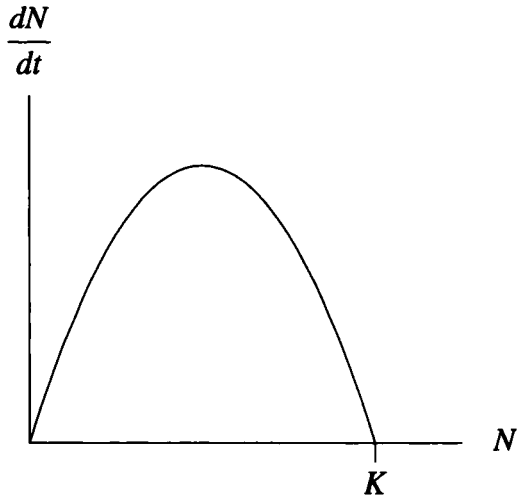


Fig. 1.5. Parabolic population growth rate.

size,

$$\frac{1}{N}\frac{dN}{dt} = r\left(1 - \frac{N}{K}\right) \tag{1.5}$$

(see Figure 1.4). This decrease in the per capita growth rate may be thought of as an extremely simple form of density-dependent regulation. Note that the per capita growth rate falls to zero at the *carrying capacity* $K$.

The population's growth rate,

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \tag{1.6}$$

is now a quadratic function of population size (see Figure 1.5). Equation (1.6) is known as the *logistic equation* or, more rarely, as the *Pearl–Verhulst equation*. It has an exact analytical solution. Figure 1.6 illustrates this solution for two different initial conditions. You are asked to find this closed-form solution in Problem 1.2. Since few nonlinear differential equations can be solved so easily, I will concentrate on a general method of analysis that emphasizes the qualitative features of the solution.

Equation (1.6) has two equilibria, $N^* = 0$ and $N^* = K$; at each of these two values, the growth rate for the population is equal to zero. Near $N^* = 0$, $N^2/K$ is small compared to $N$ so that

$$\frac{dN}{dt} \approx rN. \tag{1.7}$$

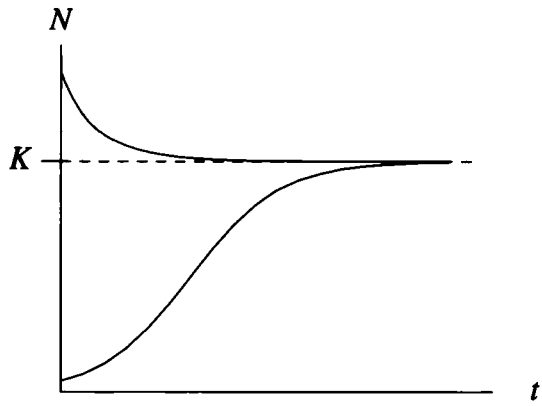


Fig. 1.6. Logistic growth.

For $r > 0$, small perturbations about $N^* = 0$ grow exponentially; the equilibrium $N^* = 0$ is unstable.

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**Problem 1.2** ***Exact solution of the logistic equation***
Show that the logistic equation has the solution

$$N(t) = \frac{K}{1 + \left(\frac{K}{N_0} - 1\right) e^{-rt}} \tag{1.8}$$

(1) treating the logistic equation as a separable equation, and
(2) treating the logistic equation as a Bernoulli equation.

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Close to $N^* = K$, we instead introduce a new variable that measures the deviation of $N$ from $K$:

$$x \equiv N - K. \tag{1.9}$$

Substituting $N = K + x$ into equation (1.6) gives us

$$\frac{dx}{dt} = -rx - \frac{r}{K}x^2, \tag{1.10}$$

and since $x$ is small for $N$ close to $K$, we have that

$$\frac{dx}{dt} \approx -rx. \tag{1.11}$$

For $r > 0$, small perturbations about $N^* = K$ *decay* exponentially; the equilibrium $N^* = K$ is asymptotically stable. For positive $r$, solutions to the

logistic equation (see Figure 1.6) are essentially a combination of exponential growth, close to zero, and of exponential decay, close to the carrying capacity.

Equations (1.7) and (1.11) imply that the solution of the logistic equation is concave up just above the origin and concave down just below the carrying capacity. It stands to reason that an inflection point lies between the origin and the carrying capacity. This inflection point can be found by setting the derivative of both sides of logistic equation (1.6) equal to zero:

$$\frac{d^2N}{dt^2} = r\left(1 - \frac{2N}{K}\right)\frac{dN}{dt} = 0. \tag{1.12}$$

It follows that the inflection point is at $N = K/2$.

### Mathematical meanderings

Consider the differential equation

$$\frac{dN}{dt} = f(N). \tag{1.13}$$

This equation is *autonomous* in that $f$ does not contain any explicit dependence on $t$. I have introduced several concepts that are useful, not only for the logistic differential equation, but for many autonomous, first-order, ordinary differential equations. Let's formalize these concepts.

*Definition* We say that $N = N^*$ is an *equilibrium point* (also known as a *fixed point*, *critical point*, *rest point*) if

$$f(N^*) = 0. \tag{1.14}$$

*Definition* An equilibrium point $N^*$ is *Lyapunov stable* if, for any (arbitrarily small) $\epsilon > 0$, there exists a $\delta > 0$ (depending on $\epsilon$) such that, for all initial conditions $N(t_0) = N_0$ satisfying $|N_0 - N^*| < \delta$, we have $|N(t) - N^*| < \epsilon$ for all $t > t_0$. In other words, an equilibrium is stable if starting close (enough) guarantees that you stay close.

*Definition* An equilibrium point $N^*$ is *asymptotically stable* (*in the sense of Lyapunov*) if it is stable and if there exists a $\rho > 0$ such that

$$\lim_{t \to \infty} |N(t) - N^*| = 0 \tag{1.15}$$

for all $N_0$ satisfying

$$|N_0 - N^*| < \rho. \tag{1.16}$$

Thus an equilibrium is asymptotically stable if all sufficiently small initial deviations produce small excursions that eventually return to the equilibrium.

At this point, the only interesting question is a practical one: is a given equilibrium point stable or unstable?

*Theorem* Suppose that $N^*$ is an equilibrium point and that $f(N)$ is a continuously differentiable function. Suppose also that $f'(N^*) \neq 0$. Then the equilibrium point $N^*$ is asymptotically stable if $f'(N^*) < 0$, and unstable if $f'(N^*) > 0$.

*Proof* Consider an equilibrium for which $f'(N^*) < 0$ and let $x(t) \equiv N(t) - N^*$. If we expand $f(N)$ about $N^*$, we obtain

$$\frac{dx}{dt} = f(N^*) + f'(N^*)x + g(x). \tag{1.17}$$

Since $N^*$ is an equilibrium, equation (1.17) reduces to

$$\frac{dx}{dt} = f'(N^*)x + g(x), \tag{1.18}$$

which may be viewed as a perturbation of a linear, constant-coefficient differential equation. Note that $g(x)$ consists of higher-order terms. In particular, $g(x)$ satisfies $g(0) = 0$ and also $g'(0) = 0$. This, along with the continuity of $g'(x)$ (which follows from the continuity of $f'(N)$), guarantees us that for each $\epsilon > 0$ there is a small $\delta$ neighborhood about zero wherein $|g'(x)| < \epsilon$. As a result,

$$g(x) = \int_0^x g'(s)\,ds \leq \epsilon |x|. \tag{1.19}$$

It follows that

$$\frac{dx}{dt} \leq f'(N^*)x + \epsilon |x|. \tag{1.20}$$

For small enough $\delta$ and $\epsilon$ and $f'(N^*) \neq 0$, the higher-order terms cannot change the sign of $dx/dt$. As a result, small enough perturbations will decay; the equilibrium is asymptotically stable. A similar argument can be made to show that $f'(N^*) > 0$ implies instability. □

Take another look at Figure 1.5. You should be able to ascertain the stability of the two equilibria *by inspection* with this theorem. What do you think happens when $f'(N^*) = 0$?

## Historical hiatus

The concepts of exponential and logistic growth arose gradually. A few people played especially important roles in the development of these concepts.

**John Graunt** (1662) was a 'collector and classifier of facts' (Hutchinson, 1980). He was also the inventor of modern scientific demography. Graunt tabulated the Weekly Bills of Mortality for London. These bills listed births and deaths; they were used as an early warning system for the plague. Using these bills, Graunt estimated a doubling time for London of 64 years. This is an extremely short period of time. Graunt posited that if the descendants of Adam and Eve

(created in 3948 BC, according to Scaliger's chronology) doubled in number every 64 years, the world should be filled with 'far more People, than are now in it.' By my calculation, this would amount to

$$2^{(1662+3948)/64} \approx 2^{87.7} \approx 2.5 \times 10^{26} \approx 200 \text{ million people/cm}^2. \quad (1.21)$$

Graunt was clearly aware of the power of exponential growth.

**Sir William Petty** (1683) faulted Graunt for ignoring the biblical flood. He started the clock with Noah ($t_0 = 2700$ BC with $N_0 = 8$). Petty also felt that Graunt's estimate for a doubling time was misleading, since much of London's increase was due to immigration. Petty estimated the doubling time for England to be between 360 and 1200 years. However, a doubling time of 360 years left Petty with a population projection,

$$8 \times 2^{12.175} \approx 36\,994, \quad (1.22)$$

that was far too small. Petty therefore proposed that the human growth rate had fallen steadily in postdiluvian times. He produced a table 'shewing how the people might have doubled in the several ages of the world'; the table exhibited a steady increase in the doubling time, much as one would expect for logistic growth.

The **Reverend Thomas Robert Malthus** (1798) is famous for having written *An Essay on the Principle of Populations*. The essence of this book may be represented with a simple quasi-equation:

$$\begin{array}{c}\text{a geometrically}\\ \text{growing}\\ \text{population}\end{array} + \begin{array}{c}\text{an arithmetically}\\ \text{growing}\\ \text{food supply}\end{array} = \begin{array}{c}\text{much}\\ \text{human}\\ \text{misery}\end{array}. \quad (1.23)$$

Many of Malthus's conclusions had already been anticipated by Graunt, Petty, and others. However, Malthus is justly famous for stating the case so clearly. Malthus's book had tremendous influence on Charles Darwin and Alfred Russel Wallace and, in effect, provided them with the material basis for natural selection.

**Pierre-François Verhulst** (1845) was a Belgian who presented an entirely modern derivation of the logistic equation. His work went unappreciated during his own lifetime and he died in relative obscurity.

**Raymond Pearl** and **Lowell Reed** (1920) rediscovered the logistic equation and launched a crusade to make the logistic equation a 'law of nature' (Kingsland, 1985). They published over a dozen papers between 1920 and 1927 promulgating this law. Some of their extrapolations and *ad hoc* pastings of logistic curves were questionable, but they did make the logistic equation famous.

The logistic equation allows us to handle limited growth in a natural way. This equation also has a long history. However, there is nothing sacred about this equation. Other models, derived differently, exhibit many of the same properties.