Population, Predation, Disease and Competition for Resources

Population, predation, disease and competition models, as well as some others, have many common features and there are a number of common tricks for building them. The simplest population model is where the change in population is proportional to the current population. If there are no restrictions on space or food, an organism reproduces to make $n$ others, on average, and those, upon maturation, reproduce to make $n$ others, and so on. If the organisms reproduce sexually, and have roughly similar food and space requirements, only half the population gives birth.

It is worth noting that this type of model also works for transmission of disease or ideas (memes) in that something is transmitted to several entities, which transmit it to several entities, and so on.

Here is a very simple model.

$\text{Pop1} := \text{diff}(P1(t), t) = k1 \cdot P1(t)$

We see that the solutions are exponential

$\text{SPop1a} := \text{dsolve}([\text{Pop1}, P1(0) = P10])$

Suppose the population doubled in 7 time units, so that $P1(7) = 2 \cdot P1(0)$. Then we solve

$K := \text{solve}(2 \cdot P10 = P10 \cdot \exp(k1 \cdot 7), k1)$

to find the constant of growth $k1$

$\text{SPop1} := \text{subs}(k1 = K, \text{SPop1a})$

Let's plot the population as it grows from 100 individuals

$\text{plot}((\text{rhs}(\text{subs}(P10 = 100, \text{SPop1})), t = 0..7);$
Let's non-dimensionalize the problem by measuring population $P_1$ in units of initial population $P_{10}$, and time in terms of the time $T$ it takes for the population to double, so that our new variables are $p = P / P_{10}$ and $\tau = t / T$. Dealing with the time first, we get

$$\frac{dP}{dT} = \frac{dT}{d\tau} = kP. \text{ The solution will be } P = C e^{Tk\tau}. \text{ The population at time } \tau = 0 \text{ is } P(0) = C e^{Tk0} = C \text{ so } P = P_0 e^{Tk\tau}. \text{ Solving for doubling time, that is, solving } 2P_0 = P_0 e^{Tk1} \text{ (remember, we want } \tau = 1 \text{ when the population has doubled) we find } k = \ln 2 / T, \text{ so the solution becomes } P = P_0 2^{\tau}. \text{ Now measuring } P \text{ in terms of initial population, so that our dimensionless population is } p = P / P_0, \text{ we arrive at the simplest possible model } p = 2^{\tau}.

Notice that the graph of this function is

```plaintext
> plot(2^(tau), tau = 0..1);
```

which is identical to the original plot up to a rescaling of the axes. In fact, notice that we begin at one initial population, which in the original was 100, and double after one time...
Of course, no real situations allow unlimited growth. In reality, there are constraints on amount of food, requirements for space, disease, predation, or other limiting factors. One way to build limited growth into a model is to multiply the dependent variable by a factor that approaches 0 as the population approaches its limit:

\[
\text{Pop2a} := \frac{\text{d}P_2(t)}{\text{d}t} = k_2 P_2(t) \left(1 - \frac{P_2(t)}{P_{2\text{max}}} \right)
\]

We can non-dimensionalize this the same way. Notice that the limiting factor is already non-dimensional, so we try \( p = \frac{P}{P_{\text{max}}} \) as our non-dimensional population. However, because the population cannot always double, as growth is limited, we must consider another non-dimensional time scaling \( \tau = \frac{t}{T} \). We'll determine \( T \) based on the form of the equation after the initial change of variables. Substituting into the limited growth equation, we get

\[
> \text{Pop2b} := \frac{\text{d}(p_2(\tau))}{\text{d}\tau} \left(\frac{P_{2\text{max}}}{T}\right) = k_2 p_2(\tau) P_{2\text{max}} \left(1 - \frac{p_2(\tau)}{P_{2\text{max}}} \right)
\]
\[ \frac{d}{dT} \frac{p2(\tau)}{P2_{\text{max}}} \]

\[ \text{Pop2b} := \frac{d}{dT} \frac{p2(\tau)}{P2_{\text{max}}} = k2 p2(\tau) P2_{\text{max}} \left( 1 - p2(\tau) \right) \]  \hspace{1cm} (6)

\[ \text{Pop2c} := \frac{d}{dT} p2(\tau) = T k2 p2(\tau) \left( 1 - p2(\tau) \right) \]  \hspace{1cm} (7)

The solution is

\[ \text{SPop2c} := \text{dsolve}\left(\{\text{Pop2c}, p2(0) = p0\}\right); \]

\[ \text{SPop2c} := p2(\tau) = -\frac{p0}{-p0 - e^{-Tk2\tau} + e^{-Tk2\tau} p0} \]  \hspace{1cm} (8)

and we see that if we let \( T = \frac{1}{k2} \), the solution simplifies to

\[ \text{SPop2d} := \text{subs}(T=1/k2, \text{SPop2c}); \]

\[ \text{SPop2d} := p2(\tau) = -\frac{p0}{-p0 - e^{-\tau} + e^{-\tau} p0} \]  \hspace{1cm} (9)

Note that \( p_0 \) is a non-dimensional parameter, because population is measured in terms of \( p_{\text{max}} \). Once again, all possible solution curves to this differential equation can be obtained from a constant rescaling of the axes.

\[ \text{plot}\left(\text{subs}(p[0]=1/10, \text{rhs(}\text{SPop2d})),\tau=0..8\right); \]
What would happen if we decided to scale population to the initial population?

\[ \text{Pop2e} := \frac{d}{d\tau} p2a(\tau) = \left( \frac{T2a}{pa[0]} \right) k2a p2a(\tau) \left( 1 - \frac{p2a(\tau) pa_0}{pmax} \right) \]

Let \( T = \frac{p_0}{k} \). Then the DE becomes

\[ \text{SPop2g} := p2a(\tau) = - \frac{pa_0 pmax}{T2a k2a \tau} \]  

\[ -pa_0^2 - e^pa_0 \ pmax + e^pa_0 \ pa_0^2 \]  

\[ \]
This is essentially the same equation but with two parameters instead of one, so the choice of \( p_{\text{max}} \) as our scaling factor is better.

**The Spruce Budworm**

If our reproducing creature is tasty, its numbers may also be limited by predation. For instance, the Spruce Budworm lives on balsam fir trees and is a pest in Canada. Its population is limited by the density of foliage on the balsam fir, but is also food for birds. The equation describing this situation is

\[
\text{Pop3a} := \frac{dB(t)}{dt} = kb B(t) \left( 1 - \frac{B(t)}{B_{\text{max}}} \right) - p(B(t))
\]

where \( p \) is some function describing the decrease in population growth due to being eaten. If \( p \) is strictly proportional to the number of budworms

\[
\text{dsolve(subs}(p(B(t))=cb*B(t),\text{Pop3a}))
\]

\[
B(t) = \frac{B_{\text{max}} e^{(-kb + cb)t} (-kb + cb)}{e^{(-kb + cb)t} + \text{Cl} B_{\text{max}} - \text{Cl} B_{\text{max}} cb}
\]

Once again, if we non-dimensionalize by changing variables to \( \tau = t / T \) and \( b = B / B_{\text{max}} \), we get

\[
\text{Pop3b} := \frac{db(\tau)}{d\tau} = \frac{Tk b(t)}{B_{\text{max}}} \left( 1 - \frac{B(t)}{B_{\text{max}}} \right) - cb B(t)
\]

\[
\text{Pop3c} := \frac{db(\tau)}{d\tau} = Tb kb b(\tau) \left( 1 - b(\tau) \right) - cb b(\tau)
\]

\[
\text{SPop3c} := \text{dsolve}([\text{Pop3c}, b(0)=b[0]])
\]

\[
\text{SPop3c} := b(\tau) = -\frac{b_0 \left( Tb kb - cb \right)}{-Tb kb b_0 - e^{-(Tb kb - cb) \tau} Tb kb + e^{-(Tb kb - cb) \tau} cb + e^{-(Tb kb - cb) \tau} Tb kb b_0}
\]

We have a couple of choices here. Let's require that \( Tb kb - cb = 1 \) so \( Tb = (1+cb)/kb \)

\[
\text{SPop3d} := \text{simplify}([\text{Pop3d}, \text{subs}(Tb = (1+cb)/kb, \text{SPop3c})])
\]

\[
\text{SPop3d} := b(\tau) = -\frac{b_0}{-b_0 - cb b_0 - e^{-\tau} + e^{-\tau} b_0 + e^{-\tau} b_0 cb}
\]

\[
\text{animate(plot, [subs(b[0]=1/10, rhs(SPop3d)), tau=0..6], cb=0..3));}
\]
Now, it turns out that predation of the spruce budworm by birds is not directly proportional to the number of budworms, but occurs on a sliding scale -- the more spruce budworms there are, the more attractive they are to birds. When there are relatively few of them, the birds start to look elsewhere for food. So we want $p$ to be a term that goes to 0 very quickly as $b(t)$ goes to 0, and approaches a constant function as the population increases. Here is an example:

```maple
plot(2*x^2/(3+x^2),x=0..9);
```
Because the left hand side has units of bugs/time, the right hand side must also.
Therefore, we write the equation

\[ B1 := \frac{dB(t)}{dt} = k_1 B(t) \left( 1 - \frac{B(t)}{B_{\text{max}}} \right) - \frac{p B(t)^2}{q^2 + B(t)^2} \]

This equation can be non-dimensionalized by putting \( b = B / A \), \( \tau = t / T \) and choosing constants so that the right hand term is made simple. Substituting these into the equation

\[ \dot{B}(t) = k_1 B(t) \left( 1 - \frac{B(t)}{B_{\text{max}}} \right) - \frac{p B(t)^2}{q^2 + B(t)^2} \]

we get

\[ \frac{db}{d\tau} = k_1 b A \left( 1 - \frac{b A}{B_{\text{max}}} \right) - \frac{pb^2 A T}{q^2 + b^2 A^2} , \]

which, upon choosing \( A = q \), \( T = \frac{q}{p} \),

\[ s = \]
\[ \frac{B_{\text{max}}}{q} \text{ and } r = \frac{k_1 q}{p} \] simplifies to \( b' = r b \left( 1 - \frac{b}{s} \right) - \frac{b^2}{1 + b^2} \). Note: this method of non-dimensionalization relies on the assumption that all constants and parameters are of the proper dimension so that we can choose the form of each undetermined scaling factor \( A, T \), and so on to make the equation simple in the way that benefits us.

Here is that non-dimensional equation

\[ b_1 := \frac{b'(t) = r b(t) \left( 1 - \frac{b(t)}{s} \right) - \frac{b(t)^2}{1 + b(t)^2}}{\text{ }} \quad (20) \]

Generate a sequence of initial conditions

\[ ICb := \{ b(0) = k/10, k = 0 \ldots 10 \} \]

\[ ICb := \{ b(0) = 0, b(0) = \frac{1}{10}, b(0) = \frac{1}{5}, b(0) = \frac{3}{10}, b(0) = \frac{2}{5}, b(0) = \frac{1}{2}, \frac{3}{5}, \frac{7}{10}, \frac{4}{5}, \frac{9}{10}, 1 \} \quad (21) \]

and plot the solutions using the DEplot command. This is a numerical procedure that also draws the slope field, which is like a vector field except the vectors have constant length.

\[ \text{DEplot(subs(s=1, r=1, b1), b(t), t=0..4, ICb, linecolor=black, thickness=1);} \]
The animate command can be used to animate any kind of plot in which there is a parameter. It can be very useful to help you see the range of behaviors of a differential equation model or any graphical representation of phenomena.

> animate(DEplot,[subs(s=1,b1),b(t),t=0..4,ICb, linecolor=black, thickness=1],r=0..3);
Another way of analyzing a model is to look at the behavior near its equilibrium points. If we set $b'$ to zero, 

$$ \frac{rb}{s} \left(1 - \frac{b}{s}\right) - \frac{b^2}{1 + b^2} = 0 $$

we can find the equilibria by looking at the intersection of the two curves on the right hand and left hand sides of the equation

$$ r \left(1 - \frac{b}{s}\right) = \frac{b}{1 + b^2}. $$

Here the left hand side is red and the right hand side is green, and we have plotted for particular values of $r$ and $s$. When the left hand side is larger than the right, the vector field along the horizontal axis points to the right. When the right hand side is larger than the left, the vector field points to the left, and using that information we can determine the stability of the various equilibrium points. For any equilibrium point if the vector field on its left points to the right and the field on its right points to the left, it is stable. If the field on its left points to the left, and the field on its right points to the right, the equilibrium point is unstable.

```plaintext
> plot([0.5*(1-b/8), b/(1+b^2)], b=0..9);
```
We can also animate the plot so we can see how the root structure changes with \( r \) and \( s \).

\[
\text{animate(plot, [[r*(1-b/8), b/(1+b^2)], b=0..9], r=0..0.6);}
\]
Here we generate a sequence of initial conditions...

> ICb1:=[seq([b(0)=k/4],k=0..20)];

\[
\begin{align*}
ICb1 & := \left[ \begin{array}{c} b(0) = 0, \\
               b(0) = \frac{1}{4}, \\
               b(0) = \frac{1}{2}, \\
               b(0) = \frac{3}{4}, \\
               b(0) = 1, \\
               b(0) = \frac{5}{4}, \\
               b(0) = \frac{3}{2}, \\
               b(0) = \frac{7}{4}, \\
               b(0) = 2, \\
               b(0) = \frac{9}{4}, \\
               b(0) = \frac{5}{2}, \\
               b(0) = \frac{11}{4}, \\
               b(0) = 3, \\
               b(0) = \frac{13}{4}, \\
               b(0) = \frac{7}{2}, \\
               b(0) = \frac{15}{4}, \\
               b(0) = 4, \\
               b(0) = \frac{17}{4}, \\
               b(0) = \frac{9}{2}, \\
               b(0) = \frac{19}{4}, \\
               b(0) = 5 \end{array} \right] 
\end{align*}
\]  

...and animate a plot with varying r and fixed s. We can see that there are one or two stable equilibria depending on the value of r:

> animate(DEplot,[subs(s=8,b1),b(t),t=0..4,ICb1, linecolor=black, thickness=1],r=0..0.5);
It is sometimes useful to look at information in the parameter plane. Here I have plotted the value of $b$ when $b'=0$ for all values of $r$ and $s$ over a range of $r$ and $s$. The number of 'sheets' of the surface give the number of equilibrium points. You can rotate this figure in space by grabbing it with the mouse.

```plaintext
> implicitplot3d(r*(1-b/s)=b/(1+b^2),r=0..1,s=1..9,b=0..8,axes=framed,style=surfacecontour,transparency=0.5);
```