Verhulst Model For Population Growth

The first model $x'(t) = rx$ is not that realistic as it either led to a population explosion or to extinction. This simple model was improved on by building into this differential equation a way to prevent the runaway growth when $r > 0$. The death rate now increases when x starts to become too large. This is reasonable as we start to use up our resources when the population is too large. Verhulst proposed the following differential equation as a mathematical model:

$$\frac{dx}{dt} = rx(1 - x/K) = rx - rx^2/K.$$

K is called the carrying capacity of the population, which is the largest sustainable population. Note now that when x is large that the second term dominates the first so the derivative $\frac{dx}{dt}$ is now negative and so the population will decrease.

Equilibrium solutions are found by setting the derivative equal to zero which gives a constant solution. The result is that you solve an algebraic equation.

$$\frac{dx}{dt} = 0 \qquad \Rightarrow \qquad rx(1 - x/K) = 0.$$

This means there are two equilibrium solutions 0 and K.

Solution by Integration. To simplify our integration take $K = 1$. Then we have

$$\frac{dx}{dt} = rx(1 - x).$$

Note that the equilibrium solutions are $x = 0$ and $x = 1$.

Following the above procedure

1. Divide both sides by $x(1 - x)$:

$$\frac{1}{x(1-x)} \frac{dx}{dt} = r$$

2. Integrate both sides with respect to time t. Note that often, differential equations are solved by integrating.

$$\int \frac{1}{x(1-x)} \frac{dx}{dt} dt = \int r dt$$

As before, the left hand integral can be simplified by changing the variable of integration to x:

$$\int \frac{1}{x(1-x)} dx = \int r dt$$

The left hand integration is done by using partial fractions:

$$\frac{1}{x(1-x)} = \frac{-1}{x(x-1)} = \frac{A}{x} + \frac{B}{x-1}$$

This implies $-1 = A(x-1) + Bx$ and gives $A = 1$ and $B = -1$. So

$$\int \Big(\frac{1}{x} - \frac{1}{x-1}\Big) dt = \ln|x| - \ln|x-1| = rt + C.$$

Combining the logarithms

$$\ln\left|\frac{x}{x-1}\right| = rt + C$$

and inverting we have

$$\frac{x}{x-1} = e^C e^{rt} = C_0 e^{rt}.$$

Let's suppose the initial population is $x(0) = 2$, then the constant C_0 can be found

$$\frac{2}{2-1} = C_0 e^0 \qquad \Rightarrow \qquad C_0 = 2.$$

and then $x/(x-1) = 2e^{rt}$. Since we don't have $x(t)$ given explicitly we algebraically solve to get

$$x(t) = \frac{2e^{rt}}{2e^{rt} - 1} = \frac{2}{2 - e^{-rt}}$$

which is the population of our species for any time t.

3. Interpretation. Let's see what happens now when $r > 0$. Evaluating the large time behavior we see that

$$\lim_{t\to\infty} x(t) = \lim_{t\to\infty} \frac{2}{2 - e^{-rt}} = 1.$$

This means a population tends toward the equilibrium population $x(t) = 1$ which is the carrying capacity for our population. This is typical behavior in many biological problems. In fact for any choice of $C_0 \neq 0$, this is true since in general

$$x(t) = \frac{C_0 e^{rt}}{C_0 e^{rt} - 1} = \frac{C_0}{C_0 - e^{-rt}}$$

which has limit 1 as $t \to \infty$ for any starting population $C_0 \neq 0$.

Problems

1. Write down the initial value problem for the Verhulst model in the case when the net growth rate is 1, the carrying capacity is 100 and the initial population at time zero is 50.

   (a) $\dfrac{dx}{dt} = x(1-(x/50)), x(0) = 100.$

   (b) $\dfrac{dx}{dt} = 100x(1-x), x(0) = 50$

   (c) $\dfrac{dx}{dt} = 2x(1-(x/50)), x(0) = 100$

   (d) $\dfrac{dx}{dt} = x(1-(x/100)), x(0) = 50$

2. What are the equilibrium solutions?

   (a) $x = 0$, $x = 50$.

   (b) $x = 0$, $x = 100$.

   (c) $x = 50$, $x = 100$.

   (d) $x = 50$, $x = 100$.

3. Now we will solve this differential equation as follows: Divide both sides by $x(1 - (x/100))$:

$$\frac{1}{x(1-(x/100))}\frac{dx}{dt} = 1$$

Integrate both sides with respect to time t.

$$\int \frac{1}{x(1-(x/100))}\frac{dx}{dt}dt = \int dt$$

As before, the left hand integral can be simplified by changing the variable of integration to x:

$$\int \frac{1}{x(1-(x/100))}dx = \int dt$$

Lastly, on the left multiply numerator and denominator by 100 to get

$$\int \frac{100}{x(100-x)}dx = \int dt$$

Complete the integration of both sides.

(a) $\ln|\dfrac{x}{100-x}| = t + C$

(b) $\ln|\dfrac{100-x}{x}| = t + C$

(c) $\ln|\dfrac{x}{x-100}| = t + C$

(d) $\ln|\dfrac{x-100}{x}| = t + C$

4. Use algebraic manipulation to solve

$$\ln|\frac{x}{100-x}| = t + C$$

to find an explicit formula for $x(t)$. You should evaluate C by requiring that $x(0) = 50$.

(a) $x(t) = \dfrac{50}{1+e^{-t}}$

(b) $x(t) = \dfrac{50}{1+e^{t}}$

(c) $x(t) = \dfrac{100}{1+e^{-t}}$

(d) $x(t) = \dfrac{100}{1+e^{t}}$

5. Find the large time limiting behavior for $x(t)$ given by

$$x(t) = \frac{100}{1 + e^{-t}}$$

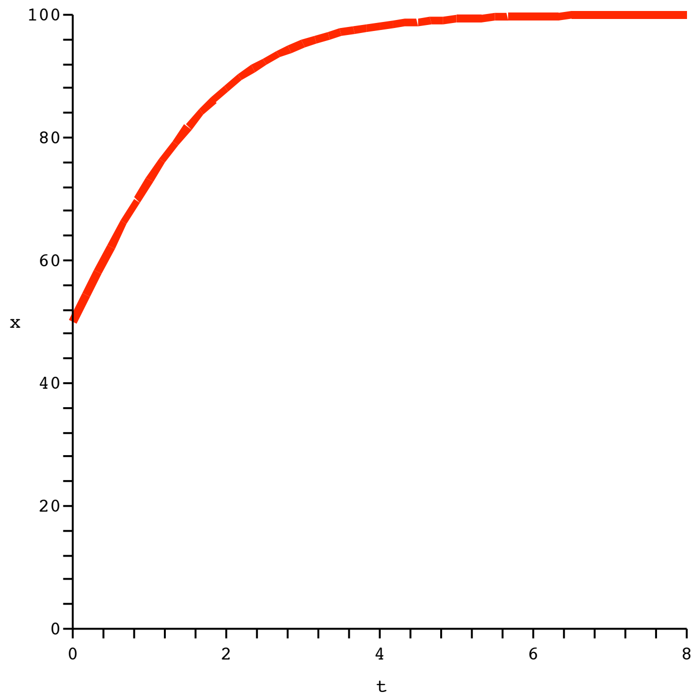
and interpret the result from a biological perspective.

(a) The population stays at its initial value of 50.

(b) The population becomes extinct eventually.

(c) The population approaches the equilibrium value of 100.

(d) A population explosion occurs.



6. Imagine a species that is hunted or fished with a yearly quota specified. In this case, the differential equation model is modified as follows

$$\frac{dx}{dt} = rx(1 - x/K) - H$$

where H is a constant and is called the harvesting rate. Let's suppose that the net growth rate is 1, the carrying capacity is 100, the harvesting rate is 21 and the initial population at time zero is 100. The initial value problem is then

$$\frac{dx}{dt} = x(1 - (x/100)) - 21,\ x(0) = 100$$

What are the equilibrium solutions?

(a) $x = 0$, $x = 50$.

(b) $x = 30$, $x = 70$.

(c) $x = 30$, $x = 100$.

(d) $x = 50$, $x = 100$.

7. We will solve this differential equation as in Question 3: Divide both sides by $x(1-(x/100))-21$:

$$\frac{1}{x(1-(x/100))-21}\frac{dx}{dt}=1$$

Integrating both sides gives:

$$\int\frac{1}{x(1-(x/100))-21}\,dx=\int dt$$

Simplifying and factoring the denominator gives

$$\int\frac{-100}{(x-30)(x-70)}dx=\int dt$$

Complete the integration of both sides.

(a) $\frac{3}{2}\ln|\frac{x-30}{x-70}| = t + C$

(b) $\frac{3}{2}\ln|\frac{x-70}{x-30}| = t + C$

(c) $\frac{5}{2}\ln|\frac{x-30}{x-70}| = t + C$

(d) $\frac{5}{2}\ln|\frac{x-70}{x-30}| = t + C$

Algebraic manipulation to then used to find an explicit formula for $x(t)$ including the evaluation of the integration constant. The solution to our harvesting problem is given by:

$$x(t) = \frac{490 - 90e^{-2t/5}}{7 - 3e^{-2t/5}}$$

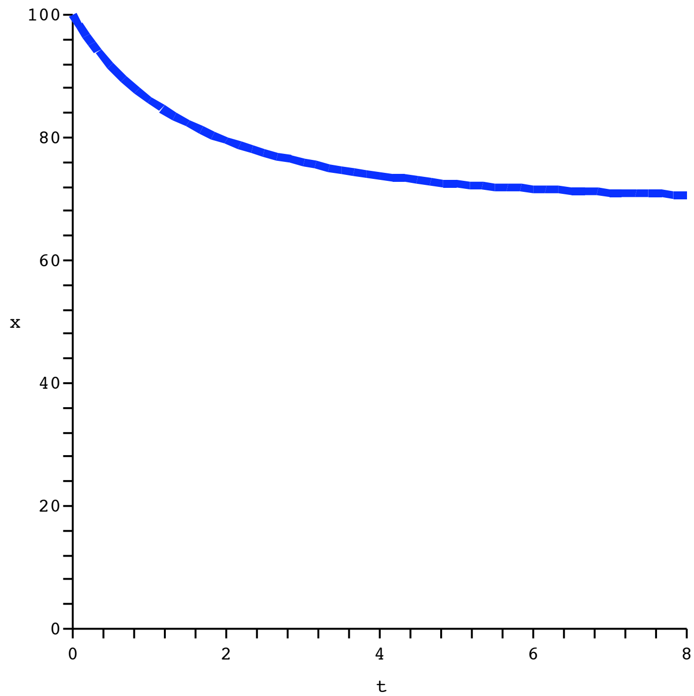
8. Find the large time limiting behavior for $x(t)$ and interpret the result from a biological perspective.

   (a) The population approaches the carrying capacity of 100.

   (b) The population becomes extinct eventually.

   (c) The population approaches the equilibrium value of 30.

   (d) The population approaches the equilibrium value of 70.



9. Now suppose that the harvesting rate is increased to 25. The initial value problem is now

$$\frac{dx}{dt} = x(1 - (x/100)) - 25,\ x(0) = 100$$

What are the equilibrium solutions in this case?

(a) $x = 0$, $x = 50$.

(b) $x = 30$, $x = 70$.

(c) $x = 50$.

(d) $x = 100$.

10. Find $x(t)$ by integrating the following:

$$\int \frac{-100}{(x^2 - 100x + 2500)} dx = \int dt$$

The general solution is then

(a) $x(t) = \dfrac{100}{t+C} + 50$

(b) $x(t) = \dfrac{100}{(t+C)^2} + 50$

(c) $x(t) = 100\ln(t-50) + C$

11. When the initial condition $x(0) = 100$, the value of $C = 2$, so that

$$x(t) = \frac{100}{t+2} + 50$$

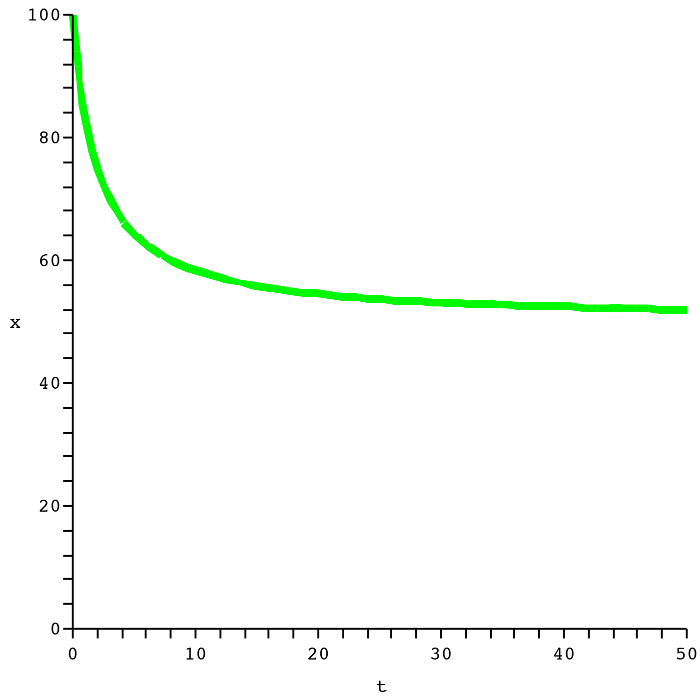
Find the large time limiting behavior and interpret the result from a biological perspective.

(a) The population approaches the carrying capacity of 100.

(b) The population becomes extinct eventually.

(c) The population approaches the equilibrium value of 50.

(d) The population approaches the equilibrium value of 70.



12. Now suppose that the harvesting rate is increased to 29. The initial value problem is now

$$\frac{dx}{dt} = x(1-(x/100)) - 29,\ x(0) = 100$$

What are the equilibrium solutions?

(a) $x = 50$.

(b) $x = 30$, $x = 70$.

(c) $x = 100$.

(d) No real values of x.

13. Find $x(t)$ by integrating the following:

$$\int \frac{-100}{(x^2 - 100x + 2900)} dx = \int dt$$

The general solution is then

(a) $-5 \arctan((x - 50)/20) = t + C$

(b) $-5 \arctan((x - 100)/50) = t + C$

(c) $-5 \ln(x - 50) = t + C$

(d) $\frac{-5}{x - 50} = t + C$

14. Use algebraic manipulation to find an explicit formula for $x(t)$.

(a) $x(t) = 20 + 50\tan(C - 5t)$

(b) $x(t) = 20 + 50\tan(C - (t/5))$

(c) $x(t) = 50 + 20\tan(C - 5t)$

(d) $x(t) = 50 + 20\tan(C - (t/5))$

The solution is

$$x(t) = 50 + 20\tan(C - (t/5)).$$

If the initial condition is applied, $x(0) = 100$, then

$$x(0) = 100 = 50 + 20\tan C$$

which means

$$C = \tan^{-1}(5/2)$$

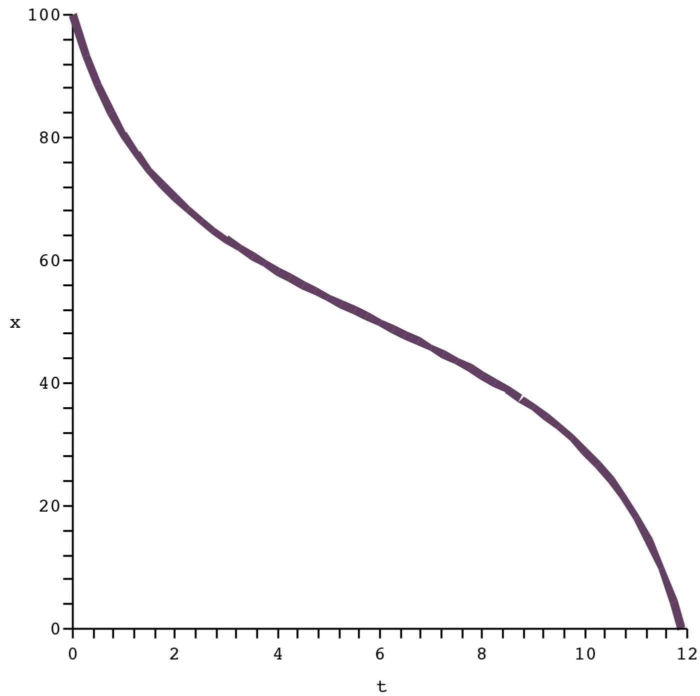
15. Find the large time limiting behavior and interpret the result from a biological perspective.

    (a) The population approaches the carrying capacity of 100.

    (b) The population becomes extinct eventually.

    (c) The population approaches the equilibrium value of 50.

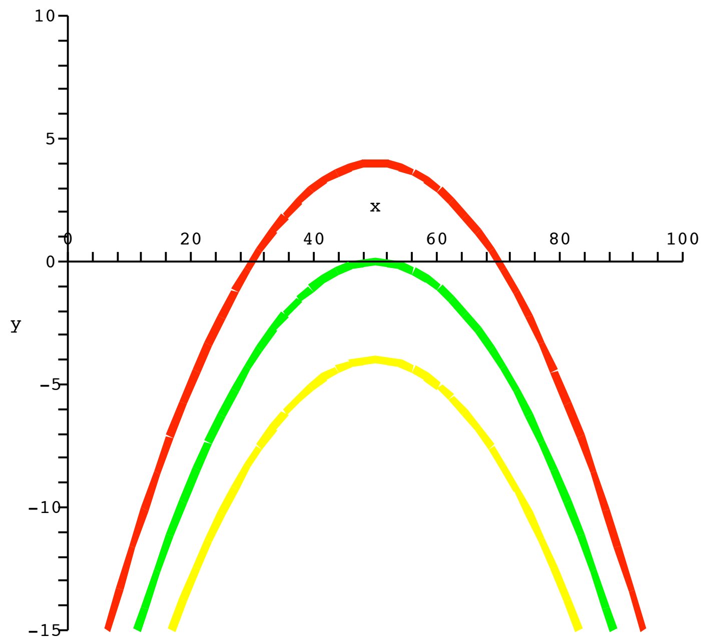
    (d) The population approaches the equilibrium value of 70.



Concluding Remarks

When $H < 25$, the harvesting rate still allows the population to tend to a constant equilibrium value. When $H = 25$, this is the cross-over point between having a sustainable population and one that goes extinct from say, over fishing. When $H > 25$, the population will always go extinct.

This can be seen by plotting x' versus x for different values of H. Note that H increases, the parabola becomes more and more negative to the point where x is a decreasing function of time leading to extinction. The red curve is $H = 21$, the green $H = 25$ and the yellow is $H = 29$.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