MODULE 2.3

# Constrained Growth

## Introduction

An animal introduced to a new environment will often reproduce at a very high rate. That is what happened when the Eurasian perch, called the ruffe (*Gymnocephalus cernuus*), was introduced to Lake Superior from an ocean-going ship's ballast. A small fish, usually 4 to 6 inches (in.) long, with sharp, menacing spines on its gill covers and dorsal fin, ruffe is a meal of last resort for most predators. Moreover, the Eurasian perch has little or no value as a fishery and is a formidable competitor. Vying with other benthivorous fish (e.g., yellow perch), they have the advantage of being more adaptable in their dietary choices, including rotifers, microcrustaceans, immature insects, larval, and small, adult fish. Interestingly, they are preyed upon on by very few species of larger fish and then only if other prey are scarce. Ruffe not only tolerate wide ranges of temperature and pH, they are also prolific breeders (6000 to 200,000 eggs/batch), spawning on a variety of substrates.

People involved in fisheries in the Great Lakes have every right to be alarmed by this intruder. When introduced to Loch Lomond, Scotland, ruffe populations increased exponentially and decimated the eggs of local salmon (Adams 1998). Although there has been no established causal association, McLean (1993) found that populations of native North American fish like yellow perch, perch-trout, and emerald shiners have all declined since the ruffe were introduced. It is hypothesized that ruffe either predate on their competitors eggs or decrease their food resources.

Because births exceed the numbers maturing and reproducing, all populations, theoretically, have the potential for exponential growth. Endemic populations increase rapidly at first, but they eventually encounter resistance from the environment—competitors, predators, limited resources, and disease. Thus, the environment tends to limit the growth of populations, so that they usually increase only to a certain level and then do not increase or decrease drastically unless a change in the environment occurs. This maximum population size that the environment can support indefinitely is termed the **carrying capacity**. Many introduced species that become pests, such as the ruffe in the Great Lakes, have a very high reproductive potential in their new environments because they are very adaptable to habitat and food sources, they have few or less-fit competitors, and few to no predators.

## Carrying Capacity

In Module 2.2, "Unconstrained Growth and Decay," we considered a population growing without constraints, such as competition for limited resources. For such a population, $P$, with instantaneous growth rate, $r$, the rate of change of the population has the following differential equation model:

$$\frac{dP}{dt} = rP$$

With initial population $P_0$, we saw that the analytical solution is $P = P_0e^{rt}$. In that module, we also developed the following finite difference equation for the change in $P$ from one time to the next, which we used in simulations:

$$\begin{aligned}\Delta P &= P(t) - P(t - \Delta t)\\ &= (r\ P(t - \Delta t))\ \Delta t\end{aligned}$$

Simulation and analytical solution graphs in Figures 2.2.2 and 2.2.3, respectively, of Module 2.2 display the exponential growth of unconstrained growth.

After developing such a model in Step 2 of the modeling process and solving the model (Step 3) as before, we should verify that the solution (Step 4) agrees with real data. However, as the introduction indicates, no confined population can grow without bound. Competition for food, shelter, and other resources eventually limits the possible growth. For example, suppose a deer refuge can support at most 1000 deer. We say that the carrying capacity ($M$) for the deer in the refuge is 1000.

**Definition** The **carrying capacity** for an organism in an area is the maximum number of organisms that the area can support.

### Quick Review Question 1

Cycling back to Step 2 of the modeling process, this question begins refinement of the population model to accommodate descriptions of population growth from the "Introduction" of this module.

**a.** Determine any additional variable and its units.

**b.** Consider the relationship between the number of individuals ($P$) and carrying capacity ($M$) as time ($t$) increases. List all the statements below that apply to the situation where the population is much smaller than the carrying capacity.

A. $P$ appears to grow almost proportionally to $t$.

B. $P$ appears to grow almost without bound.
C. $P$ appears to grow faster and faster.
D. $P$ appears to grow more and more slowly.
E. $P$ appears to decline faster and faster.
F. $P$ appears to decline more and more slowly.
G. $P$ appears to grow almost linearly with slope $M$.
H. $P$ is appears to be approaching $M$ asymptotically.
I. $P$ appears to grow exponentially.
J. $dP/dt$ appears to be almost proportional to $P$.
K. $dP/dt$ appears to be almost zero.
L. The birth rate is about the same as the death rate.
M. The birth rate is much greater than the death rate.
N. The birth rate is much less than the death rate.

**c.** List all the choices from Part b that apply to the situation where the population is close to but less than the carrying capacity.

**d.** List all the choices from Part b that apply to the situation where the population is close to but greater than the carrying capacity.

## Revised Model

In the revised model, for an initial population much lower than the carrying capacity, we want the population to increase in approximately the same exponential fashion as in the earlier unconstrained model. However, as the population size gets closer and closer to the carrying capacity, we need to dampen the growth more and more. Near the carrying capacity, the number of deaths should be almost equal to the number of births, so that the population remains roughly constant. To accomplish this dampening of growth, we could compute the number of deaths as a changing fraction of the number of births, which we model as $rP$. When the population is very small, we want the fraction to be almost zero, indicating that few individuals are dying. When the population is close to the carrying capacity, the fraction should be almost $1 = 100\%$. For populations larger than the carrying capacity, the fraction should be even larger so that the population decreases in size through deaths. Such a fraction is $P/M$. For example, if the population $P$ is 10 and the carrying capacity $M$ is 1000, then $P/M = 10/1000 = 0.01 = 1\%$. For a population $P = 995$ close to the carrying capacity, $P/M = 995/1000 = 0.995 = 99.5\%$; and for the excessive $P = 1400$, $P/M = 1400/1000 = 1.400 = 140\%$.

Thus, we can model the instantaneous rate of change of the number of deaths ($D$) as the fraction $P/M$ times the instantaneous rate of change of the number of births ($r$), as the following differential equation indicates:

$$\frac{dD}{dt} = \left(r\frac{P}{M}\right)P$$

The differential equation for the instantaneous rate of change of the population subtracts this value from the instantaneous rate of change of the number of births, as follows:

$$\frac{dP}{dt} = \underbrace{(rP)}_{births} - \underbrace{\left(r\frac{P}{M}\right)P}_{deaths}$$

or

$$\frac{dP}{dt} = r\left(1 - \frac{P}{M}\right)P \tag{1}$$

For the discrete simulation, where $P(t - 1)$ is the population estimate at time $t - 1$, the number of deaths from time $t - 1$ to time $t$ is

$$\Delta D = \left(r\frac{P(t-1)}{M}\right)P(t-1) \quad \text{for } \Delta t = 1$$

In general, we approximate the number of deaths from time $(t - \Delta t)$ to time $t$ by multiplying the corresponding value by $\Delta t$, as follows:

$$\Delta D = \left(r\frac{P(t-\Delta t)}{M}\right)P(t-\Delta t)\Delta t$$

where $P(t - \Delta t)$ is the population estimate at $(t - \Delta t)$. Thus, the change in population from time $(t - \Delta t)$ to time $t$ is the difference of the number of births and the number of deaths over that period:

$$\Delta P = \text{births} - \text{deaths}$$

$$\Delta P = \underbrace{\left(rP(t-\Delta t)\right)\Delta t}_{\text{births}} - \underbrace{\left(r\frac{P(t-\Delta t)}{M}\right)P(t-\Delta t)\Delta t}_{\text{deaths}}$$

$$= (r\Delta t)\left(1 - \frac{P(t-\Delta t)}{M}\right)P(t-\Delta t)$$

or

$$\Delta P = k\left(1 - \frac{P(t-\Delta t)}{M}\right)P(t-\Delta t), \text{ where } k = r\Delta t \tag{2}$$

Differential equation (1) and difference equation (2) are called **logistic equations**. Figure 2.3.1 displays the S-shaped curve characteristic of a logistic equation, where the initial population is less than the carrying capacity of 1000. Figure 2.3.2 shows how the population decreases to the carrying capacity when the initial population is 1500. Thus, the model appears to match observations from the "Introduction" qualitatively. To verify a particular model, we should estimate parameters, such as birth rate, and compare the results of the model to real data.

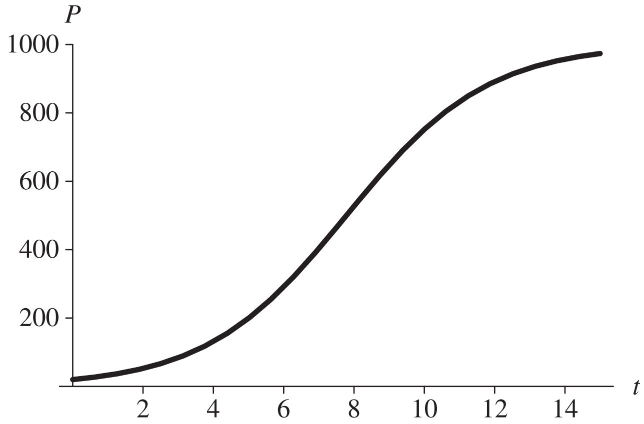


**Figure 2.3.1** Graph of logistic equation, where initial population is 20, carrying capacity is 1000, and instantaneous rate of change of births is 50%, with time ($t$) in years

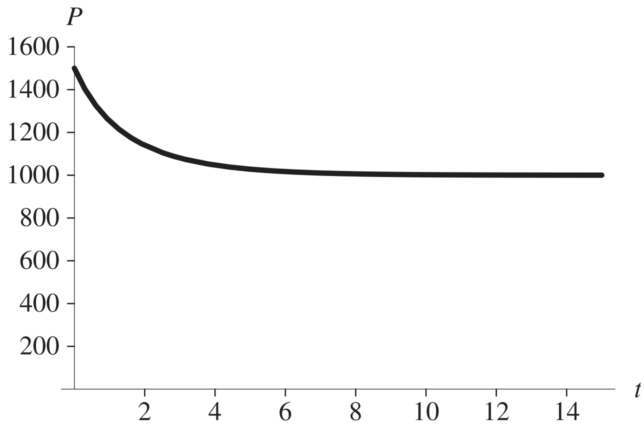


**Figure 2.3.2** Graph of logistic equation, where initial population is 1500, carrying capacity is 1000, and instantaneous rate of change of births is 50%, with time ($t$) in years

## Quick Review Question 2

**a.** Complete the difference equation to model constrained growth of a population $P$ with respect to time $t$ over a time step of 0.1 units, given that the population at time $t - \Delta t$ is $p \leq 1000$, the carrying capacity is 1000, the instantaneous rate of change of births is 105%, and the initial population is 20.
$\Delta P = \rule{1.5em}{0.4pt}(\rule{1.5em}{0.4pt}\ \rule{1.5em}{0.4pt}\ \rule{2.5em}{0.4pt})(p)(0.1)$

**b.** What is the maximum population?

**c.** Suppose the population at time $t = 5$ yr is 600 individuals. What is the population, rounded to the nearest integer, at time 5.1 yr?

## Equilibrium and Stability

The logistic equation with carrying capacity $M = 1000$ has an interesting property. If the initial population is less than 1000, as in Figure 2.3.1, the population increases to a limit of 1000. If the initial population is greater than 1000, as in Figure 2.3.2, the population decreases to the limit of 1000. Moreover, if the initial population is 1000, we see from Equation (1) that $P/M = 1000/1000 = 1$ and $dP/dt = r(1 - 1)P = 0$. In discrete terms, $\Delta P = 0$. A population starting at the carrying capacity remains there. We say that $M = 1000$ is an **equilibrium** size for the population because the population remains steady at that value or $P(t) = P(t - \Delta t) = 1000$ for all $t > 0$.

**Definitions** An **equilibrium solution** for a differential equation is a solution where the derivative is always zero. An **equilibrium solution** for a difference equation is a solution where the change is always zero.

### Quick Review Question 3

Give another equilibrium size for the logistic differential equation (1) or logistic difference equation (2).

Even if an initial positive population does not equal the carrying capacity $M = 1000$, eventually, the population size tends to that value. We say that the solution $P = 1000$ to the logistic equation (1) or (2) is **stable**. By contrast, for a positive carrying capacity, the solution $P = 0$ is **unstable**. If the initial population is close to but not equal to zero, the population does not tend to that solution over time. For the logistic equation, any displacement of the initial population from the carrying capacity exhibits the limiting behavior of Figure 2.3.1 or 2.3.2. In general, we say that a solution is stable if for a small displacement from the solution, $P$ tends to the solution.

**Definition** Suppose that $q$ is an equilibrium solution for a differential equation $dP/dt$ or a difference equation $\Delta P$. The solution $q$ is **stable** if there is an interval $(a, b)$ containing $q$, such that if the initial population $P(0)$ is in that interval, then

1. $P(t)$ is finite for all $t > 0$;
2. As time, $t$, becomes larger and larger, $P(t)$ approaches $q$.

The solution $q$ is **unstable** if no such interval exists.

## Exercises

**1.** Using calculus, solve the following:
**a.** The differential equation (1),

$$\frac{dP}{dt} = r\left(1 - \frac{P}{M}\right)P$$

where the carrying capacity, $M$, is 1000, $P_0 = 20$, and the instantaneous rate of change of the number of births, $r$, is 50%
**b.** The differential equation (1) in general

**2.** Consider $dy/dt = \cos(t)$.
**a.** Give all the equilibrium solutions.
**b.** Using calculus, find a function $y(t)$ that is a solution.
**c.** Give the most general function $y$ that is a solution.

**3.** It has been reported that a mallard must eat 3.2 ounces (oz) of rice each day to remain healthy. On the average, an acre of rice in a certain area yields 110 bushels (bu) per year; and a bushel of rice weighs 45 lb. Assuming that in the area 100 acres (ac) of rice are available for mallard consumption and mallards eat only rice, determine the carrying capacity for mallards in the area (Reinecke).

**4.** The **Gompertz differential equation**, which follows, is one of the best models for predicting the growth of cancer tumors:

$$\frac{dN}{dt} = kN\ln\left(\frac{M}{N}\right), \quad N(0) = N_0$$

where $N$ is the number of cancer cells and $k$ and $M$ are constants.
**a.** As $N$ approaches $M$, what does $dN/dt$ approach?
**b.** Make the substitution $u = \ln(M/N)$ in the Gompertz equation to eliminate $N$ and convert the equation to be in terms of $u$.
**c.** Using calculus, solve the transformed differential equation for $u$.
**d.** Using the relationship between $u$ and $N$ from Part b, convert your answer from Part c to be in terms of $N$. The result is the solution to the Gompertz differential equation.
**e.** Using calculus, verify that $N(t) = Me^{\ln\left(\frac{N_0}{M}\right)e^{-kt}}$ is the solution to the Gompertz differential equation.
**f.** Using the solution in Part e, what does $N$ approach as $t$ goes to infinity?

**5. a.** Graph $y = e^{-t}$.
Match each of the following scenarios to a differential equation that might model it.

A. $dP/dt = 0.05P$ B. $dP/dt = 0.05P + e^{-t}$
C. $dP/dt = 0.05(1 - e^{-t})P$ D. $dP/dt = 0.05P - 0.0003P^2 - 400$
E. $dP/dt = 0.05e^{-t}P$ F. $dP/dt = 0.05P - 0.0003P^2$

**b.** At first, a bacteria colony appears to grow without bound; but because of limited nutrients and space, the population eventually approaches a limit.
**c.** Because of degradation of nutrients, the growth of a bacterial colony becomes dampened.
**d.** A bacterial colony has unlimited nutrients and space and grows without bound.
**e.** Because of adjustment to its new setting, a bacterial colony grows slowly at first before appearing to grow without bound.
**f.** Each day, a scientist removes a constant amount from the colony.

**6.** Write an algorithm for simulation of constrained growth similar to Algorithm 1 for simulation of unconstrained growth in Module 2.2.

## Projects

*For additional projects, see Module 7.4, "What Goes Around Comes Around—The Carbon Cycle"; Module 7.5, "A Heated Debate—Global Warming"; and Module 7.6, "Plotting the Future: How Will the Garden Grow."*

1. Develop a model for constrained growth.
2. Develop a model for the mallard population in Exercise 3. Have a converter or variable for the number of acres of rice available for mallard consumption, and from this value, have the model compute the carrying capacity. Report on the effect of decreasing the number of acres of rice available (Reinecke).
3. In some situations, the carrying capacity itself is dynamic. For example, the performance of airplanes had one carrying capacity with piston engines and a higher limit with the advent of jet engines. Many think that human population growth over a limited period of time follows such a pattern as technological changes enable more people to live on the available resources. In such cases, we might be able to model the carrying capacity itself as a logistic. Suppose $M_1$ is the first carrying capacity, and $M_1 + M_2$ is the second. The differential equation for the carrying capacity $M(t)$ as a function of time $t$ would be as follows:

$$\frac{dM(t)}{dt} = a(M(t) - M_1)\left(1 - \frac{M(t) - M_1}{M_2}\right) \text{ for some constant } a > 0$$

By using $M(t)$, we have a logistic for the carrying capacity as well as a logistic for the population. Figure 2.3.3 displays population, $P(t)$, in black and $M(t)$ in color with the first carrying capacity $M_1 = 20$; the second, $M_1 + M_2 = 70$; and an inflection point for $M$ at $t = 450$. Notice that we get a "bilogistic," or "doubly logistic," model for $P(t)$.

Develop a model for the following scenario. First, generate an appropriate logistic carrying capacity, $M(t)$. Then, use this dynamic carrying capacity to limit the population.

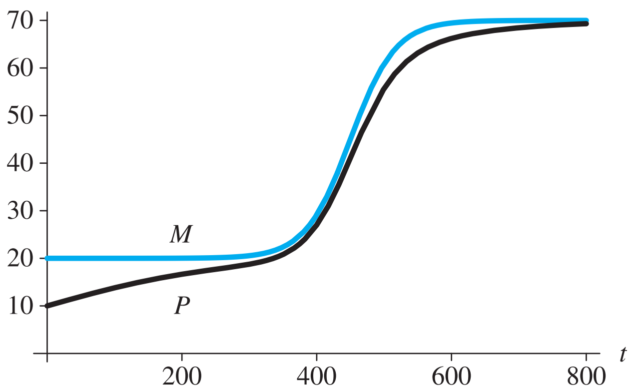


**Figure 2.3.3** Graphs of functions for carrying capacity, $M(t)$, and population, $P(t)$, with time ($t$) in years

In a population study of England from 1541 to 1975, starting with a population of about 1 million, early islanders appear to have a carrying capacity of around 5 million people. However, beginning about 1800 with the advent of the Industrial Revolution, the carrying capacity appears to have increased to about 50 million people. The change in the concavity from concave up to concave down for this new logistic appears to occur in about 1850 (Meyer and Ausubel 1999).

**4.** Refer to Project 3 for a description of a logistic carrying-capacity function. Using that information, develop a model for the Japanese population from the year 1100 to 2000. With an initial population of 5 million, the island population was mainly a feudal society that leveled off to about 35 million. The industrial revolution came to Japan in the latter part of the nineteenth century, and the population rose rapidly over a 77-yr period, with the inflection point occurring about 1908 (Meyer and Ausubel 1999).

**5.** Develop a model for the number of trout in a lake initially stocked with 400 trout. These fish increase at a rate of 15%, and the lake has a carrying capacity of 5000 trout. However, vacationers catch trout at a rate of 8%.

**6.** It has been estimated that for the Antarctic fin whale, $r = 0.08$, $M = 400{,}000$, and $P_0 = 70{,}000$ in 1976. Model this population. Then, revise the model to consider harvesting the whales as a percentage of $rM$. Give various values for this percentage that lead to extinction and other values that lead to increases in the population. Estimate the **maximum sustainable yield**, or the percentage of $rM$ that gives a constant population in the long term (Zill 2013).

**7.** Army ants on a 17-km$^2$ island forage at a rate of 1500 m$^2$/day, clearing the area almost completely of other insects. Once the ants have departed, it takes about 150 days for the number of other insects to recover in the area. Assume an initial number of 1million army ants and a growth rate of 3.6%, where the unit of time is a week. Model the population.

## Answers to Quick Review Questions

**1. a.** carrying capacity, say $M$, in units of the population, such as deer or bacteria

**b.** B. $P$ appears to grow almost without bound.
C. $P$ appears to grow faster and faster.
I. $P$ appears to grow exponentially.
J. $dP/dt$ appears to be almost proportional to $P$.
M. The birth rate is much greater than the death rate.

**c.** D. $P$ appears to grow more and more slowly.
H. $P$ is appears to be approaching $M$ asymptotically.
K. $dP/dt$ appears to be almost zero.
L. The birth rate is about the same as the death rate.

**d.** F. $P$ appears to decline more and more slowly.
H. $P$ is appears to be approaching $M$ asymptotically.
K. $dP/dt$ appears to be almost zero.

L. The birth rate is about the same as the death rate.

**2. a.** $\Delta P = 1.05(1 - p/1000)(p)(0.1)$

**b.** 1000 individuals

**c.** 625 individuals because $P + \Delta P = 600 + 1.05(1 - 600/1000)\ 600(0.1) =$ 625.2 individuals

**3.** 0 because $dP/dt = r(1 - P/M)P = r(1 - 0)0 = 0$

## References

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