

Population Dynamics

Notes by Holly Hirst

We will begin by modeling the change in the population of a single species over time. Let's suppose we have a field full of rabbits. We'll let

$P(t)$ = the population of rabbits at time t .
There are 10 rabbits to start, so $P(0) = 10$.

Model 0: "the more the merrier"

In this most simple model, we assume that the more rabbits present, the more rabbits will be born. More mathematically, the change in P over time is proportional to the number of rabbits present:

$$\frac{dP}{dt} = kP;$$
$$P(0) = 10.$$

Before we begin to investigate this model, we need to talk about how to estimate the parameter, k . The first question is, *what exactly does k tell us?* Look at it again this way:

$$\frac{P'}{P} = k$$

The change in population per unit of population is equal to k . In other words, k tells us how fast the population is changing at any given population level. So a good description of k is that it is the *rate of growth* of the population (or of decrease if k is negative). If we look at k as a fraction, for example 0.5 or one half, we can say that at each time step, there is a new rabbit for every two rabbits already in the population at the beginning of that time step. Obviously, k is dependent on the time step we are using, and for example if the time step is in minutes, k is probably smaller than one half.

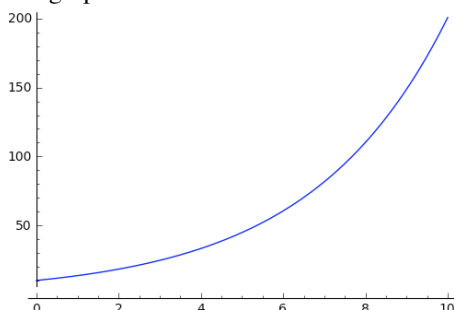
In general, parameter estimation is a difficult problem when dealing with biological or sociological models (rather than models from physics, where some measurement can often give us the parameter value). We will use the value 0.3 for now for k , keeping in mind that an actual value for k would involve field work and observations, collecting data to use to estimate an appropriate growth factor.

In Sage, we need to declare the variable t and the function p . Then build the differential equation – notice that we gave it a name "diffeq." Once we have those things entered, we can ask for the solution using the "desolve" command.

```
var('t')
p=function('p',t)
diffeq = diff(p, t) == 0.3*p
desolve(diffeq,p, [0,10])
```

The output: $10 * e^{(3/10 * t)}$

Let's look at a graph of this solution:



This model makes sense, at least early in the time span for our population. As time gets larger the population grows without bound, clearly a limitation of this model. How can we fix this? Let's add death.

Model 1/2: Adding Death as proportional to the number of rabbits.

The simplest way to add death is to think of it in the same way as we did birth in model 0: The more rabbits the more crowded, so the more likely a rabbit will die.

$$\frac{dP}{dt} = kP - dP ;$$
$$P(0) = 10 .$$

This is a good idea, but notice that we will have the same model as before:

$$\frac{dP}{dt} = kP - dP = (k - d)P = \hat{k}P .$$

Again we would have the derivative or difference quotient equal to a constant times P . Which would yield the same result at Model 0. What else can we try?

Model 1: Competition between individuals

Let the death term be proportional to the number of possible 2-rabbit interactions. Using a combinatorial argument, we can figure out this number:

There are P possible rabbits to choose for interacting rabbit number one and $(P-1)$ possible rabbits for interacting rabbit number two – and which order the rabbits are chosen shouldn't matter, so we have:

$$\frac{dP}{dt} = kP - d \frac{P(P-1)}{2} ;$$
$$P(0) = 10 .$$

Changing the equation in Sage, and using $d = 0.01$:

```
diffeq = diff(p,t) == 0.3*p - 0.01*p*(p-1)/2
```

```
Output: -200/61*log(p(t) - 61) + 200/61*log(p(t)) == -200/61*I*pi + t +
200/61*log(10) - 200/61*log(51)
```

Ick! This is not solved for p . Is there another approach? We can solve numerically using the Runge-Kutta 4 Method:

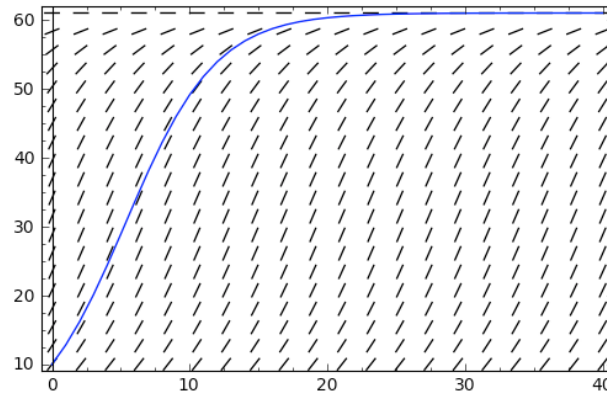
```
var('t')
p=function('p',t)
diffeq = diff(p, t) == 0.3*p - 0.01*p*(p-1)/2
desolve_rk4(diffeq,p, ics=[0,10],step=1, end_points=40)
```

This gives us list of points from $t = 0$ to $t = 40$ with steps of 1:

```
[[0, 10], [1, 12.816863229], [2, 16.1755543197], [3, 20.0482018878], [4,
24.344482145], [5, 28.9114669606], [6, 33.5510187397], [7,
38.0521945855], [8, 42.2282148708], [9, 45.9449334039], [10,
49.1325450093], [11, 51.7806490926], [12, 53.9229492775], [13,
55.6191592185], [14, 56.9394300394], [15, 57.9534901665], [16,
58.7244225125], [17, 59.3059673485], [18, 59.742075187], [19,
60.0676765943], [20, 60.309972272], [21, 60.4898337992], [22,
60.6231057487], [23, 60.7217228297], [24, 60.7946234196], [25,
60.8484737919], [26, 60.8882303767], [27, 60.9175699787], [28,
60.9392155999], [29, 60.9551813927], [30, 60.9669558406], [31,
60.9756382192], [32, 60.9820399677], [33, 60.9867598404], [34,
60.9902395353], [35, 60.9928048266], [36, 60.9946959546], [37,
60.9960900639], [38, 60.9971177643], [39, 60.99787535], [40,
60.9984338121]]
```

It would be more helpful to have a plot, and `desolve` allows us to do that in one command, and we can include a slope field diagram as well:

```
desolve_rk4(diffeq,p, ics=[0,10],step=1, end_points=40, output='slope_field')
```



This is more realistic behavior – the population levels off over time – in this case at around 60. What other ways can we incorporate death?

Model 2: Maximum Sustainable Population

Let's assume that, rather than fighting over scarce resources as in the two-rabbit interaction model above, the species we are studying has less offspring when resources are scarce, and hence the model should reflect a slowing birth rate as some maximum population is approached. The difference equation version in this case would be something like:

$$\frac{dP}{dt} = k(\text{**insert slowing factor here**})P ;$$

$$P(0) = 10 .$$

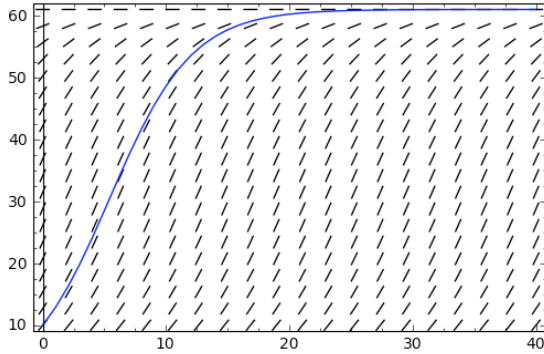
What slowing factor would work? Something that is around 1 when P is small and goes to 0 as the maximum population, M , is approached:

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

$$P(0) = 10 .$$

Let's assume the maximum population is 61, as appears to be the case in the previous model:

```
var('t')
p=function('p',t)
diffeq = diff(p, t) == 0.3*(1-p/61)*p
desolve_rk4(diffeq,p, ics=[0,10],step=1, end_points=40, output='slope_field')
```



Interesting! This model gives the same rough shape as the two-rabbit interaction model. This is not a coincidence. Look at the algebraic simplifications of the right hand sides of the two equations – both are in the form constant times P minus constant times P squared; in effect, the same model.

Conclusions: We have seen that we can model one species populations by making relatively simple assumptions and obtain solution curves that reflect our notions on what makes sense for a population growth curve. We have glossed over the problems of parameter estimation (finding values for the birth rate, death rate and maximum population numbers) – these numbers can be difficult to estimate, and require careful data collection.

Problems

- (1) Adding Harvesting:
 - (a) Modify the "two rabbit interaction" competition model to include the following idea: Each time step, one rabbit is added to the stew pot. Solve the model, print the graph and describe what happens, commenting on the maximum sustaining population.
 - (b) Using the idea in (a), how many rabbits can be harvested each time step before we drive them to extinction?
 - (c) How does the model change if the number of rabbits harvested is proportional to the total number of rabbits present? Say, we harvest 25% of the rabbits each time step.
- (2) Parameter Sensitivity: Experiment with the values of the parameters in the "maximum sustainable population" competition model.
 - (a) What happens if the initial number of rabbits is higher than M ? The same as M ?
 - (b) What happens as k is increased and decreased?
- (3) Parameter Sensitivity: Experiment with the values of the parameters in the "maximum sustainable population" competition model. Can you find values for M and for k so that this model yield the same data as the "interaction" competition model?
- (4) Population: NASA is interested in the population dynamics of a proposed moon base. Answer the questions below based upon the an appropriate model for population growth. Back up your answers using appropriate graphs. Assume that the maximum sustainable population on the base is 100,000 people, the on-base birth rate per year is $11/10,000$ and the initial population is 30,000.
 - (a) How does the population change over the first 15 years of operation? About when does the population reach 90% of the maximum sustainable?
 - (b) NASA plans to send up approximately 500 "immigrants" per year. How would you model this? How does this affect the population? Using your model, about when is 90% of the maximum sustainable population reached now?
- (5) A species of sandhill crane indigenous to North America (*Grus canadensis*) was declared an endangered species in 1916. These birds do considerable crop damage when their numbers are increased, so hunting permits were allowed starting in 1961. The primary question of interest is: How many permits should be sold per year? We have the following data from R. Miller and D. Botkin based on their population study from 1974:
 - ❖ maximum sustainable population $\approx 194,600$
 - ❖ current population $\approx 190,000$
 - ❖ population rate $\approx 5.07 \times 10^{-7}$ (for time in years)

We want to build in a model that incorporates these data along with an additional term for the hunting limit (supposing the a constant number are killed each year). We want to choose this number so that the species doesn't go extinct. Find a good hunting license number.

Interacting Species

Now we want to look at two species that interact: x is the prey and y is the predator. Now we have two equations instead of one, each with increase rate and decrease rate terms.

$$\frac{dx}{dt} = in_x - out_x$$
$$\frac{dy}{dt} = in_y - out_y$$

So how should we model these four terms? Here are some ideas -- in historical order.

Original Lotka-Volterra Model: (Volterra 1927)

$$\frac{dx}{dt} = b_x x - d_x xy$$
$$\frac{dy}{dt} = b_y xy - d_y y$$

Volterra set the prey (x) increase to simple Malthusean and had the predator (y) affect the prey through the death term. He set the birth term of the predator proportional to both the predators present and the prey present, since predators would have a hard time reproducing without food. Notice the four parameters: b_x , b_y , d_x , and d_y . These can be interpreted as the population birth rates and death rates for each of the species.

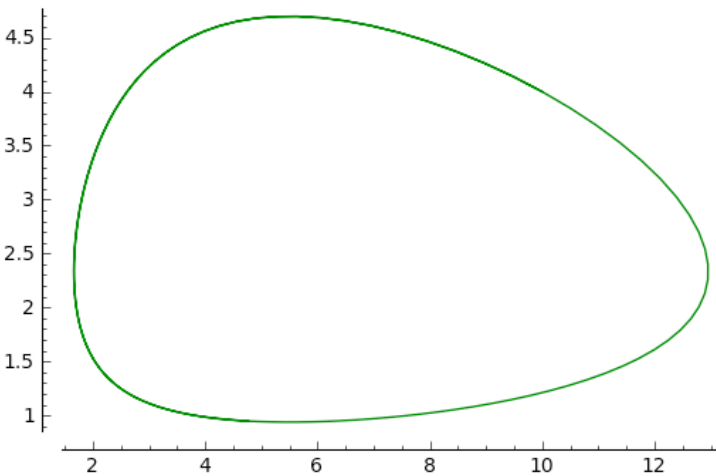
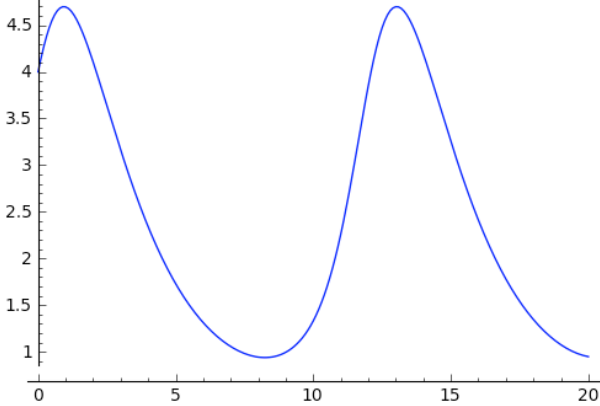
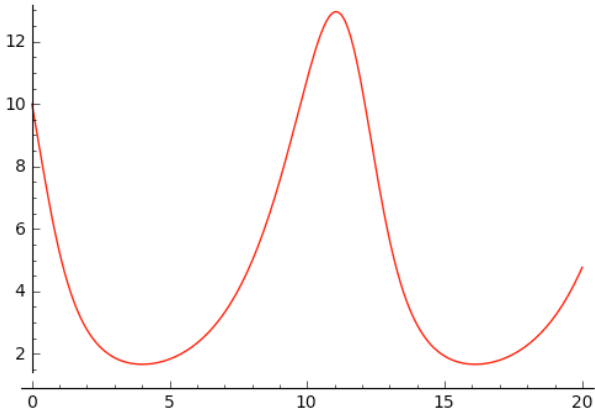
Suppose the predator species is wolves and the prey species is rabbits, and let us start with 10 rabbits, 4 wolves, rabbit birth and death rates of 0.7 and 0.3, and wolf birth and death rates of 0.08 and 0.44.

```
x,y,t=var('x y t')
sol=desolve_system_rk4([0.7*x - 0.3*x*y,0.08*x*y - 0.44*y],[x,y],
    ics=[0, 10, 4],ivar=t,end_points=20)
```

These commands generate a list of triples, and if we want to plot points we have to decide what to plot: (t, x) , (t, y) or (x, y) :

```
txpoints=[ [i,j] for i, j, k in sol]
typoints=[ [i,k] for i, j, k in sol]
xypoints=[ [j,k] for i, j, k in sol]
list_plot(txpoints, plotjoined=true, color='red')
list_plot(typoints, plotjoined=true, color='blue')
list_plot(xypoints, plotjoined=true, color='green')
```

Notice that the populations cycle, with the predator peaking right after the prey:



Competition in the Prey (1930s):

The primary objection to the LV Model was that the prey (x) would increase without bound if the predators died out. What if competition among the prey is also incorporated, using a maximum sustainable prey population (M)?

$$\frac{dx}{dt} = b_x \left(1 - \frac{x}{M}\right) x - d_x xy$$

$$\frac{dy}{dt} = b_y xy - d_y y$$

Try generating a solution: The populations cycle, with the predator peaking right after the prey, but the cycles die off, approaching a stable population.

Leslie (1950s):

- (a) There is no upper limit to the relative rate of increase of predator
- (a) Predator should do worse as the predator to prey ratio increases

Leslie fixed these by removing the prey dependency in the birth of the predators and changing the death term for the predator to have both the number of predators and the ratio of predators to prey.

$$\frac{dx}{dt} = b_x x - d_x xy$$
$$\frac{dy}{dt} = b_y xy - d_y y \frac{y}{x}$$

Try generating a solution: The populations cycle, with the predator peaking right after the prey, but the cycles die off even more quickly, approaching a stable population.

May (1960s):

May liked both the Leslie model and the competition model and combined them, but also noted the following: The prey death term implies that for a given y , the number of prey eaten is proportional to the number of prey present. This implies that predators are never not hungry. He fixed this by adding a piece to the prey death that would control this term.

$$\frac{dx}{dt} = b_x \left(1 - \frac{x}{M}\right) x - d_x y \frac{x}{1+x}$$
$$\frac{dy}{dt} = b_y xy - d_y y \frac{y}{x}$$

Problems – Part 2

- (1) Finish the development of May's model, using the same parameter values as in the other models. Explain why the prey death term now allows for wolves to become satiated by looking at the limit of this term as x gets very large, but y stays fixed. Comment on the similarities and differences in behavior between May and the other models.
- (2) For each of the models above, experiment with changing each of the parameters and record your observations. Write a summary of your findings from these experiments, and comment on whether your observations make sense given what you expected. Do all of the parameters seem to govern the same qualitative behavior regardless of the particular model?
- (3) Another graph that can be examined in the case where there are two independent variables is the *phase plane* which is the scatterplot of x versus y . Generate these graphs, and look at what information is conveyed by them.

Other Models using Systems of Equations

Competitive Hunter Model. In the situation where we have two species who compete for the same resources (rather than one being the food source for the other), we can build a two equation model in a similar fashion. The birth terms do not involve interaction between the species (i.e., only x is present in the birth term for the x equation), but the death terms for each involve both species. Build a model that reflects this situation. What are the parameters? What units are involved in each term? What happens to the populations? Experiment with parameter values and report your findings.

Mutualism Model. In the situation where we have two species whose survival depends on their mutual cooperation, we can build a two equation model in a similar fashion. The death terms would not involve interaction (i.e., only x is present in the death term for the x equation), but the birth terms for each involve both species. Build a model that reflects this situation. What are the parameters? What units are involved in each term? What happens to the populations? Experiment with parameter values and report your findings.

Battle Model. In a battle, we can model the actions (and subsequent army strengths) in the same way as we did for predator-prey interaction, except that the "birth terms" -- which are now better called "reinforcement terms" -- would not involve any interaction, and the "death terms" -- which might still be called death terms -- are really only dependent on the strength of the opposing army. Build a model that reflects this situation. What are the parameters? What units are involved in each term?

(a) What happens to the armies? Experiment with parameter values and report your findings.

(b) Army X is about to attack army Y. Army Y has 1000 troops and army X has 3000 troops, but army Y has superior weaponry and training, making each Y soldier 1.65 more effective than an X soldier. This can be interpreted as the time it takes an X to kill a Y being 1.65 times longer. Model this situation and comment on who "wins."

Economic Model. Here is an idea for a simple model for an economy in which all means of production are socially owned. Consider the following assumptions (originally proposed by G. A. Feldman):

- (6) The economy is divided into two sectors, Producer goods (where goods which will be used or invested in both sectors are produced), and Consumer goods (where goods which will be consumed by the population are produced).
- (7) The annual rate of output from each sector is proportional to the amount invested in that sector. The constants of proportionality can be assumed to be the same for each sector – in fact, the reciprocal of this constant is called the *marginal capital coefficient*.
- (8) The output from the producer sector is split in some proportion and invested in both the producer and the consumer sectors. The output from the consumer sector is consumed (i.e., not invested).
- (9) The sum of the outputs from the producer and consumer sectors is called the national income.

Please develop such a model and provide an analysis of and explanation for all parameters used. What are relative rates of growth of the sectors and the national income tending toward over time? (relative rate of growth can be thought of as rate of change relative to current size)

Epidemic Model. Another common situation which can be modeled using a system of equations is a general model for a rapidly spreading epidemic, in which persons who get the disease die from it (e.g., the ebola virus). We need a model that incorporates the following assumptions:

- 1) Healthy people get sick at a rate proportional to both the number of healthy people and the number of sick people.
- 2) Sick people die at a constant rate.

(a) Develop such a model and provide an analysis of and explanation for all parameters used.

(b) What if the disease allows for people to recover and then be immune (for example, measles)? Then we would need to consider three populations: Susceptible, Ill, and Recovered (SIR). Model this situation thinking in the following way: The number of susceptible people is declining at a rate proportional to the number of infected people, the number of infected people is growing at a rate proportional to the number of times infected people come in contact with susceptible people with people who are recovering being subtracted out of the infected pool, and the number of recovered people is growing at a rate proportional to the number of infected people. Develop such a model and provide an analysis of and explanation for all parameters used.