

Subject: Zoology

Production of Courseware
e-Content for Post Graduate Courses



Paper : 12 Principles of Ecology
Module : 08b Life Table, Fecundity Table and Survivorship curves, Part-II



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Content:

1. Learning Outcomes
2. Introduction
3. Survivorship curve
 - 3.1. Convex type curve
 - 3.2. Diagonal type curve
 - 3.3 Concave type curve
4. Mortality curve
5. Fecundity curve
6. Determination of net reproductive rate
7. Summary

1. Learning Outcomes

- After studying this module, you shall be able to:
- Understand quantitative aspect of population ecology.
- Understand different parameters that derive population change.
- Understand different types of survivorship curve.
- Construct fecundity table and its various components.
- Know about net reproductive rate (R_0), intrinsic capacity of increase (r) and generation time (G)

2. Introduction

For a population, the surviving individuals are more significant for a population than the dead individuals; the death rate can be represented by **survivorship curves** or **life tables**, both of which provide an estimate of organisms surviving at various ages. The data obtained from a cohort life table can be represented as survivorship curve for a given population which describes age specific mortality through survivorship. The life tables and survivorship curves are derived from data obtained from a cohort of a species at given period of time under certain environmental conditions. In the previous module we studied about concept and construction of life table and in this module we shall understand survivorship curve and also learn about fecundity table.

3. Survivorship curve

The life table can be represented on a semi-logarithmic paper in which the proportion of surviving individuals (l_x) is plotted on the vertical axis (Y-axis) on a logarithmic scale and age class (x) is plotted on the horizontal axis (X-axis) on the arithmetic scale. This representation is called as survivorship curve.

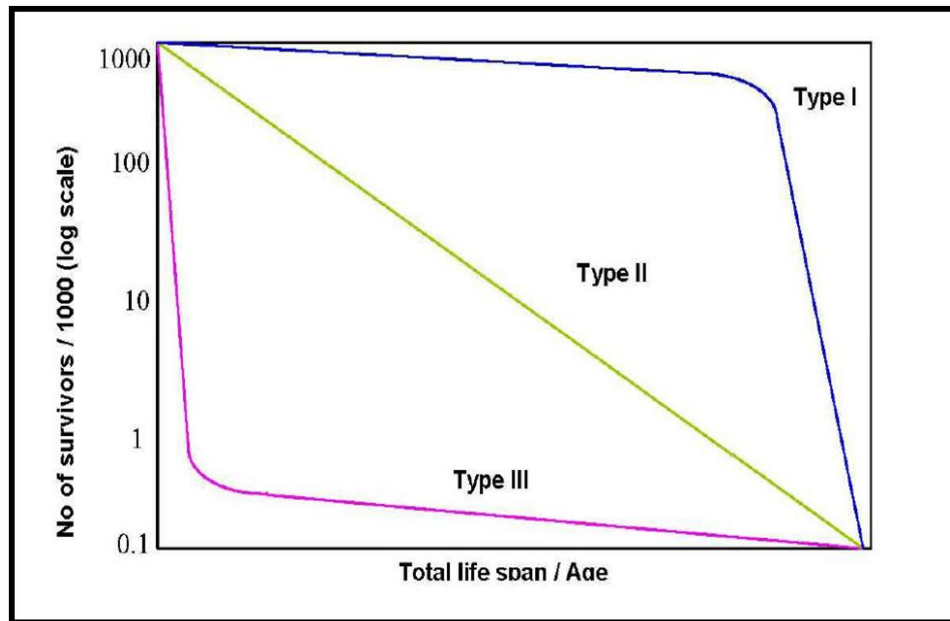


Figure.1: Hypothetical survivorship curves on a semi-log plot (after R. Pearl, 1928).

It can be categorized into three types (figure 1), which can be used as a standard at which real life survivorship curves of different organisms can be compared. It represents the different nature of survivors in different types of populations.

3.1 Highly convex curve

This type of curve (type-I) is the characteristic of the species in which the mortality rate of the population is low up to the end of the life span (old age). Thus, such species survive throughout their life span with low mortality rate in young and adult individuals. Many species of large animals such as deer, mountain sheep, man and small rotifers show such curves (figure 2).

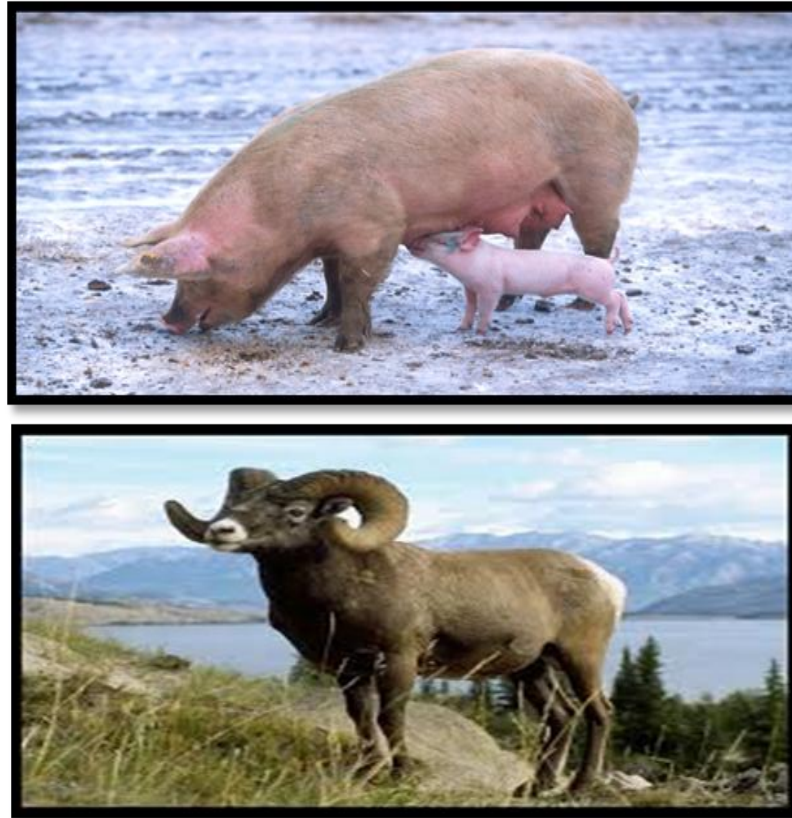


Figure.2: Animals showing type-I survivorship curve (pig on top and mountain sheep on bottom).

Among various large-sized perennial plants, generally they die after reaching reproductive phase within a period of old age. A population which is characterized by a Type I survivorship usually exhibit low birth rates. This is due to the fact that mostly all young individuals survive to perform reproductive event and their high birth rate would lead to "runaway" population growth.

3.2 Diagonal curve

This type of curve (type II) indicates an age-specific constant survivorship, *i.e.*, a constant rate of mortality occurs at every age. Such a curve is characteristic of some animals such as hydra, gull, American robin adult birds, rodents, and reptiles, as well as many perennial plants etc. exhibit this type of curve (figure 3).



Figure.3: Animals showing type-II survivorship curve (rodent on top and American robin on bottom).

3.3 Highly concave curve

This type of curve (type- III) is the characteristic of those species in which mortality rate is high during the early life stages. Some birds, oysters, shell fish, many insects, oak tree and fishes exhibit this type of survivorship curve (figure 4). In oysters, higher mortality occurs due to high predation in the early age as well as adverse environmental conditions. In case of holometabolous insects, stair type of survivorship curve is obtained as different stages of insects in their life history exhibit great variation in their survival.

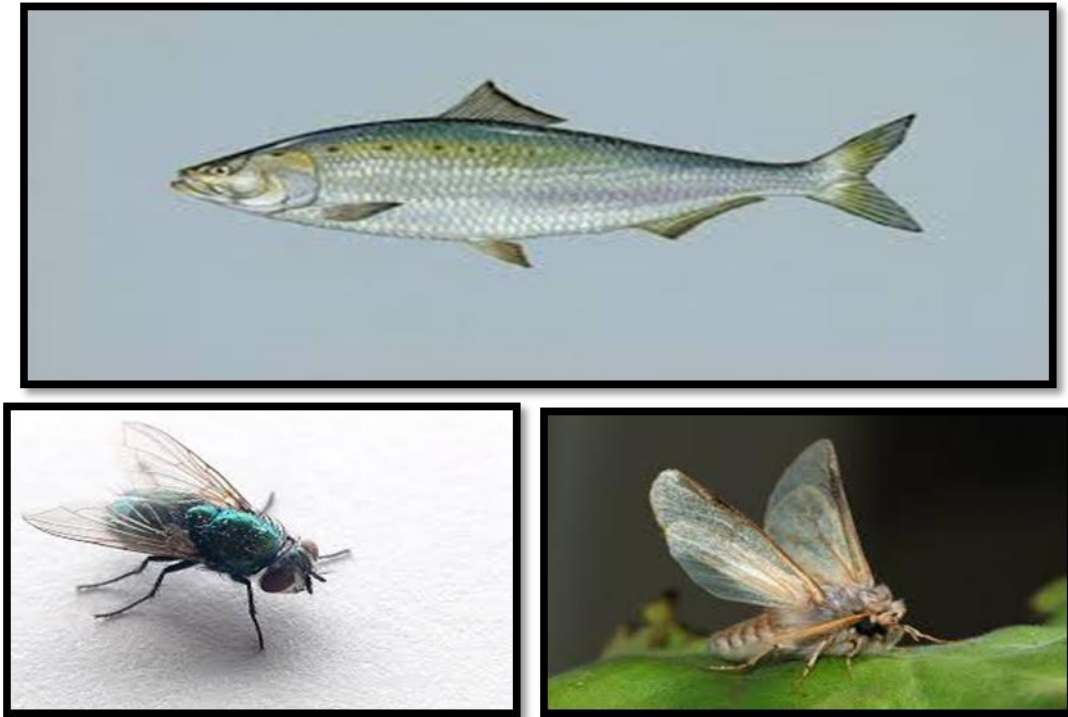
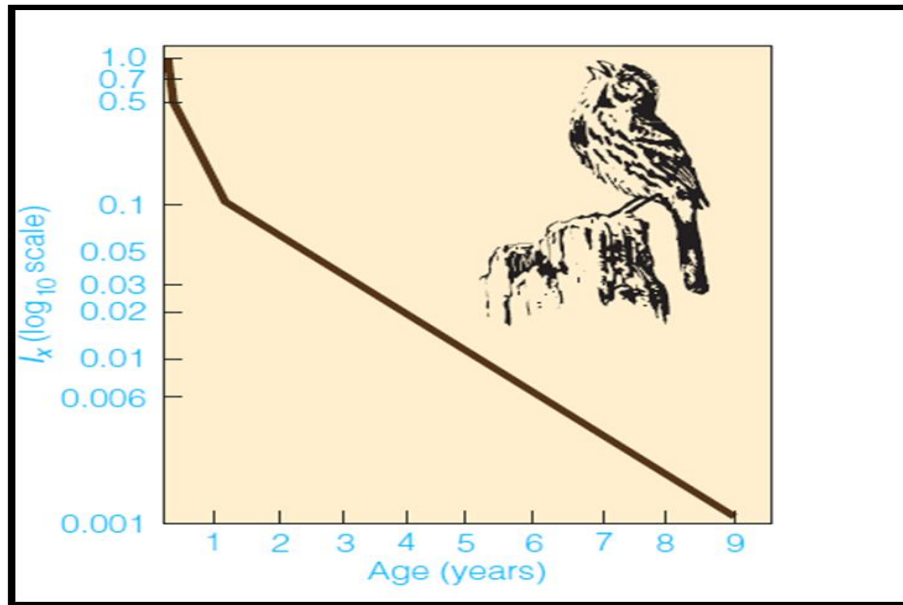


Figure.4: Animals showing type-III survivorship curve (fishes, insects etc).

Many birds, mice and rabbits show a slightly concave or sigmoid curve due to higher mortality in the young individuals; however, mortality is low when they reach to the adult stages. The population which is characterized by Type-III curve (concave) often required high birth rates to maintain the constant population size. The high birth rates make sure that sufficient numbers of young individuals survive to reach at reproductive age to ensure that the population can continues to maintain itself.

Analyzing the shape of the survivorship curve is very important to find out the critical periods in the life history of the organisms. When the line of the survivorship curve becomes steeper, it denotes the increase in mortality rate of the individuals due to some environmental factors or some developmental effects on the population. For example, Salmon fish produce several thousand eggs in its one time reproductive event, but only few young ones are able to survive and reach the adult stage. Suppose, if only one egg out of 10,000 eggs survived to reach adult stage, it indicates that only 0.01% of the total invested energy is represented in the next generation. Most of the larger animals survived for several years and invest their energy

in repeated reproductive events are considered as **iteroparous** whereas, many species of plants, insects and different microorganisms, after a single reproductive effort one or both individuals die, are considered as **semelparous** which represents ultimate expenditure of energy to produce maximum number of eggs.



**Figure.5: Survivorship curve of the song sparrow (*Melospiza melodia*). The curve is typical of birds.
(Adapted from Johnston 1956.)**

These three types of generalized survivorship curves can be used to compare the survival of a species. In fact, no population in the real world has a constant age-specific survival rate throughout the whole life span. Many species in their life history exhibit components of all three types of generalized survivorship curves. For example, in song sparrow (*Melospiza melodia*), there is high mortality in juvenile stage (type III survivorship curve) and in adult stage it becomes linear (type II curve) (Figure 5). The Survivorship curve for the gray squirrel is presented in figure 6.

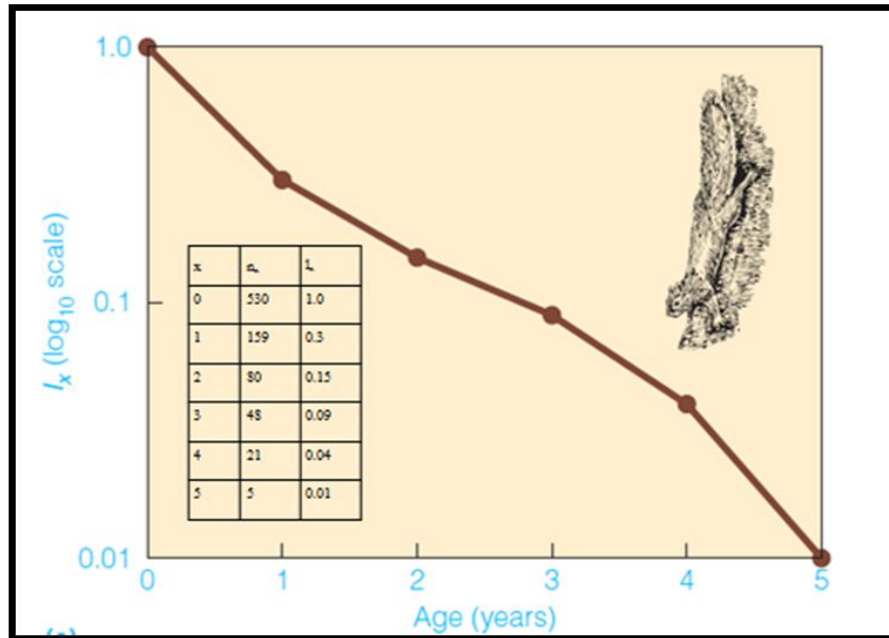


Figure.6: Survivorship curve of gray squirrel (Source: Smith and Smith, 2012)

A slightly concave or sigmoid survivorship curve is characteristic of many birds, mice and rabbits. In these animals, the mortality rate is high during the younger stage but becomes lower and almost constant in the adult stage (1 year or older). In some holometabolous insects (*i.e.*, insects with complete metamorphosis), such as butterflies, the survival rate differs in successive life-history stages and the curve becomes the **stair-step** type survivorship curve, the initial, middle and final steep segments represent the egg population and short lived adult stages and the two middle flatter segments represent the larval and pupal stages which exhibit less mortality. Some earthworm's species also exhibit stair-step type survivorship curve. Lastly, crowding (high density) in certain populations such as black tail deer population may influence the shape of survivorship curve.

The survivorship curve of human population is highly convex. This has become possible because of increased medical care, better hygiene, improved nutrition, and so on. The average life span of an Indian male has gone up from 30 years (before 1947) to 58 years now. But maximum longevity has not gone up very much in any society.

4. Mortality curve

When mortality rate (q_x) of the life table is plotted against age (x), it is called as mortality curve (Figure 7). Mortality curve has two phases, the first phase is juvenile phase, where mortality rate is high and second phase is post juvenile phase in which mortality rate first decreases with increase in age and then mortality rate increases with age after a period of low mortality. Usually, the mortality curve is j-shaped and such curve indicates the rate of mortality through the slope of line is more as compare to survivorship curve.

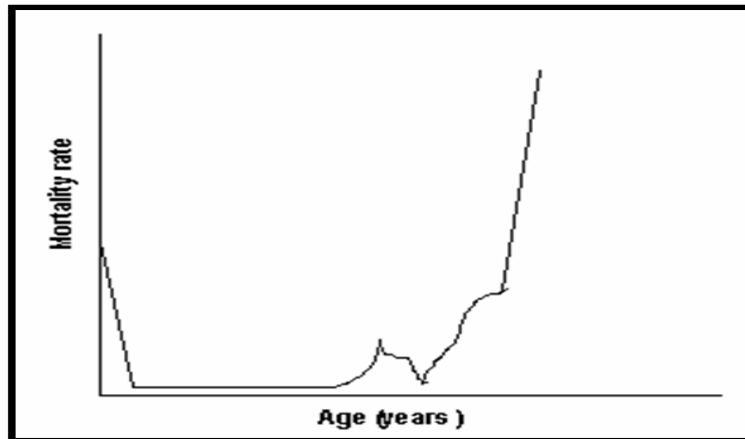


Figure.7: Hypothetical mortality curve.

Mortality curves for the life tables presented in figure 8 (gray squirrel). For the gray squirrel cohort, the curve consists of two parts: the first part is a juvenile phase where mortality rate is high and second phase is a post-juvenile phase in which mortality rate decreases with increasing age until mortality reaches to some low point and then again it start increasing.

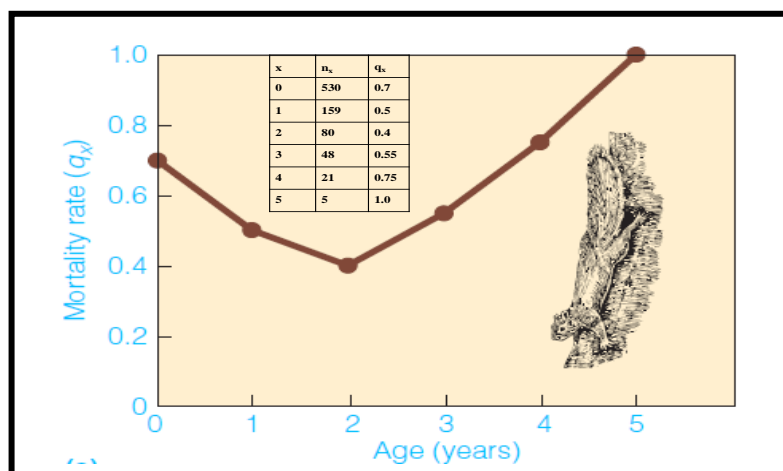


Figure.8: mortality curves for (a) gray squirrel population, (Source: Smith and Smith, 2012)

5. Fecundity table

A life table demonstrates the mortality schedule of a population. The next step in the life table is to combine the mortality and reproduction to estimate the net population change. Alfred Lokta (1925) derived one demographic parameter called intrinsic capacity of increase. Any population in the nature has its mean longevity, growth, mortality and speed of development. These parameters are not constant for any species. Their mean value is determined by innate quality of the organisms and their surrounding environment.

Due to fluctuation in environment such as winter and summer, the population cannot grow continuously (population increases in favourable conditions and decreases in adverse condition). The organisms have great intrinsic capacity of increase; however, in nature there is always a balance in the population size. For example, female *Helicoverpa armigera*, a polyphagous pest can produce 1200-1600 eggs in its life time; even then there is a balance in the population size of this pest due to environment and biological agents. Therefore, in nature there is actual rate of change of population occurs in response to environment, age structure and genetic composition.

A standard convention in the study of populations is to express birthrates as births/1000 population/per unit time. This is calculated by dividing the number of births over given time period by the population size at the beginning and multiplying by 1000. This will represent the crude birthrate and this can be further improved by taking two important factors. First, in sexually reproducing population, only females give birth to young ones. Second, the number of birth given by female varies with age. Hence, birthrate can be expressed as the number of births per female of age x . As the size of population is increased due to reproduction by females, the age-specific birthrate can be further modified by determining mean number of females born to a female in each age group (bx). Following given data for age-specific birthrates of gray squirrel population can be used to construct fecundity life table (table 1):

x	bx
0	0
1	2
2	3
3	3
4	2
5	0
Sum	10

Table.1: Age specific birthrate of gray squirrel population

At the beginning (age 0), females did not produce any offsprings, so the value of bx is 0. At age 1, female produces an average of two female offsprings. Females of ages 2 and 3, the average number of female offspring produced (bx) increases to 3 and after that bx declines to 2 when female reaches to age 4. By the age of 5, females cannot produce offsprings, therefore, the value of bx is again reaches to zero. The summation of bx values of all age group provides an estimate of the average number of female offspring produced by female in her lifetime. It is called as gross reproductive rate. In the above example, the gross reproductive rate of gray squirrel population is 10. However, in this example, value assumes that the maximum survival of female squirrel is 5 years. Now, next step is to measure net reproductive rate that integrate the age-specific birthrate and the probability of survival of female to any specific age.

After knowing the fertility schedule (bx) and proportion surviving (lx), another important parameter, net reproductive rate (R_0) can be calculated.

$$\text{Net reproductive rate } (R_0) = \frac{\text{Number of female offspring produced in generation } t+1}{\text{Number of female offspring produced in generation } t}$$

Net reproductive rate is thus the multiplication rate per generation and it can be calculated by multiplying lx and bx schedules and summing over all age groups.

$$R_0 = \sum_0^{\infty} (l_x b_x)$$

If net reproductive rate is 1.0, the population is replacing itself and if rate is below 1.0, the population will not replace itself.

6. Determination of net reproductive rate (R_0)

The age specific birth rate of gray squirrel population can be used for constructing a fecundity or fertility table. The fecundity table uses the survivorship column (l_x) and age-specific birthrates (b_x) from the life table data. In the fecundity table, initially b_x increases with the age, whereas, proportion survivorship (l_x) declines with each age group (table 2). To adjust for mortality, each b_x value is multiplied by its corresponding proportion survival (l_x) values. The resulting value ($l_x b_x$) gives the average number of female offsprings produced in each age class, adjusted for survivorship.

Table.2: Fecundity table of gray squirrel population.

x	l_x	b_x	$l_x b_x$
0	1.0	0.0	0.00
1	0.3	2.0	0.60
2	0.15	3.0	0.45
3	0.09	3.0	0.25
4	0.04	2.0	0.08
5	0.01	0.0	0.00
Σ		10.0	1.40

Therefore, the value of b_x for one year old female is 2, but when it is adjusted for survival (l_x), the value declines to 0.6. Similarly, for female of age group 2, the value of b_x is 3 and $l_x b_x$ value declines to 0.45. It represents that the survival of adult females is poor. The values of $l_x b_x$ are summed over all ages at which reproduction occurs that will give net reproductive rate.

$$R_0 = \Sigma l_x b_x = 1.40$$

Therefore the net reproductive rate of Gray squirrel population is 1.4. If value of R_0 is greater than 1, females are more than replacing themselves. In this example, R_0 value of gray squirrel suggests a growing population of females.

The difference between gross reproductive rate and net reproductive rates (10 and 1.4, respectively) reflects that only a small proportion of female gray squirrel will survive to the maximum age and produce 10 female offspring. As the value of R_0 is a function of the age-specific birth rate and survivorship, it is a product of life history characteristics: the reproduction time, allocation to reproduction, trade-off between the size and number of offspring produced and the level of parental care. Therefore, net reproductive rate (R_0) provides a means of evaluating individual (fitness) and population consequences of specific life history characteristics. The fecundity table of human females in the united state is presented in the table 3. If human population of the United State continues to grow at these rates, it would multiply 1.039 times in each generation.

Table.3: Fecundity table for women in United State (Source: statistical abstract of the United States 2007)

Age group	Age (x)	Proportion surviving (l_x)	Number female offsprings per female aged x per 5 year period (b_x)	$l_x b_x$
0-9	5.0	0.994	0.000	0.000
10-14	12.5	0.994	0.002	0.002
15-19	17.5	0.993	0.143	0.142
20-24	22.5	0.991	0.286	0.283
25-29	27.5	0.990	0.286	0.283
30-34	32.5	0.998	0.216	0.213
35-39	37.5	0.985	0.092	0.090
40-44	42.5	0.981	0.018	0.017
45-49	47.5	0.974	0.008	0.007
50 and more	--	--	0.000	0.000
			$R_0 = \sum_0^{\infty} (l_x b_x) = 1.039$	

In the natural condition environment is always fluctuating (sometimes favourable and sometime unfavourable). When environmental conditions are favourable, there is increase in population size and if conditions are adverse population number declines. Therefore in the natural state, a population shows the actual change that can vary from positive to negative due to change in social structure, age distribution, genetic composition or change in environmental factor.

An organism innate capacity of increase (Malthusian parameter) depends on its fertility, longevity and development speed. These processes are integrated with natality rate and mortality rate. The natality rate can be explained by birth schedule, egg or seed production of the population. The number of female offsprings produced by per female aged x to $x+1$ is considered as fertility schedule (b_x). Usually females are counted for fertility schedule and demographers considers only females as a population which further produces more females.

Table.4: The following given hypothetical data can be used to illustrate how the intrinsic capacity of increase (r) can be calculated from biological data.

x	l_x	b_x	$(l_x)(b_x)$	$(x)(l_x)(b_x)$
0	1	0	0	0
1	1	2	2	2
2	1	1	1	2
3	1	2	0	0
4	0	--	--	--
			$R_0 = \sum l_x b_x = 3$	

The value of l_x and b_x from the tables are sufficient to allow calculation of intrinsic capacity of increase in number (r). First step is to calculate the net reproductive rate (R_0) which is already explained above in this module. For the given data, net reproductive rate is 3 which clearly indicate that the population can triple its size in each generation (table 4). But how long is a generation? The length of a generation (G) can be explained as the mean period between the birth of parents and the production of the offspring. Dublin and Lotka in 1925 defined the mean length of a generation by the formula:

$$G = \frac{\sum l_x b_x x}{\sum l_x b_x} = \frac{\sum l_x b_x x}{R_0}$$

For the given hypothetical data the value of G is 1.3 years. Knowing the value of R_0 and G , we can calculate intrinsic capacity of increase (r) by applying the formula:

$$r = \log_e(R_0)/G$$

$$r = \log_e(3)/1.3 = 0.82 \text{ per individual per year}$$

The capacity for increase is an instantaneous rate that can be converted to more familiar finite rate by the formula:

$$\text{Finite rate of increase} = \lambda = e^r$$

Any component of the environment such as temperature, humidity, rainfall may affect natality and mortality rates and hence r .

Example: Fecundity Table for a *Gambusia holbrooki* population.

x (days)	n_x	L_x	b_x	$l_x b_x$	$l_x b_{xx}$
0	759	1.000	00.00	0.00	0.00
30	629	0.829	00.00	0.00	0.00
60	439	0.578	00.00	0.00	0.00
90	199	0.262	24.00	6.29	566.32
120	79	0.104	00.00	0.00	0.00
150	19	0.025	29.00	0.73	108.00
180	4	0.005	32.00	0.17	30.36
210	1	0.001	00.00	0.00	0.00
240	0	0.000	00.00	0.00	0.00
			Sum	7.19	705.57
				$R_0 = 7.19$ offsprings	
				$G = 98.17$ days	
				$r = 0.02$ individual/day	

7. Summary

- A population can be defined as a group of individuals belonging to the same species.
- The surviving individuals are more significant for a population than the dead; the death rate can be represented by survivorship curves.
- Survivorship curves can be classified into three types. It represents the different nature of survivors in different types of populations.
- Type-I or convex curve is present in the population of those species which exhibit low mortality rate up to the end of their life.
- Type-II curve indicates an age-specific constant rate of mortality.
- Type-III curve is the characteristic of those species in which mortality rate is high during the early life stages. These three types of generalized survivorship curves can be used to compare the survival of a species.
- When mortality rate is plotted against age, it is called as mortality curve. It has two phases, juvenile phase and post juvenile phase.
- Any population in the nature has its mean longevity, growth, mortality and speed of development. Due to fluctuation in environment such as winter and summer, the population cannot grow continuously
- A standard convention in the study of populations is to express birthrates as births/1000 population/per unit time.
- After knowing the fertility schedule (bx) and proportion surviving (lx), another important parameter, net reproductive rate (R_0) can be calculated.
- Net reproductive rate is thus the multiplication rate per generation.
- An organism innate capacity of increase depends on its fertility, longevity and development speed. These processes are integrated with natality rate and mortality rate.
- The length of a generation (G) can be explained as the mean period between the birth of parents and the production of the offspring.