

2

Population Models

A population is a group of individuals of the same species that occupy a particular area. As an individual grows by gaining weight, so a population grows by gaining individuals. Changes in population size and composition result from interactions between individuals of the same species, interactions between individuals of different species, interactions with the environment, disease, food supply, etc.

The variable N is used to indicate the size of population. Population changes with time, so N is a function of time. We use t to indicate the time of reference. Hence $N(t)$ indicates the number of individuals in the population at time, t . We use $t = 0$ to indicate the starting point. Given the present population N_0 and a rule f for evolution $f:(N, t) \rightarrow N$ which is the model, it is possible to tell where the population will be in the immediate future. The model can be described using:

- Continuous-time dynamical System (Differential Equation)
- Discrete-time dynamical System (Difference Equation)

2.1

Determinants of Population Change

In modeling population change, it is useful to know the determinants of change in the particular population under investigation. The four general determinants are births (B), death (D), immigration (I) and emigration (E). Population increases when new individuals are added, and decreases when individuals of the population leave, hence, births and immigration are considered as inflows while deaths and emigration are outflows.

Net change in population = inflow-outflow

$$\Delta N = B + I - (D + E)$$

$$N(t + 1) = N(t) + B + I - D - E \quad 2.1$$

If the inflow is greater than the outflow, the population will grow. If the outflow is higher than the inflow, it will shrink. If the two are in balance, the population size will not change, or will remain constant.

2.1.1

Continuous- Time Model and Discrete-Time Model

When generations do not overlap or all births occur at fixed intervals, discrete models are useful. For example, many insects and annual plants reproduce only once per year. The descendants that survive form the base for the population for the next year. These populations have discrete generations and are modeled with difference equations or discrete dynamical systems (Gotelli, 2009). In difference equation, time is viewed as an ordinal index at discrete points.

For a discrete model in natural time unit t , the population at $t+1$ is related to the population at time t by the equation;

$$N(t+1) = N(t) + B - D + I - E \quad 2.2$$

Continuous population models are useful where births can occur at any time, as with humans (Weiss, 2009). In differential equation, time is used as a continuous variable. For a continuous model, the population change is given by;

$$\frac{dN}{dt} = B - D + I - E \quad 2.3$$

The change in a population is discontinuous but for large population this change is relatively small compared to the total population from t to $t+1$. It can therefore be approximated by a continuous function, making it possible to model this change in population with differential equations. We present both the difference equation and differential equation versions of

- The Exponential Population Model
- The Logistic Population Model

With the assumption that our population, N is large, we focus on their differential equation versions.

2.2

The Exponential Population Model

The exponential population model is also known as the **Malthusian population model**. There is a reasonable consensus among ecologists that the exponential model is a good candidate for the first principle of population dynamics (e.g., Ginzburg 1986, Berryman 1999). Turchin (2001) formulates this principle as follows: “a population will grow (or decline) exponentially as long as the environment experienced by all individuals in the population remains constant”.

The model makes a few assumptions.

1. The population is a closed system i.e. there is no migration

$$I = E = 0$$

Normally, this assumption does not hold in nature but it is mathematically convenient and allows us to focus on the details of the dynamics of a local population.

2. The birth and death rates are constant, i.e.

$$B = bN \quad 2.4$$

$$D = dN \quad 2.5$$

where b and d are constants. Hence the population grows at a constant rate r ,

where $r = b - d$.

3. There is no difference in the birth and death rates due to age, sex or size.
4. There is no spontaneous generation, i.e. if $N(0) = 0$, then there is nobody around to start reproducing, and so $N = 0$ for all time.

The discrete-time version of the exponential model is given by

$$\begin{aligned} N(t+1) &= N(t) + B - D \\ &= N(t) + bN(t) - dN(t) \\ &= (1 + b - d)N(t) \\ N(t+1) &= (1 + r)N(t) \end{aligned} \quad 2.6$$

hence,

$$\begin{aligned}
 N(1) &= (1+r)N(0) \\
 N(2) &= (1+r)N(1) = (1+r)^2 N(0) \\
 N(3) &= (1+r)N(2) = (1+r)^3 N(0) \\
 &\vdots \\
 &\vdots
 \end{aligned}$$

The population at time t is given by

$$N(t) = (1+r)^t N(0) \tag{2.7}$$

The continuous-time version of the exponential model is given by

$$\begin{aligned}
 \frac{dN}{dt} &= B - D \\
 &= bN(t) - dN(t) \\
 &= (b-d)N(t) \\
 &= rN(t)
 \end{aligned} \tag{2.8}$$

Eq.(2.8) is a first order differential equation whose independent variable, t does not appear explicitly.

Our objective now is to show how geometric methods can be used to obtain important qualitative information directly from the differential equation in Eq.(2.8).

2.2.1

Equilibria and local Stability

We set $f(N)=0$ and solve for the equilibrium N^* .

$$\begin{aligned}
 f(N) &= rN = 0 \\
 N^* &= 0.
 \end{aligned}$$

When $r>0$, $f(N)>0$ for values to the right of zero on the phase line and $f(N)<0$ for values to the left of zero. When $r<0$, $f(N)<0$, for values to the right of zero on the phase line and $f(N)>0$ for values to the left of zero.

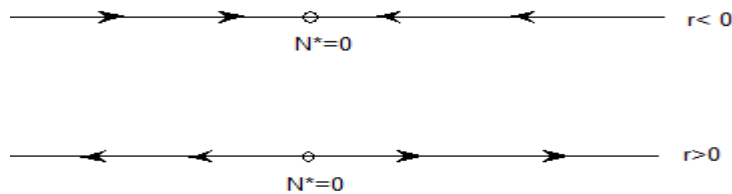


Figure 2.1 Phase line of the exponential model.

To determine the stability of $N^*=0$, we find the slope $f'(N)$ at N^*

$$f'(N^*) = r.$$

We conclude that $N^*=0$ is an unstable equilibrium when $r>0$ since $f'(0)=r >0$ and a stable equilibrium when $r<0$ since $f'(0)=r < 0$. In fact, the qualitative structure and the stability of the zero equilibrium change when r is varied.

Given an initial population of 100 with r ranged from -0.02 to 0.02, Figure 2.2 shows the trajectory using MATLAB. Given several initial populations N_0 , Figure 2.3 gives the direction field using MAPLE.

The Exponential Growth Curve

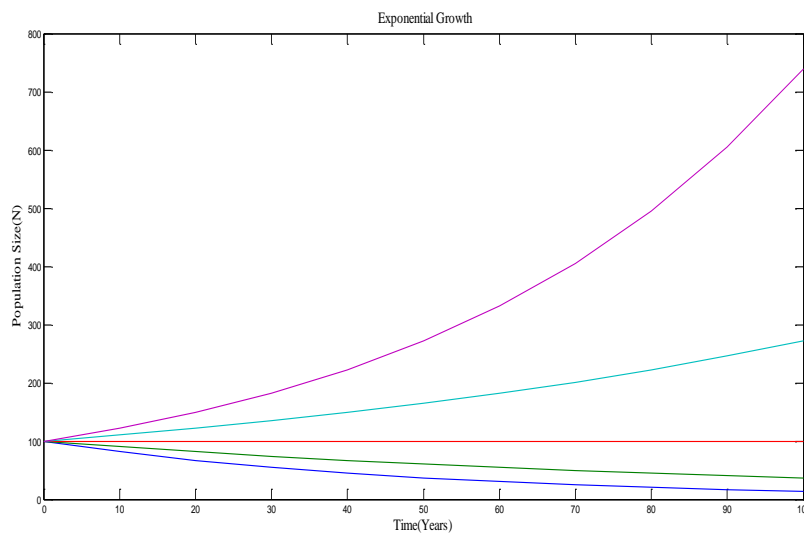


Figure 2.2 Exponential growth curves for an initial population of 100 individuals with different growth rates. The r is estimated at -0.02, -0.01, 0.00, 0.01, 0.02 (below to above).

Direction Field of Exponential Model

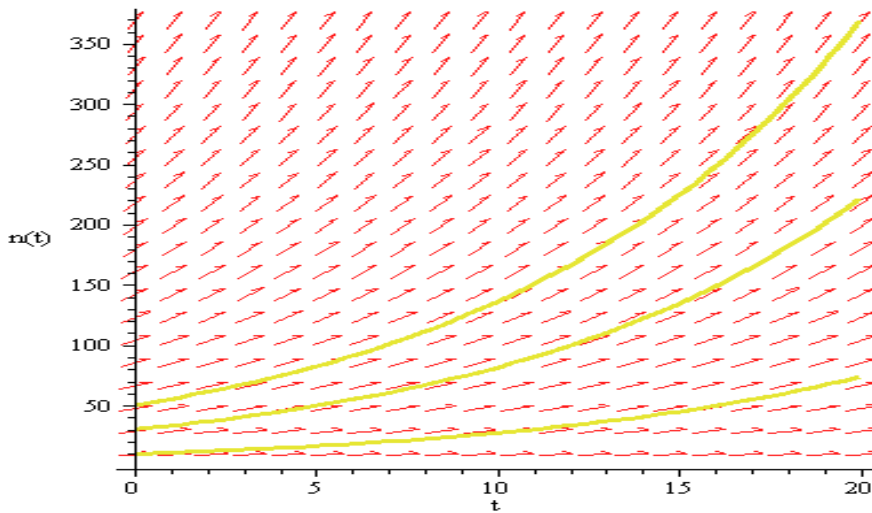


Figure 2.3 initial populations 10,30 and 50 and growth rate 0.1.

We solve Eq.(2.8) using separation of variables and integrating both sides of the equation,

$$\frac{dN}{dt} = rN$$

$$\int \frac{1}{N} dN = \int r dt$$

$$\ln N = rt + c_1$$

$$N = Ce^{rt} \quad \text{where } C = e^{c_1}$$

Applying the initial condition $N(0) = N_0$ with $r > 0$, we have

$$N = N_0 e^{rt} \tag{2.9}$$

$$\lim_{t \rightarrow \infty} N = \infty$$

Therefore the population grows for all time.

2.2.2

Limitations of the Exponential Population Model

Most simple species at the initial stages of population growth (usually over a short period of time) exhibit this exponential growth (Wiess, 2009). Some examples include:

1. US population from 1650 to 1800 (Pearl, 1920).

2. UK population from 1781 to 1851 (Ronald Shone, 2002).

A population undergoing exponential growth grows without bounds but in reality this is not so. No population grows exponentially forever because of limited resources. While the population grows exponentially, the resources such as food, water, space, etc on which they depend remain constant or only increase arithmetically. Thus, the demand for resources will eventually exceed the supply and population growth, being dependent on the resource supply, must cease (Berryman, 1992). Therefore the exponential model cannot be considered as a realistic model for any real-life population but rather provides the starting point for a mathematical description of dynamics of population systems (Turchin, 2001).

2.3

The Logistic Population Model

In an attempt to take account of the assumption resulting from limited space and resources, the Belgian mathematician Pierre François Verhulst introduced a new population model in 1838. Verhulst began by reasoning that in the early states of growth, a population would increase exponentially until such time when crucial resources, in this case farmland, became limiting (Kingsland, 1982). His work did not receive much attention until many years later, when it was rediscovered by the American biologist Raymond Pearl (Himonas and Howard, 2003). Although, according to Kingsland, the logistic curve stands out in the history of population ecology as one of the more fruitful and at the same time criticized model of population growth because of its over simplicity, it remains the central theoretical construct for single-species populations and it describes the dynamics of many single-species populations in both laboratory and field (Berryman, 1992).

Since the logistic model was derived from the exponential model, it makes the same assumptions in addition to the following;

-The amount of competition is proportional to the number of encounters between organisms, which in turn is proportional to the square of the population.

2.3.1

The Discrete-Time Logistic Model

The discrete-time version of the logistic model may be expressed in this form

$$N_{t+1} = F(N_t) \quad 2.10$$

Here the population in the $t+1$ generation depends on the population in the t generation.

$$N_{t+1} = N_t (r - k N_t)$$

The equation is a first-order, nonlinear difference equation. When $k=0$, it describes a population growing purely exponentially (for $r > 1$); for $k \neq 0$, the quadratic nonlinearity produces a growth curve with a hump, the steepness of which is tuned by the parameter r . This model was introduced into the population dynamics literature by the ecologist, Robert May in 1976. It was popularized in his seminal 1976 paper in part, as a discrete-time model analogous to the logistic equation first created by P. F. Verhulst. By writing $X = kN/r$, the logistic equation can be written as

$$X_{t+1} = rX_t (1 - X_t) \quad 2.11$$

Eq.(2.11) is attractive to mathematicians because of its simplicity. In practical applications, it has the disadvantage that it requires X to remain on the interval $0 < X < 1$. If X exceeds unity, subsequent iterations diverge towards $-\infty$, (which means the population becomes extinct). Therefore it is difficult to find examples of populations which are well modeled by this model (May, 1976).

We find the fixed points of the discrete model. It is the value at which there is no change from one iteration to the next.i.e

$$\begin{aligned} X_e &= F(X_e) & 2.12 \\ X_e &= rX_e(1 - X_e) \\ X_e &= rX_e - rX_e^2 \\ X_{e_1} &= \frac{r-1}{r} \quad \text{and} \quad X_{e_2} = 0 \end{aligned}$$

The characterization of the behavior of the discrete model near fixed points can be found in Devaney (1989) and May (1976).

1. If $f'(X_e) > 1$, then the solutions of the discrete model grow away from the equilibrium (monotonically). Thus, the fixed point is unstable.
2. If $0 < f'(X_e) < 1$, then the solutions of the discrete model approach the equilibrium (monotonically). Thus, the fixed point is stable.
3. If $-1 < f'(X_e) < 0$, then the solutions of the discrete model oscillate about the fixed point and approach it. Thus, the fixed point is stable.
4. If $f'(X_e) < -1$, then the solutions of the discrete model oscillate but move away from the equilibrium. Again, the fixed point is unstable.

Returning to the discrete logistic model, we analyse the local stability of the difference equation by examining the partial derivatives of F with respect to X evaluated at each equilibrium point X_e .

$$\lambda(X_e) = \left[\frac{\partial F}{\partial X} \right]_{X=X_e} \quad 2.13$$

Substituting X_e into Eq.(2.13) yields

$$\begin{aligned} \lambda(X_{e_1}) &= r - 2r \left(\frac{r-1}{r} \right) = 2 - r \\ \lambda(X_{e_2}) &= r - 2r(0) = r \end{aligned}$$

From the list of characterisations above, it follows that

- If $0 \leq r < 1$, the fixed point $X_{e_2} = 0$ is globally attracting, i.e. $\lim_{t \rightarrow \infty} X_t = 0$ for all X . The population will eventually die, independent of the initial population.
- If $1 < r < 2$, then $-1 < \lambda(X_{e_1}) < 1$, the fixed point X_{e_1} is stable and the population will quickly approach this value.
- If $2 < r < 3$, the population will also eventually approach X_{e_1} , but first will fluctuate around that value for some time.

- If $r > 1$, then $\lambda(X_{e_2}) > 1$ and implies $X_{e_2} = 0$ is unstable
- When $r = 1$ then $\lambda(X_{e_1}) = \lambda(X_{e_2}) = 1$ and $X_{e_1} = X_{e_2} = 0$ is a non hyperbolic fixed point.

For values of r between 3.57 and 4, chaos is observed.

We will not spend much time on discussing the discrete model but it has a rich bifurcation structure (period doubling bifurcations) and complicated dynamics (including chaotic behavior). For a rigorous treatment of the logistic map, see May (1976) and Devaney (1989).

2.3.2

The Continuous – Time Logistic model

The Continuous-time version of the model is given by

$$\frac{dN}{dt} = rN - kN^2 \quad 2.14$$

which is sometimes called the Verhulst equation but more commonly known as the logistic equation or logistic Model of growth. It is a first order quadratic, autonomous differential equation. Unlike the exponential model, this is nonlinear.

The equation involves two constants r and k . The first of these is the intrinsic growth rate, and it is the relative rate at which the population would grow if there were no restrictions; It plays the same role as the constant r in the exponential model. The constant k called the damping factor reflects the damping effect on growth caused by competition for resources between members of the population. In general, the parameter k is small relative to the parameter r . However, as the population size grows and competition becomes greater, the second term kN^2 becomes more significant. The growth in population is dampened as kN^2 becomes more significant.

We let $K = \frac{r}{k}$ and write Eq. (2.14) as

$$\begin{aligned} \frac{dN}{dt} &= rN - \frac{r}{K} N^2 \\ \frac{dN}{dt} &= rN \left(1 - \frac{N}{K}\right) \end{aligned} \quad 2.15$$

The interpretation of K will become clear shortly.

2.3.3

Equilibria and Local Stability

We start by drawing the graph of dN/dt versus N where $f(N) = r(1 - N/K)N$. The graph is the parabola as shown in Figure 2.4. The intercepts are $(0, 0)$ and $(K, 0)$, corresponding to the equilibria of Eq. (2.15), and the vertex of the parabola is $(K/2, rK/4)$.

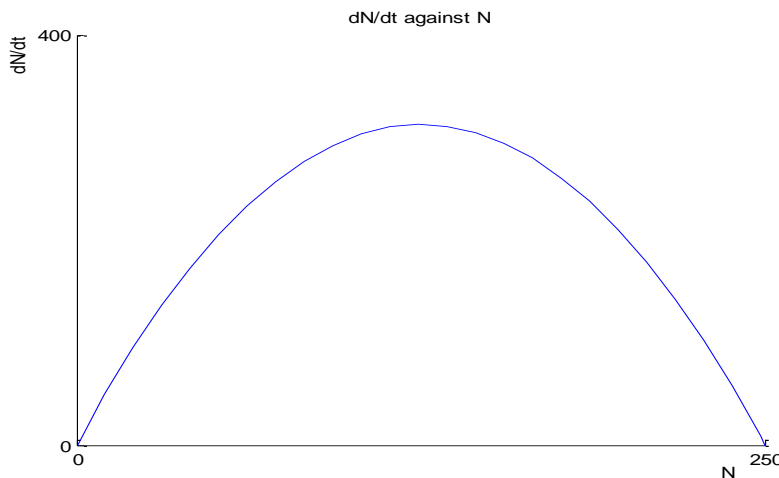


Figure 2.4 logistic growth curve. dN/dt versus N .

Using linear stability;

$$f'(N) = rN\left(\frac{-1}{K}\right) + r\left(1 - \frac{N}{K}\right) \quad 2.16$$

$$f'(0) = r \quad N=0 \text{ repeller}$$

$$f'(K) = -r \quad N=K \text{ attractor}$$

Hence, the equilibrium $N = K$ is a stable equilibrium for Eq.(2.15). This means that after a long time the population approaches K regardless of the initial population size, as long as it is positive. On the other hand, initial populations that start very near zero grow away as t increases. We say that $N = 0$ is an unstable equilibrium.

The graph of Eq.(2.15) has the following features. For $0 < N < K/2$, f is positive, f' are positive so the trajectories are concave up. For $N > K$, f is negative and f' is negative so the trajectories are concave up. For $K/2 < N < K$, the trajectories

are concave down since f is positive and f' is negative. At $N = K/2$, f' is zero so it is an inflection point. This is shown in Figure 2.6.

Direction field of the logistic Equation

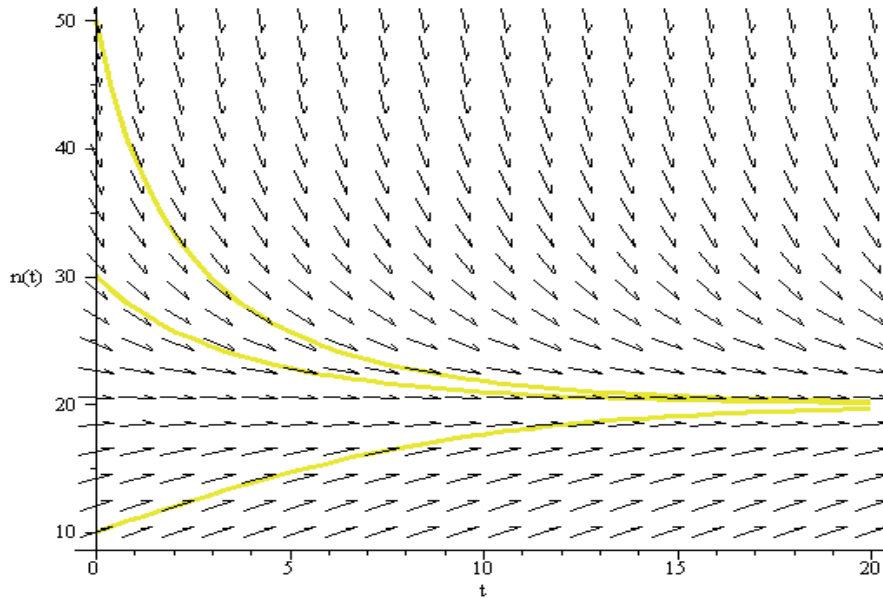


Figure 2.5 direction field of $dN/dt = r(1 - N/K)N$ with $r = 0.2$, $k = 0.01$ and initial population of 10,30 and 50.

The behaviour of trajectories in Figures 2.3 and 2.5 are strikingly different at least for large values of t . No matter how small the nonlinear term in the logistic model, trajectories of this equation approach a finite value as $t \rightarrow \infty$, whereas trajectories of the exponential model grow (exponentially) without bound as $t \rightarrow \infty$. For each $N_0 > 0$, the solution approaches the equilibrium $N = K$ as $t \rightarrow \infty$. In Figure 2.5, all trajectories approach the value 20 as t increases.

We investigate how varying the parameter r affects the stability of the equilibria. Eq.(2.15) may equivalently be written in dimensionless form by letting

$$x = \frac{N}{K},$$

Then we have

$$\begin{aligned} \frac{1}{K} \frac{dN}{dt} &= r \frac{N}{K} \left(1 - \frac{N}{K}\right) \\ \frac{dx}{dt} &= rx(1 - x) \end{aligned} \tag{2.17}$$

Allowing r to be positive, negative and zero, the plot of Eq.(2.17) is shown in Figure 2.6. As shown by the arrows, when $r < 0$, there are two equilibria, an unstable equilibrium at $x^* = 1$ and a stable equilibrium at $x^* = 0$. As r increases, the unstable equilibrium approaches the origin, and coalesces with it when $r = 0$. Finally, when $r > 0$, a new equilibrium is created in addition to the origin. The origin now an unstable equilibrium and $x^* = 1$ is a stable equilibrium.

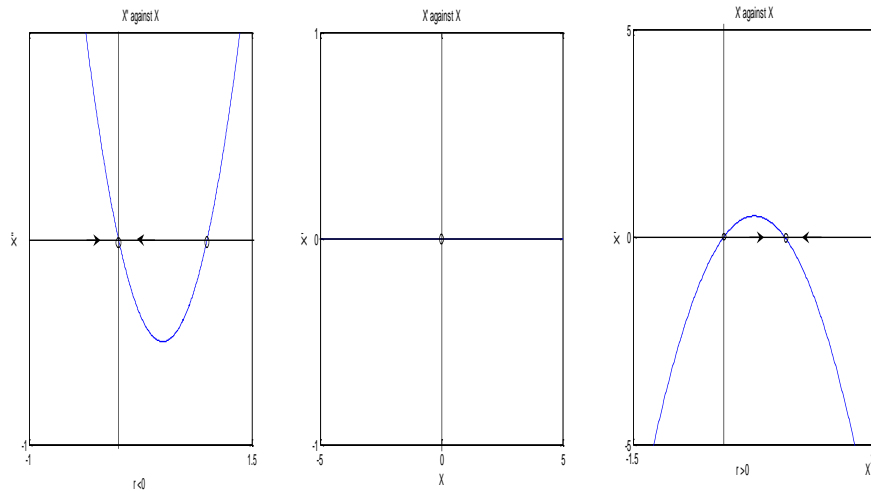


Figure 2.6. vector field of x' as r varies. For all r , $x^*=0$ is an equilibrium.

We observe that $x^* = 0$ exist regardless of the value of r . It only changes its stability as r is varied. This kind of bifurcation is the transcritical bifurcation.

We solve Eq. (2.15) explicitly for $N(t)$ by separation of variables subject to the initial condition $N(0) = N_0$.

$$\frac{1}{N(1 - \frac{N}{K})} dN = r dt$$

$$\int \frac{1}{N(1 - \frac{N}{K})} dN = \int r dt = rt + c_1$$

Using a partial fraction expansion on the left side and integrating both sides, we obtain,

$$\begin{aligned} \frac{1}{N(1-\frac{N}{K})} &= \frac{1}{N} + \frac{\frac{1}{K}}{(1-\frac{N}{K})} \\ \int \frac{1}{N(1-\frac{N}{K})} dN &= \int \frac{1}{N} dN + \int \frac{\frac{1}{K}}{(1-\frac{N}{K})} dN \\ &= \ln|N| - \ln\left|1-\frac{N}{K}\right| \\ &= \ln\left|\frac{N}{1-\frac{N}{K}}\right| \\ \ln\left|\frac{N}{1-\frac{N}{K}}\right| &= rt + c_1 \\ \Rightarrow \frac{N}{1-\frac{N}{K}} &= Ce^{rt} \quad \text{where } C=e^{c_1} \end{aligned} \tag{2.18}$$

Applying the initial condition $N(0)=N_0$, we have

$$C = \frac{N_0}{1-\frac{N_0}{K}}$$

Substituting C in Eq.(2.18), we have

$$\frac{N}{1-\frac{N}{K}} = \frac{N_0}{1-\frac{N_0}{K}} e^{rt}$$

Simplifying further,

$$\begin{aligned} N(1-\frac{N_0}{K}) &= N_0 e^{rt} - N_0 \frac{N}{K} e^{rt} \\ N(1-\frac{N_0}{K} + \frac{N_0}{K} e^{rt}) &= N_0 e^{rt} \\ \therefore N(t) &= \frac{N_0 K e^{rt}}{K - N_0 + N_0 e^{rt}} \end{aligned}$$

$$N(t) = \frac{N_0 K}{N_0 + (K - N_0)e^{-rt}} \quad 2.19$$

In particular, if $N_0 = 0$, then Eq.(2.19) requires that $N(t) = 0$ for all t .

If $N_0 > 0$ and $t \rightarrow \infty$ then

$$\lim_{t \rightarrow \infty} N(t) = K = \frac{r}{k} \quad 2.20$$

This confirms the stability analysis. Since K is the upper bound that is approached, but not exceeded, by growing populations starting below this value, it is referred to as the **saturation level**, or the **environmental carrying capacity** for the given population.

2.3.4

Limitations of the Logistic Model

Both Pearl (1924) and Lotka (Berryman, 1992) considered the logistic equation as the ‘law of population growth’. For the entire US population from 1790 to 1950, a logistic model was determined with the magnitude of r being 0.03134 and the value of K being 197 million. Starting with population of 3.929 million in 1790, the predicted population size in 1950 was 149 million. The actual population in 1950 was 151 million (Quinn, 1999), illustrating the good approximation of the Logistic model.

Ecologists such as Turchin (2001), however disagree with the consideration of the logistic equation as a law citing its failure to describe the growth of many real populations because natural populations rarely reach the equilibrium population K but constantly fluctuate.

According to Gause (1934), the logistic model looks like a good candidate since it accurately describes the growth of populations growing under a particular set of conditions (Berryman, 1992).