Chapter 2: Population Ecology

Learning Outcomes - At the end of this chapter, students will be able to:

• Define the variables in the exponential and logistic growth equations.
• Use the exponential and logistic equations to predict population growth rate.
• Compare the environmental conditions represented by the exponential growth model vs. the logistic growth model.
• Define carrying capacity and be able to label the carrying capacity on a graph.
• Compare density-dependent and density-independent factors that limit population growth and give examples of each.
• Interpret survivorship curves and give examples of organisms that would fit each type of curve.

Chapter outline

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2.1 Population Ecology

Ecology is a sub-discipline of biology that studies the interactions between organisms and their environments. A group of interbreeding individuals (individuals of the same species) living and interacting in a given area at a given time is defined as a population. These individuals rely on the same resources and are influenced by the same environmental factors. Population ecology, therefore, is the study of how individuals of a particular species interact with their environment and change over time. The study of any population usually begins by determining how many individuals of a particular species exist, and how closely associated they are with each other. Within a particular habitat, a population can be characterized by its population size ($N$), defined by the total number of individuals, and its population density, the number of individuals of a particular species within a specific area or volume (units are number of individuals/unit area or unit volume). Population size and density are the two main characteristics used to describe a population. For example, larger populations may be more stable and able to persist better than smaller populations because of the greater amount of genetic variability, and their potential to adapt to the environment or to changes in the environment. On the other hand, a member of a population with low population density (more spread out in the habitat), might have more difficulty finding a mate to reproduce compared to a population of higher density. Other characteristics of a population include dispersion – the way individuals are spaced within the area; age structure – number of individuals in different age groups and; sex ratio – proportion of males to females; and growth – change in population size (increase or decrease) over time.

2.2 Population Growth Models

Populations change over time and space as individuals are born or immigrate (arrive from outside the population) into an area and others die or emigrate (depart from the population to another location). Populations grow and shrink and the age and gender composition also change through time and in response to changing environmental conditions. Some populations, for example trees in a mature forest, are relatively constant over time while others change rapidly. Using idealized models, population ecologists can predict how the size of a particular population will change over time under different conditions.

2.2.1 Exponential Growth

Charles Darwin, in his theory of natural selection, was greatly influenced by the English clergyman Thomas Malthus. Malthus published a book (An Essay on the Principle of Population) in 1798 stating that populations with unlimited natural resources grow very rapidly. According to the Malthus’ model, once population size exceeds available resources, population growth decreases dramatically. This accelerating pattern of increasing population size is called exponential growth, meaning that the population is increasing by a fixed percentage each year. When plotted (visualized) on a graph showing how the population size increases over time, the result is a J-shaped curve (Figure 2.1). Each individual in the population reproduces by a certain amount ($r$) and as the population gets larger, there are more individuals reproducing by that same amount (the fixed percentage). In nature, exponential growth only occurs if there are no external limits.

One example of exponential growth is seen in bacteria. Bacteria are prokaryotes (organisms whose cells lack a nucleus and membrane-bound organelles) that reproduce by fission (each individual cell splits into two new cells). This process takes about an hour for many bacterial species. If 100 bacteria are placed in a large flask with an unlimited supply of nutrients (so the nutrients will not
become depleted), after an hour, there is one round of division and each organism divides, resulting in 200 organisms - an increase of 100. In another hour, each of the 200 organisms divides, producing 400 - an increase of 200 organisms. After the third hour, there should be 800 bacteria in the flask - an increase of 400 organisms. After ½ a day and 12 of these cycles, the population would have increased from 100 cells to more than 24,000 cells. When the population size, \( N \), is plotted over time, a J-shaped growth curve is produced (Figure 2.1). This shows that the number of individuals added during each reproduction generation is accelerating – increasing at a faster rate.

![Figure 2.1: The “J” shaped curve of exponential growth for a hypothetical population of bacteria. The population starts out with 100 individuals and after 11 hours there are over 24,000 individuals. As time goes on and the population size increases, the rate of increase also increases (each step up becomes bigger). In this figure “r” is positive.](image)

This type of growth can be represented using a mathematical function known as the **exponential growth model**:

\[
G = r \times N \quad \text{(also expressed as } \frac{dN}{dt} = r \times N)\]

In this equation

- \( G \) (or \( \frac{dN}{dt} \)) is the **population growth rate**, it is a measure of the number of individuals added per time interval time.
- \( r \) is the **per capita rate of increase** (the average contribution of each member in a population to population growth; per capita means “per person”).
- \( N \) is the **population size**, the number of individuals in the population at a particular time.
Per capita rate of increase (r)

In exponential growth, the population growth rate \( G \) depends on population size \( (N) \) and the per capita rate of increase \( (r) \). In this model \( r \) does not change (fixed percentage) and change in population growth rate, \( G \), is due to change in population size, \( N \). As new individuals are added to the population, each of the new additions contribute to population growth at the same rate \( (r) \) as the individuals already in the population.

\[
r = (\text{birth rate} + \text{immigration rate}) - (\text{death rate and emigration rate}).
\]

If \( r \) is positive (> zero), the population is increasing in size; this means that the birth and immigration rates are greater than death and emigration.

If \( r \) is negative (< zero), the population is decreasing in size; this means that the birth and immigration rates are less than death and emigration rates.

If \( r \) is zero, then the population growth rate \( (G) \) is zero and population size is unchanging, a condition known as zero population growth. “\( r \)” varies depending on the type of organism, for example a population of bacteria would have a much higher “\( r \)” than an elephant population. In the exponential growth model \( r \) is multiplied by the population size, \( N \), so population growth rate is largely influenced by \( N \). This means that if two populations have the same per capita rate of increase \( (r) \), the population with a larger \( N \) will have a larger population growth rate than the one with a smaller \( N \).

2.2.2 Logistic Growth

Exponential growth cannot continue forever because resources (food, water, shelter) will become limited. Exponential growth may occur in environments where there are few individuals and plentiful resources, but soon or later, the population gets large enough that individuals run out of vital resources such as food or living space, slowing the growth rate. When resources are limited, populations exhibit logistic growth. In logistic growth a population grows nearly exponentially at first when the population is small and resources are plentiful but growth rate slows down as the population size nears limit of the environment and resources begin to be in short supply and finally stabilizes (zero population growth rate) at the maximum population size that can be supported by the environment (carrying capacity). This results in a characteristic S-shaped growth curve (Figure 2.2). The mathematical function or logistic growth model is represented by the following equation:

\[
G = r \times N \times [1 - \frac{N}{K}]
\]

Where,

\( K \) is the carrying capacity – the maximum population size that a particular environment can sustain (“carry”). Notice that this model is similar to the exponential growth model except for the addition of the carrying capacity.

In the exponential growth model, population growth rate was mainly dependent on \( N \) so that each new individual added to the population contributed equally to its growth as those individuals previously in the population because per capita rate of increase is fixed. In the logistic growth model, individuals’ contribution to population growth rate depends on the amount of resources available (K). As the number of individuals \( (N) \) in a population increases, fewer resources are available to each
individual. As resources diminish, each individual on average, produces fewer offspring than when resources are plentiful, causing the birth rate of the population to decrease.

Figure 2.2: Shows logistic growth of a hypothetical bacteria population. The population starts out with 10 individuals and then reaches the carrying capacity of the habitat which is 500 individuals.

**Influence of K on population growth rate**

In the logistic growth model, the exponential growth \((r \times N)\) is multiplied by fraction or expression that describes the effect that limiting factors \((I - N/K)\) have on an increasing population. Initially when the population is very small compared to the capacity of the environment \((K)\), \(1 - N/K\) is a large fraction that nearly equals 1 so population growth rate is close to the exponential growth \((r \times N)\). For example, supposing an environment can support a maximum of 100 individuals and \(N = 2\), \(N\) is so small that \(I - N/K (1 - 2/100 = 0.98)\) will be large, close to 1. As the population increases and population size gets closer to carrying capacity \((N\) nearly equals \(K)\), then \(1 - N/K\) is a small fraction that nearly equals zero and when this fraction is multiplied by \(r \times N\), population growth rate is slowed down. In the earlier example, if the population grows to 98 individuals, which is close to (but not equal) \(K\), then \(1 - N/K (1 - 98/100 = 0.02)\) will be so small, close to zero. If population size equals the carrying capacity, \(N/K = 1\), so \(1 - N/K = 0\), population growth rate will be zero (in the above example, \(1 - 100/100 = 0\)). This model, therefore, predicts that a population’s growth rate will be small when the population size is either small or large, and highest when the population is at an intermediate level relative to \(K\). At small populations, growth rate is limited by the small amount of individuals \((N)\) available to reproduce and contribute to population growth rate whereas at large populations, growth rate is limited by the limited amount of resources available to each of the large number of individuals to enable them reproduce successfully. In fact, maximum population growth rate \((G)\) occurs when \(N\) is half of \(K\).
Yeast is a microscopic fungus, used to make bread and alcoholic beverages, that exhibits the classical S-shaped logistic growth curve when grown in a test tube (Figure 2.3). Its growth levels off as the population depletes the nutrients that are necessary for its growth. In the real world, however, there are variations to this idealized curve. For example, a population of harbor seals may exceed the carrying capacity for a short time and then fall below the carrying capacity for a brief time period and as more resources become available, the population grows again (Figure 2.4). This fluctuation in population size continues to occur as the population oscillates around its carrying capacity. Still, even with this oscillation, the logistic model is exhibited.

**Figure 2.3**: Graph showing amount of yeast versus time of growth in hours. The curve rises steeply, and then plateaus at the carrying capacity. Data points tightly follow the curve. The image is a micrograph (microscope image) of yeast cells.

**Figure 2.4**: Graph showing the number of harbor seals versus time in years. The curve rises steeply then plateaus at the carrying capacity, but this time there is much more scatter in the data. A photo of a harbor seal is shown.
2.3 Factors limiting population growth

Recall previously that we defined density as the number of individuals per unit area. In nature, a population that is introduced to a new environment or is rebounding from a catastrophic decline in numbers may grow exponentially for a while because density is low and resources are not limiting. Eventually, one or more environmental factors will limit its population growth rate as the population size approaches the carrying capacity and density increases. Example: imagine that in an effort to preserve elk, a population of 20 individuals is introduced to a previously unoccupied island that’s 200 km$^2$ in size. The population density of elk on this island is 0.1 elk/km$^2$ (or 10 km$^2$ for each individual elk). As this population grows (depending on its per capita rate of increase), the number of individuals increases but the amount of space does not so density increases. Suppose that 10 years later, the elk population has grown to 800 individuals, density = 4 elk/ km$^2$ (or 0.25 km$^2$ for each individual). The population growth rate will be limited by various factors in the environment. For example, birth rates may decrease due to limited food or death rate increase due to rapid spread of disease as individuals encounter one another more often. This impact on birth and death rate in turn influences the per capita rate of increase and how the population size changes with changes in the environment. When birth and death rates of a population change as the density of the population changes, the rates are said to be density-dependent and the environmental factors that affect birth and death rates are known as density-dependent factors. In other cases, populations are held in check by factors that are not related to the density of the population and are called density-independent factors and influence population size regardless of population density. Conservation biologists want to understand both types because this helps them manage populations and prevent extinction or overpopulation.

The density of a population can enhance or diminish the impact of density-dependent factors. Most density-dependent factors are biological in nature (biotic), and include such things as predation, inter- and intraspecific competition for food and mates, accumulation of waste, and diseases such as those caused by parasites. Usually, higher population density results in higher death rates and lower birth rates. For example, as a population increases in size food becomes scarcer and some individuals will die from starvation meaning that the death rate from starvation increases as population size increases. Also as food becomes scarcer, birth rates decrease due to fewer available resources for the mother meaning that the birth rate decreases as population size increases. For density-dependent factors, there is a feedback loop between population density and the density-dependent factor.

Two examples of density-dependent regulation are shown in Figure 2.5. First one is showing results from a study focusing on the giant intestinal roundworm (*Ascaris lumbricoides*), a parasite that infects humans and other mammals. Denser populations of the parasite exhibited lower fecundity (number of eggs per female). One possible explanation for this is that females would be smaller in more dense populations because of limited resources and smaller females produce fewer eggs.
Figure 2.5: (a) Graph of number of eggs per female (fecundity), as a function of population size. In this population of roundworms, fecundity (number of eggs) decreases with population density. (b) Graph of clutch size (number of eggs per “litter”) of the great tits bird as a function of population size (breeding pairs). Again, clutch size decreases as population density increases. (Photo credits: Worm image from Wikimedia commons, public domain image; bird image from Wikimedia commons, photo by Francis C. Franklin / CC-BY-SA-3.0)

Density-independent birth rates and death rates do NOT depend on population size; these factors are independent of, or not influenced by, population density. Many factors influence population size regardless of the population density, including weather extremes, natural disasters (earthquakes, hurricanes, tornadoes, tsunamis, etc.), pollution and other physical/abiotic factors. For example, an individual deer may be killed in a forest fire regardless of how many deer happen to be in the forest. The forest fire is not responding to deer population size. As the weather grows cooler in the winter, many insects die from the cold. The change in weather does not depend on whether there is a population size of 100 mosquitoes or 100,000 mosquitoes, most mosquitoes will die from the cold regardless of the population size and the weather will change irrespective of mosquito population density. Looking at the growth curve of such a population would show something like an exponential growth followed by a rapid decline rather than levelling off (Figure 2.6).
Figure 2.6: Weather change acting as a density-independent factor limiting aphid population growth. This insect undergoes exponential growth in the early spring and then rapidly die off when the weather turns hot and dry in the summer.

In real-life situations, density-dependent and independent factors interact. For example, a devastating earthquake occurred in Haiti in 2010. This earthquake was a natural geologic event that caused a high human death toll from this density-independent event. Then there were high densities of people in refugee camps and the high density caused disease to spread quickly, representing a density-dependent death rate.

Q: Can you think of other density-dependent (biological) and density-independent (abiotic) population limiting factors?

2.4 Life Tables and Survivorship

Population ecologists use life tables to study species and identify the most vulnerable stages of organisms’ lives to develop effective measures for maintaining viable populations. Life tables, like Table 2.1, track survivorship, the chance of an individual in a given population surviving to various ages. Life tables were invented by the insurance industry to predict how long, on average, a person will live. Biologists use a life table as a quick window into the lives of the individuals of a population, showing how long they are likely to live, when they’ll reproduce, and how many offspring they’ll produce. Life tables are used to construct survivorship curves, which are graphs showing the proportion of individuals of a particular age that are now alive in a population. Survivorship (chance of surviving to a particular age) is plotted on the y-axis as a function of age or time on the x-axis. However, if the percent of maximum lifespan is used on the x-axis instead of actual ages, it is possible to compare survivorship curves for different types of organisms (Figure 2.7). All survivorship curves start along the y-axis intercept with all of the individuals in the population (or 100% of the individuals...
surviving). As the population ages, individuals die and the curves goes down. A survivorship curve never goes up.

**Table 2.1**: Life Table for the U.S. population in 2011 showing the number who are expected to be alive at the beginning of each age interval based on the death rates in 2011. For example, 95,816 people out of 100,000 are expected to live to age 50 (0.983 chance of survival). The chance of surviving to age 60 is 0.964 but the chance of surviving to age 90 is only 0.570.

<table>
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<th>Age (years)</th>
<th>Number Living at Start of Age Interval</th>
<th>Number Dying During Interval</th>
<th>Chance of Surviving Interval</th>
<th>Chance of Dying During Interval</th>
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</thead>
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<td>606</td>
<td>0.993942</td>
<td>0.006058</td>
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<tr>
<td>1-5</td>
<td>99394</td>
<td>105</td>
<td>0.988946</td>
<td>0.001054</td>
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<td>5-10</td>
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<td>0.999397</td>
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<td>0.995704</td>
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<td>475</td>
<td>0.995176</td>
<td>0.004824</td>
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<tr>
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<td>553</td>
<td>0.994362</td>
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</table>

**SOURCE**: CDC/NCHS, National Vital Statistics System.

Survivorship curves reveal a huge amount of information about a population, such as whether most offspring die shortly after birth or whether most survive to adulthood and likely to live long lives. They generally fall into one of three typical shapes, Types I, II and III (Figure 2.7a). Organisms that exhibit Type I survivorship curves have the highest probability of surviving every age interval until old age, then the risk of dying increases dramatically. Humans are an example of a species with a Type I survivorship curve. Others include the giant tortoise and most large mammals such as elephants. These organisms have few natural predators and are, therefore, likely to live long lives. They tend to produce only a few offspring at a time and invest significant time and effort in each offspring, which increases survival.

In the Type III survivorship curve most of the deaths occur in the youngest age groups. Juvenile survivorship is very low and many individuals die young but individuals lucky enough to survive the first few age intervals are likely to live a much longer time. Most plants species, insect
species, frogs as well as marine species such as oysters and fishes have a Type III survivorship curve. A female frog may lay hundreds of eggs in a pond and these eggs produce hundreds of tadpoles. However, predators eat many of the young tadpoles and competition for food also means that many tadpoles don’t survive. But the few tadpoles that do survive and metamorphose into adults then live for a relatively long time (for a frog). The mackerel fish, a female is capable of producing a million eggs and on average only about 2 survive to adulthood. Organisms with this type of survivorship curve tend to produce very large numbers of offspring because most will not survive. They also tend not to provide much parental care, if any.

**Type II** survivorship is intermediate between the others and suggests that such species have an even chance of dying at any age. Many birds, small mammals such as squirrels, and small reptiles, like lizards, have a Type II survivorship curve. The straight line indicates that the proportion alive in each age interval drops at a steady, regular pace. The likelihood of dying in any age interval is the same.

In reality, most species don’t have survivorship curves that are definitively type I, II, or III. They may be anywhere in between. These three, though, represent the extremes and help us make predictions about reproductive rates and parental investment without extensive observations of individual behavior. For example, humans in less industrialized countries tend to have higher mortality rates in all age intervals, particularly in the earliest intervals when compared to individuals in industrialized countries. Looking at the population of the United States in 1900 (*Figure 2.7b*), you can see that mortality was much higher in the earliest intervals and throughout, the population seemed to exhibit a type II survivorship curve, similar to what might be seen in less industrialized countries or amongst the poorest populations.

**Figure 2.7:** (a) Survivorship curves show the distribution of individuals in a population according to age. Humans and most large mammals have a Type I survivorship curve because most death occurs in the older years. Birds have a Type II survivorship curve, as death at any age is equally probable. Trees have a Type III survivorship curve because very few survive the younger years, but after a certain age, individuals are much more likely to survive. (b) Survivorship curves for the US population for 1900, 1950, 2000, 2050, 2100


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This material has been modified from the OpenStax Biology textbook.
POPULATION ECOLOGY PRACTICE PROBLEMS

1. If a population is experiencing exponential growth, what happens to \( N \), \( r \) and \( G \) over time (increase, decrease or stay the same)?

2. At the beginning of the year, there are 7650 individuals in a population of beavers whose per capita rate of increase for the year is 0.18. What is its population growth rate at the end of the year?

3. A zebrafish population of 1000 individuals lives in an ecosystem that can support a maximum of 2000 zebrafish. The per capita rate of increase for the population is 0.01 for the year. What is the population growth rate?

4. In a scenario where: \( r = 0.25; \ K = 18,000; \)
   a. What is \( G \) when i) \( N = 4,500; \) ii) \( N = 9,000; \) and iii) \( N = 13,500? \)
   b. Which \( N \) level results in the highest population growth rate and why?

5. A chipmunk population is experiencing exponential growth with a population growth rate of 265 individuals/year, and a per capita rate of increase of 0.15. How many chipmunks are currently in this population?

6. Scientists discovered a new species of frog and were able to estimate its population at 755 individuals. At the end of the year, 105 frogs were added to this population. Assuming the population is undergoing exponential growth, what is the per capita rate of increase?

Test your skills (extra challenge)

7. At the beginning of the year, a wildlife area that is 1,000,000 ha in size has a population of 90 Brown bears with a per capita growth rate of 0.02. It’s estimated that brown bears need a territory of about 10 km\(^2\) per individual (note: 1 km\(^2\) = 100 ha). Use this information to answer the following questions.
   a. What is the density of brown bears in this wildlife preserve currently?
   b. What is the carrying capacity of the preserve?
   c. What is the population growth rate for this year?

8. A wildlife ranch currently has a population of polar bears whose death rate is 0.05 and birth rate is 0.12 per year. This particular ranch is isolated from other suitable habitats so there’s no immigration into or emigration from this population. This population is experiencing logistic growth and currently has 550 bears. If the population growth rate for the year was 36 bears, what is the carrying capacity of the preserve?