

## Density-dependent growth:

In reality, population cannot grow exponentially over time because of limited resources and/or competition for these with other species. Generally, population is found to be stable or to reach a limit if it is observed ~~for~~ over a long period. Hence question arises on the validity of exponential growth model of population leading to a modification of it.

### Background:

Individuals have to compete for the <sup>available</sup> limited resources with the growing of population. In other words, the environment can support a limited number of individuals. This number is known as the carrying capacity for the population and is usually denoted by  $K$  in biological literature. Technically, it is defined as <sup>(density)</sup> that population for which per capita birth rate and the per-capita death rate ~~are equal~~ <sup>are equal</sup> ~~including~~ external factors like harvesting or interaction with other population are included. Here, we will introduce an additional death rate due to resource limitation to curb the exponential growth so that the population is stabilized.

Formulating the differential equation:  
 The following word-equation describes the population as before,

$$\left\{ \begin{array}{l} \text{rate of} \\ \text{change in} \\ \text{population} \end{array} \right\} = \left\{ \begin{array}{l} \text{rate of} \\ \text{births} \end{array} \right\} - \left\{ \begin{array}{l} \text{rate of} \\ \text{deaths} \end{array} \right\}$$

we assume constant <sup>per-capita</sup> birth rate =  $\beta$  ①

So that-

$$\left\{ \begin{array}{l} \text{rate of} \\ \text{births} \end{array} \right\} = \beta x(t)$$

where  $x(t)$  is population at any time.  
 Instead of constant per-capita death rate, we ~~to~~ are to increase it as the population increases. To model their behaviour, we assume a linear dependence of the per-capita death rate on the population size is

$$\left\{ \begin{array}{l} \text{per-capita} \\ \text{death} \\ \text{rate} \end{array} \right\} = \alpha + \theta x(t)$$

where  $\alpha > 0$  is the natural per-capita death rate and  $\theta > 0$  is the per-capita dependence of deaths on the population size. It is to be noted that as  $x \rightarrow 0$ , per-capita death rate  $\rightarrow \alpha$  and as  $x$  increases, per-capita death rate also increases.

$$\therefore \left\{ \begin{array}{l} \text{rate of} \\ \text{deaths} \end{array} \right\} = \alpha x(t) + \theta x^2(t). \quad \text{--- (2)}$$

$\therefore$  (1) becomes

$$\frac{dx}{dt} = \beta x - \alpha x - \theta x^2$$

$$\text{or } \frac{dx}{dt} = r x - \theta x^2 \quad \text{where } r = \beta - \alpha \text{ is the reproduction rate.}$$

(3) is the mathematical model for density-dependent growth. (3)

Alternative formulation:

The population may also be described

$$\text{as } \left\{ \begin{array}{l} \text{rate of} \\ \text{change in} \\ \text{population} \end{array} \right\} = \left\{ \begin{array}{l} \text{rate} \\ \text{of} \\ \text{births} \end{array} \right\} - \left\{ \begin{array}{l} \text{normal} \\ \text{rate of} \\ \text{deaths} \end{array} \right\} - \left\{ \begin{array}{l} \text{rate of} \\ \text{deaths} \\ \text{by} \\ \text{crowding} \end{array} \right\}.$$

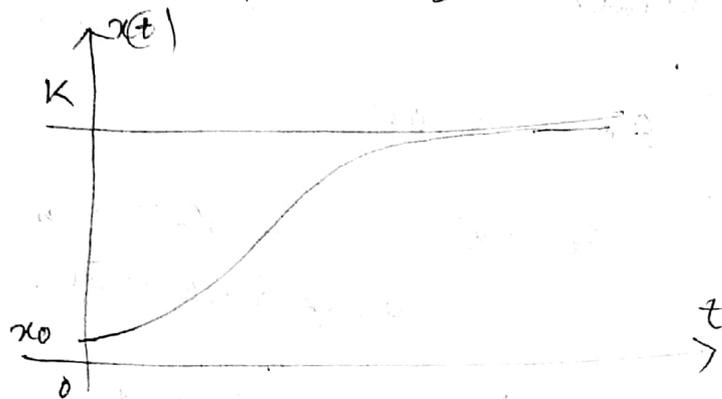
$$\text{Here, } \left\{ \begin{array}{l} \text{extra rate} \\ \text{of deaths} \\ \text{by crowding} \end{array} \right\} = \theta x^2, \text{ for } \theta > 0.$$

then the same equation (3) is obtained.

& sketch of the general solution of (3) without solving the equation.

Let initial population is  $x_0$ . we have  $\frac{dx}{dt} > 0$  for  $x < K$  and thus the population is increasing. The rate of growth increases initially and then

and then as the population approaches the carrying capacity  $K$ , it slows down. The sketch is given below



Ref - 10.6

§ The Logistic equation:

Let  $K = \frac{r}{\theta}$ . Then (3) becomes

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

$$\Rightarrow \frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) \quad \text{--- (4)}$$

(4) is a non-linear differential equation. It is called the logistic equation and is also referred to as the limited growth model or the density dependent model. Here it is considered that  $r > 0$  and  $K > 0$  so that the population values are positive.

§ Interpretation of the parameters:

Recall the equation of unrestricted population growth, namely

$$\frac{dx}{dt} = rx$$

It can be written as

$$\frac{dx}{dt} = \phi(x) \cdot x$$

where  $\phi(x)$  represents a population dependent per-capita growth rate. Comparing this with (4), we set

$$\phi(x) = r \left(1 - \frac{x}{K}\right).$$

Here  $\phi(x)$  is a linear function of  $x$  and  $\phi(x) \rightarrow 0$  as population  $x \rightarrow K$  the carrying capacity and as  $x \rightarrow 0$ ,  $\phi(x) \rightarrow r$ .

Graphically, this form represents a straight line passing through  $(0, r)$  and  $(K, 0)$ . If  $x < 0$ , then  $x > K$  and the population  $x$  decreases as it approaches the carrying capacity  $K$ .

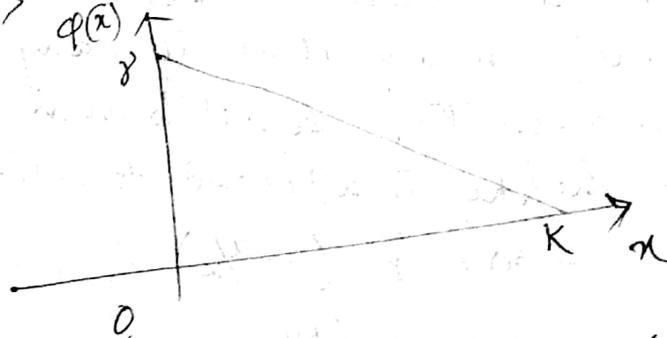


Fig. 10.7 The simplest assumption for a population dependent per-capita growth rate is a straight line.

### Equilibrium solution and stability:

An observation of the levelling of a population over time shows that the rate of change of population approaches zero, i.e.  $\frac{dx}{dt} \rightarrow 0$ . Thus any value of the population  $x$

growth  $\neq$  zero rate of change of population is called equilibrium point or equilibrium solution.

Then, equilibrium solutions are constant solutions where the rate of increase (births) exactly balances the rate of decrease (deaths).

$\therefore$  Equilibrium solutions satisfy

$$\frac{dx_e}{dt} = 0$$

$$\Rightarrow r x_e \left(1 - \frac{x_e}{K}\right) = 0 \quad \text{--- (5)}$$

$\Rightarrow$  Either  $x_e = 0$  or  $x_e = K$

We shall be interested on that value which are stable. For stable solutions stability means that if any body starts near the equilibrium solution then he/she is attracted towards that.

$$\text{let } f(x) = r x \left(1 - \frac{x}{K}\right)$$

For local stability,

$$f'(x_e) < 0 \quad [x_e = 0 \text{ or } K]$$

$$\text{But } f'(x) = r - \frac{2rx}{K}$$

$$\therefore f'(0) = r \quad \text{and } f'(K) = -r \quad \text{for } r > 0.$$

Hence the solution  $x = 0$  is always unstable and equilibrium solution  $x = K$  is always stable.

It can further be shown that - even if we are not near to the equilibrium solutions, these stability conditions still holds here.

Again, for the equation

$$\frac{dx}{dt} = r x \left(1 - \frac{x}{K}\right),$$

we observe that - the rate of change of  $x$  is always positive for  $x < K$ . This shows that population is increasing with time and will approach the equilibrium  $x = K$ . Similarly, if  $x > K$ ,  $\frac{dx}{dt} < 0$ , showing that the population is always decreasing towards  $x = K$ .

When the population always approaches the equilibrium <sup>population</sup> position, then the equilibrium is called globally stable.

The equilibrium is unstable if it is the population is repelled from the equilibrium. For  $0 < x < K$ ,  $\frac{dx}{dt} > 0$  and hence the equilibrium point at  $x = 0$  is globally unstable.

From this model, it is found that all populations approach the equilibrium value  $K$ , the carrying capacity for the population.

The carrying capacity and stable equilibrium point of population coincide in this case.

Ex. 10.13 Solve the logistic differential equation

$$\frac{dx}{dt} = r x \left(1 - \frac{x}{k}\right) \quad (4)$$

given the initial condition  $x(0) = x_0$ .

Solution.

The equation is

$$\frac{dx}{dt} = \frac{r x (k-x)}{k}$$

$$\Rightarrow \frac{k}{x(k-x)} dx = r dt$$

$$\Rightarrow \left(\frac{1}{x} + \frac{1}{k-x}\right) dx = r dt$$

[assuming  $x \neq 0, x \neq k$ ]

$$\Rightarrow \int \left(\frac{1}{x} + \frac{1}{k-x}\right) dx = \int r dt$$

$$\Rightarrow \ln|x| - \ln|k-x| = rt + C$$

$$\Rightarrow \left|\frac{x}{k-x}\right| = C_1 e^{rt} \quad [C_1 = e^C]$$

Assuming  $0 < x < k$ , we get

$$x = C_1 e^{rt} (k-x) \quad \text{--- (i)}$$

Using the initial condition  $x(0) = x_0$ ,

$$\text{we get } x_0 = C_1 e^0 (k-x_0)$$

$$\Rightarrow C_1 = \frac{x_0}{k-x_0}$$

$$\therefore x = \frac{x_0}{k-x_0} e^{rt} (k-x)$$

$$\text{or } \left(1 + \frac{x_0}{K-x_0} e^{\gamma t}\right) x = \frac{Kx_0 e^{\gamma t}}{K-x_0}$$

$$\text{or } \frac{K-x_0+x_0 e^{\gamma t}}{K-x_0} x = \frac{Kx_0 e^{\gamma t}}{K-x_0}$$

$$\Rightarrow \left(K-x_0+x_0 e^{\gamma t}\right) x = Kx_0 e^{\gamma t}$$

$$\Rightarrow x = \frac{Kx_0 e^{\gamma t}}{K-x_0+x_0 e^{\gamma t}}$$

$$= \frac{K}{\frac{K-x_0+x_0 e^{\gamma t}}{x_0 e^{\gamma t}}}$$

$$= \frac{K}{1 + \frac{K-x_0}{x_0} e^{-\gamma t}}$$

$$= \frac{K}{1 + \mu e^{-\gamma t}} \quad \text{where } \mu = \frac{K}{x_0} - 1. \quad \text{--- (ii)}$$

Note: If  $0 < K < x$ ,

$$\text{then } x = C_1 e^{\gamma t} (x-K)$$

with the initial condition  $x(0) = x_0$ ,

$$\text{we have } x_0 = C_1 (x_0 - K)$$

$$\Rightarrow C_1 = \frac{x_0}{x_0 - K}$$

giving the ~~above~~ <sup>same</sup> solution when (ii) (as above)

10.10.5  
 § 3.3. Limited growth with harvesting.

There is an utmost importance ~~the effect~~ Harvesting a population on a regular basis extremely affects the many industries such as fishing industry, etc. ~~pose the questions~~ ~~will~~ such as with a high harvesting rate destroy the population or a low harvesting rate destroy the existence of the industry?

Formulation of the equation:

Let us consider a constant harvesting rate in our logistic model. Then the balance of law leads to the word equation

$$\left\{ \begin{array}{l} \text{rate of} \\ \text{change in} \\ \text{population} \end{array} \right\} = \left\{ \begin{array}{l} \text{rate} \\ \text{of} \\ \text{births} \end{array} \right\} - \left\{ \begin{array}{l} \text{normal} \\ \text{rate of} \\ \text{deaths} \end{array} \right\} - \left\{ \begin{array}{l} \text{rate of} \\ \text{deaths} \\ \text{by crowding} \end{array} \right\} - \left\{ \begin{array}{l} \text{rate of} \\ \text{deaths} \\ \text{by harvesting} \end{array} \right\}$$

————— (3-3.1)

The differential equation representing the word equation 3-3.1 is

$$\frac{dx}{dt} = \beta x - \alpha x^2 - h$$

where  $x(t)$  is the population at any time  $t$ ,  $\beta =$  constant birth rate,  $\alpha =$  constant per capita death rate,

constant dependence  
 $\alpha =$  per-capita death ~~rate~~ in the population  
 size and is positive

$\beta =$  constant  
 $h =$  rate of ~~deaths~~ by harvesting ...  
 $\beta$  = total number caught per unit time  
 or deaths due to harvesting per unit  
 time.

$$\text{or } \frac{dx}{dt} = \gamma x - \frac{\gamma}{K} x^2 - h$$

where  $\gamma = \beta - \alpha$  is the reproduction  
 rate

and  $K = \frac{\gamma}{\alpha}$  is the carrying capacity  
 of population.

$$\text{or } \frac{dx}{dt} = \gamma x \left(1 - \frac{x}{K}\right) - h \quad \leftarrow \textcircled{3.3.2}$$

Solution of equation (3.3.2) for  $\gamma=1, K=10,$

$$h = \frac{9}{10} \quad \text{and} \quad x(0) = x_0.$$

Then (3.3.2) become

$$\frac{dx}{dt} = x \left(1 - \frac{x}{10}\right) - \frac{9}{10}$$

$$= \frac{-1}{10} (x^2 - 10x + 9)$$

$$= -\frac{1}{10} (x-1)(x-9)$$

$$\Rightarrow \frac{dx}{(x-1)(x-9)} = -\frac{1}{10} dt$$

$$\Rightarrow \frac{1}{10} \int \left( \frac{1}{x-9} - \frac{1}{x-1} \right) dx = -\frac{1}{10} \int dt$$

$$\frac{1}{8} (\log |x-9| - \log |x-1|) = -\frac{1}{10}t + C$$

$$\Rightarrow \frac{1}{8} \log \left| \frac{x-9}{x-1} \right| = -\frac{1}{10}t + C$$

$$\Rightarrow \log \left| \frac{x-9}{x-1} \right| = -\frac{8}{10}t + 8C$$

$$\Rightarrow \log \left| \frac{x-9}{x-1} \right| = -\frac{4}{5}t + \log b, \quad \log b = 8C$$

$$\Rightarrow \left| \frac{x-9}{x-1} \right| = b e^{-\frac{4}{5}t}$$

When  $t=0$ ,  $x=x_0$

$$\therefore \left| \frac{x_0-9}{x_0-1} \right| = b$$

$$\therefore \frac{x-9}{x-1} = \frac{x_0-9}{x_0-1} e^{-\frac{4}{5}t}$$

$$= b e^{-\frac{4}{5}t}$$

$$\Rightarrow \frac{x-9+x-1}{x-9-x+1} = \frac{b e^{-\frac{4}{5}t} + 1}{b e^{-\frac{4}{5}t} - 1}$$

$$\Rightarrow \frac{2x-10}{-8} =$$

$$\frac{x-1}{x-9} = \frac{1}{b e^{-\frac{4}{5}t}}$$

$$\Rightarrow \frac{x-1+x-9}{x-1-x+9} = \frac{1 + b e^{-\frac{4}{5}t}}{1 - b e^{-\frac{4}{5}t}}$$

$$\Rightarrow \frac{2x-10}{8} = \frac{1 + b e^{-\frac{4}{5}t}}{1 - b e^{-\frac{4}{5}t}}$$

$$\Rightarrow x-5 = \frac{4 + 4b e^{-\frac{4}{5}t}}{1 - b e^{-\frac{4}{5}t}}$$

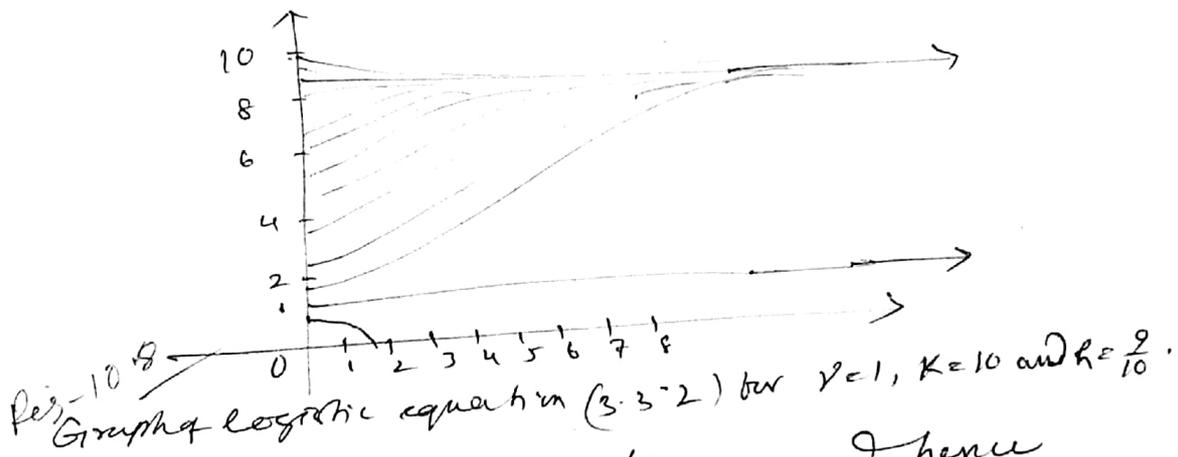
$$\Rightarrow x = \frac{4 + 4be^{-\frac{4t}{5}}}{1 - be^{-\frac{4t}{5}}} + 5$$

$$\Rightarrow x = \frac{4 + 4be^{-\frac{4t}{5}} + 5 - 5be^{-\frac{4t}{5}}}{1 - be^{-\frac{4t}{5}}}$$

$$\Rightarrow x(t) = \frac{9 - be^{-\frac{4t}{5}}}{1 - be^{-\frac{4t}{5}}}$$

where  $b = \left| \frac{x_0 - 9}{x_0 - 1} \right|$ .

Biometrical  
Interpretation Illustration with the help of graph. [Maple or Matlab].



If  $1 < x < 9$ , then  $\frac{dx}{dt} > 0$  and hence the population increases. If  $x > 9$ , then  $\frac{dx}{dt} < 0$  and the population decreases. If  $x=1$  or  $9$ , then as  $x' \rightarrow 0$ , the population doesn't change.

Conclusion

- \* For stability of population, the harvesting rate must be less than the carrying capacity.
- \* For a harvesting rate ~~which~~ <sup>causes</sup> ~~causes~~ the

population to decrease <sup>below</sup> a critical level, the threshold level (at which <sup>our model predicts</sup> the problem is) ~~predicts~~ that the population will become extinct.

Thus, the concept of threshold level is critical to many industries.