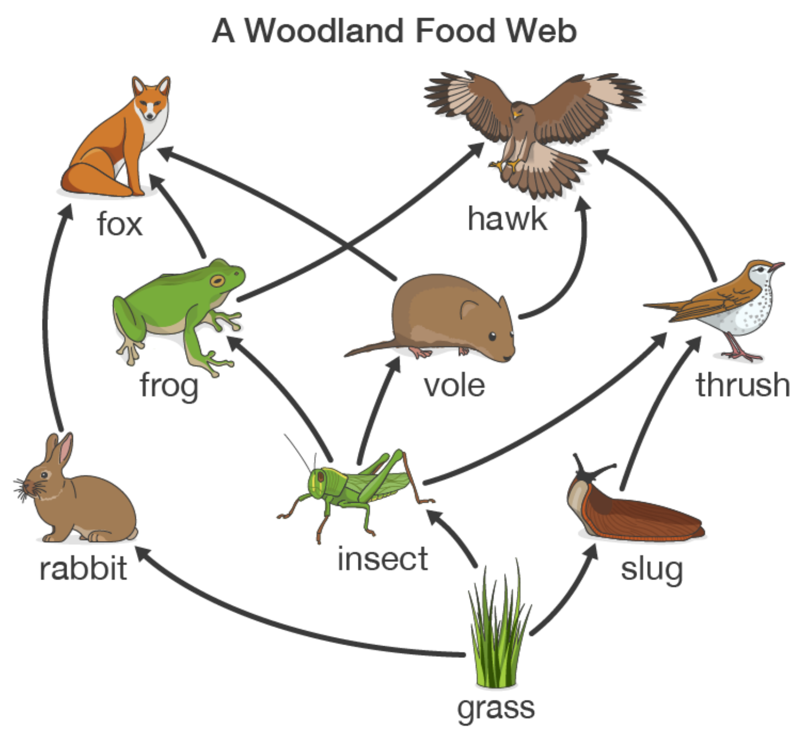
Eat or Be Eaten

Models of Population Growth and Competition
MATH3304: Elementary Differential Equations
https://people.sc.fsu.edu/~jburkardt/latex_src/math3304_2024/growth.pdf



Predators and their prey

Growth Famine Death

Differential equations can simulate population changes.

- *Exponential ODE: Pure growth or decay;*
- *Logistic ODE: Growth with a "ceiling";*
- *Predator-Prey ODE: Two species compete.*

1 The exponential growth equation

Many animal populations have a natural growth rate. As long as there is plenty of food and no external pressures, the population will increase by the same relative amount at fixed time intervals. We might observe that every 10 days, a population of rats increases by 8 percent. A corresponding differential equation for the population $p(t)$ would describe the instantaneous growth by

$$\frac{dp}{dt} = r\,p(t)$$

where r is the growth parameter. We may assume that at some time t_0, we measured the population $p_0 = p(t_0)$.

Our prediction problem then is to determine the population $p(t)$ at any future time, given our information at time t_0 and our model for how the population grows with the rate r.

2 A computed exponential growth solution

We can use a simple forward Euler ODE solver to fill in the predictions of this growth model for a population. At time $t_0, 0$, let's start with $p_0 = 100$ Tribbles and assume the growth rate is $r = 0.05$. We write

```
r = 0.05
for i = 0 : 100
  if ( i == 0 )
    t = 0.0
    p = 100.0
  else
    dt = 0.01
    dp = r * p * dt
    t = t + dt
    p = p + dp
  end
  tvec(i+1) = t
  pvec(i+1) = p
end
plot ( tvec , pvec )
```

For this example, our plot doesn't look very exciting! Growth is happening, but not very noticeably. Assuming our approach is correct, what can we do to see a sharp increase in population?

3 An exact exponential growth solution

It turns out that, for the growth differential equation, we can actually work out an exact solution. The result is probably no surprise, but the technique, called *separation of variables*, is a useful tool which we will need for another problem soon:

$$\begin{aligned}
\frac{dy}{dt} &= r\,y && \text{Differential equation}\\
\frac{dy}{y} &= r\,dt && \text{Separation of variables } y \text{ and } t\\
\int \frac{dy}{y} &= \int r\,dt && \text{Indefinite integrals}\\
\ln(y) &= r\,t + c_1 && \text{Antiderivatives, } c_1 \text{ arbitrary constant}\\
y &= c_2 e^{r\,t} && \text{Exponentiate, } c_2 = e^{c_1}\\
y &= y_0\, e^{r\,(t-t_0)} && \text{Apply our initial condition}
\end{aligned}$$

So our formula for the future population involves the exponential function:

$$p(t) = p_0\, e^{r(t-t_0)}$$

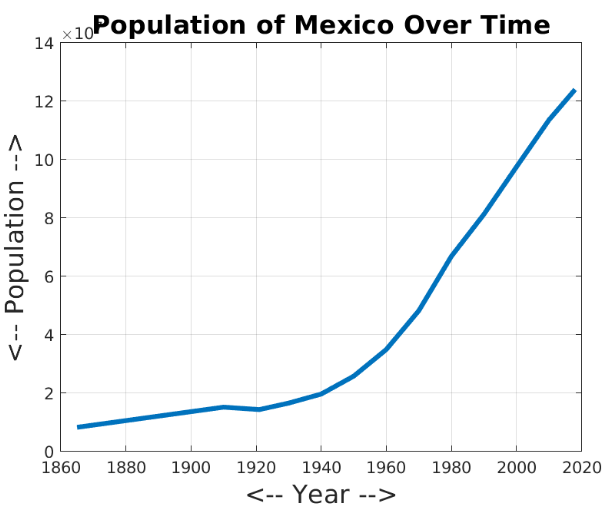
4 An exponential growth example

This result suggests that the growth equation cannot be a general model of population; assuming r is positive, a population will grow infinitely large, which is not believable. However, in many cases, the growth equation does seem to match the behavior of a population that is (temporarily) experiencing unrestrained growth.

Here is some population data for Mexico:

```
Year  Population
----  ----------
1865     8259080
1910    15160369
1921    14334780
1930    16552722
1940    19653552
1950    25791017
1960    34923129
1970    48225238
1980    66846833
1990    81249645
2000    97483412
2010   113580528
2018   123982528
```

A plot of the data suggests that, for some value of r, an exponential growth curve would be a reasonable match for the statistics until about 1980, when perhaps a linear growth rate takes over.



Population statistics for Mexico

Assignment: Plot the Mexico population data. Write a function which, given values of t_0, p_0, t and r, will return a prediction for Mexico's population $p(t)$ at any time t. Use the initial values $t_0 = 1865$ and $p_0 = 8259080$. Try to estimate a value for r so tha4 a plot of your function roughly matches the data. You can estimate r by thinking as follows:

$$p(1940) = p(1865) * e^{r*(1940-1865)}$$

If you can solve this equation, you will get a rough idea of what r might be, and then you can try to improve your plot by making small adjustments to that value.

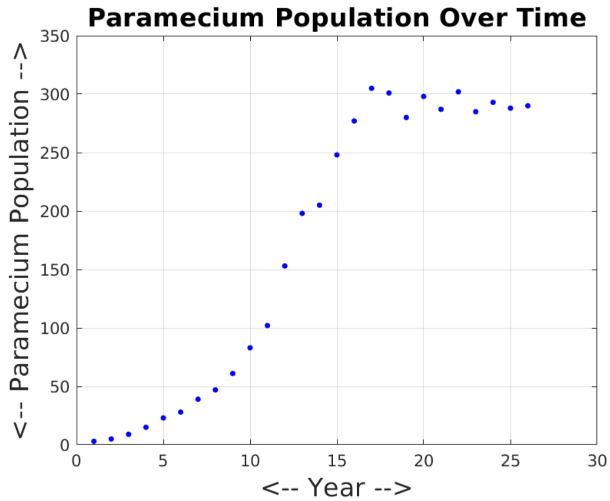
5 Logistic growth

The explosive growth we saw in the exponential example can occur in real populations for a limited time only; the model solution goes to infinity, but we know that can't happen. At some point, the growth potential must be resisted by some limits, such as a shortage of food or space or some other resource. This means that the population lives in an environment with a limited *carrying capacity*; that is, there is maximum population that can survive long term.

6 Logistic growth example

As an example, here is a table of the Paramecium population in a test tube at a biology lab. The data and plot strongly suggest that a period of exponential growth is followed by a tendency to stick near a fixed population of about 300 individuals.

```
        Paramecium
Hours   Population
------  ----------
  1,      3
  2,      5
  3,      9
  4,     15
  5,     23
  6,     28
  7,     39
  8,     47
  9,     61
 10,     83
 11,    102
 12,    153
 13,    198
 14,    205
 15,    248
 16,    277
 17,    305
 18,    301
 19,    280
 20,    298
 21,    287
 22,    302
 23,    285
 24,    293
 25,    288
 26,    290
```



Paramecium population data

7 Logistic growth equation

To construct a better mathematical model for cases where we know a limit exists, we must somehow control the growth value r, so that it begins to tap the brakes as the limit is approached. We can see one way to do this by looking at the **logistic differential equation**. If we know that our system can sustain a maximum population of y_max, then we want to adjust the growth equation so that, at low populations, the growth rate is r, but as we approach the maximum population, the effective growth rate decreases to zero. We can achieve this by including a factor of the form $(1 - \frac{y}{y_{max}})$, which adjusts r in this way.

Our logistic differential equation is then:

$$\frac{dy}{dt} = y\,r\,(1 - \frac{y}{y_{max}})$$

To complete the problem, we need to specify values for the growth rate r, the maximum population y_{max}, and the initial conditions

$$t_0 = ?$$
$$y(t_0) = ?$$

8 Logistic growth exact solution

The general logistic equation can be solved exactly. In some of the following steps, we will silently rearrange and redefine constants to simplify the final result.

$$
\begin{aligned}
\frac{dy}{dt} &= r\,y\,(1 - \frac{y}{y_{max}}) && \text{Differential equation} \\
\frac{y_{max}\,dy}{y(y_{max}-y)} &= r\,dt && \text{Separation of variables} \\
\int \frac{y_{max}\,dy}{y(y_{max}-y)} &= \int r\,dt && \text{Indefinite integrals} \\
\frac{1}{y_{max}} \int (\frac{1}{y} + \frac{1}{(y_{max}-y)})dy &= \int r\,dt && \text{Partial fractions} \\
\frac{1}{y_{max}}(\ln(y) - \ln(y_{max}-y)) &= r\,t + c_1 && \text{Antiderivatives, } c_1 \text{ is an arbitrary constant} \\
\frac{y}{y_{max}-y} &= c_2 e^{(rt+y_{max})} = c_3\,e^{rt} && \text{Exponentiate, } c_3 \text{ combines } c_2 \text{ and } e^{y_{max}} \\
y(t) &= \frac{y_{max}}{1+ce^{-rt}} && \text{Algebra, solving for } y \text{ for any initial condition}
\end{aligned}
$$

From the resulting formula, we can see that, assuming $0 \leq r$, we have $y(t) \rightarrow y_{max}$, $t \rightarrow \infty$, as we should expect. The initial condition information will tell us how to set the constant c.

9 Logisic model fitting

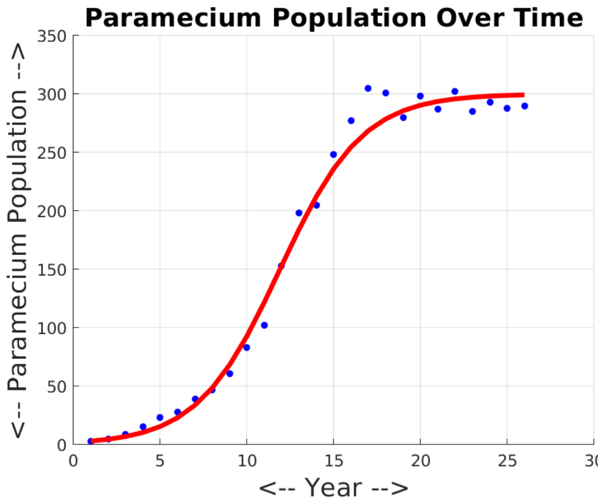
To compare the logistic equation with our paramecium data, we can make reasonable guesses for $t_0 = 1$ and $y_0 = 3$ and $y_{max} = 300$. We can adjust the formula so that the exponential involves $(t - t_0)$. Now plugging our initial data allows us to determine the constant c:

$$
\begin{aligned}
y(t_0) &= \frac{y_{max}}{1 + ce^{-r(t-t_0)}} \\
3 &= \frac{300}{1+c} \\
c &= 99
\end{aligned}
$$

but now we need an estimate of r. We want to use data from the part of the graph where the population is still rising strongly. We might consider $y(12) = 153$. Plugging this into our equation allows us to estimate r:

$$
\begin{aligned}
153 &= \frac{300}{1 + 99e^{-r(11)}} \\
1 + 99e^{-r(11)} &= \frac{300}{153} \\
e^{-r(11)} &= (\frac{300}{153} - 1)/99 \\
-11r &= \ln((\frac{300}{153} - 1)/99) \\
r &= -0.4214
\end{aligned}
$$

And now that we have all the constants in our formula, we can evaluate it and compare it to our original data:



Paramecium population data and logistic formula

We can conclude that the logistic model is a good fit to our data, especially during the growth phase. It tapers off smoothly at the end, although our data actually seems to wiggle above and below the maximum value of 300 that we estimated.

10 Logistic approximate solution by Euler

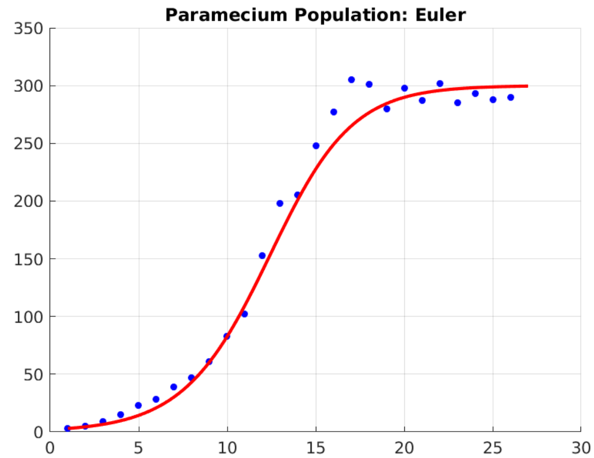
We were lucky that in this case, it was possible to use the method of separation of variables to get a general solution to our differential equation. But usually, we are simply given a differential equation with initial conditions, and asked to estimate the solution for future times, without being able to determine a formula for the solution. Instead, we must be satisfied with a computational result, that is, a table of estimated values $(t_i), y_i)$ produced by an ODE solver.

Knowing only the differential equation, and the initial value, we can use the Euler method to draw a partial, approximate picture of the solution over time.

```
r = 0.4214        <-- Set two constants we need
pmax = 300.0

for i = 0 : 100
  if ( i == 0 )
    t = 1.0       <-- Set the initial condition
    p = 3.0
  else
    dt = 0.26                              <-- Set dt so we get to t = 27
    dp = r * p * ( 1.0 - p / pmax ) * dt   <-- Right hand side of the ODE
    t = t + dt
    p = p + dp
  end
  tvec(i+1) = t
  pvec(i+1) = p
end
plot ( tvec, pvec )
```

The Euler method starts knowing only the initial condition, and the direction field. It uses this information to estimate the solution at a sequence of time values. Typically, the error between this estimate and the true solution will grow as time increases, particularly if the solution grows large, or varies strongly. For this paramecium problem, our results look reasonably close:



Paramecium population data and Euler prediction

11 Predator Prey equation

The logistic equation can simulate a population whose exponential growth is eventually inhibited by a maximum population limit. This represents a fairly simple barrier. In nature, a more interesting example of a population limit occurs when a prey population shares space with a predator. The prey population tends to increase with reproduction, but decrease through predation (being eaten!). Instead of a model which simply rises towards a ceiling, we now might observe two competing populations that rise and fall repeatedly.

Let $p_1(t)$ and $p_2(t)$ represent the sizes of the prey and predator populations at time t. We can assume that, if left alone, the prey population will grow at some rate α; on the other hand, if left alone, the predators will die off, at a rate of $-\gamma$. The difference is that the prey only need grass to eat, and there is always enough (no logistic worry today!). But the predators will starve on their own, and can only survive by predation, that is, meeting and eating a prey.

Predation occurs when a prey and a predator meet; one dies, and the other gets fed. We need to add a term to both population equations that models the frequency and cost or benefit of predation.

If we assume the predators and prey encounter each other at random, then the frequency of predation must be proportional to $p_1(t) * p_2(t)$; that is, if we double the number of rabbits, or double the number of foxes, the number of encounters will double.

The cost of predation to the prey, which we can describe as β, is a negative effect because each death reduces the prey population; the product of the cost and the frequency gives us a term to be subtracted from the prey population equation. Similarly, the benefit of predation, labeled δ, will be a positive effect multiplying the predation frequency, and added to the predator equation.

Thus we use four positive parameters, α, β, γ, and δ, to describe the pair of differential equations that control the two populations:

$$\frac{dp_1}{dt} = \alpha * p_1 - \beta * p_1 * p_2$$
$$\frac{dp_2}{dt} = -\gamma * p_2 + \delta * p_1 * p_2$$

Although these equations look quite new, we can rearrange them so that they look as versions of the exponential growth equation in which the r coefficient has become more complicated, (no longer constant):

$$\frac{dp_1}{dt} = (\alpha - \beta * p_2) * p_1 \qquad r_1 = (\alpha - \beta * p_2)$$
$$\frac{dp_2}{dt} = (-\gamma + \delta * p_1) * p_2 \qquad r_2 = (-\gamma + \delta * p_1)$$

so if p_2 decreases, the prey population grows faster; if p_1 decreases, the predator population dies away faster.

Considering this new version of the equations, we can see that there must be a **steady state** solution, where $r_1 = r_2 = 0$, and the two populations never change in size. Two other possible trends are obvious: if p_1 ever becomes 0, then the predators must exponentially die off; if p_2 ever becomes 0, the prey goes into exponential growth and explodes to infinity.

12 Predator Prey approximate solution by Euler

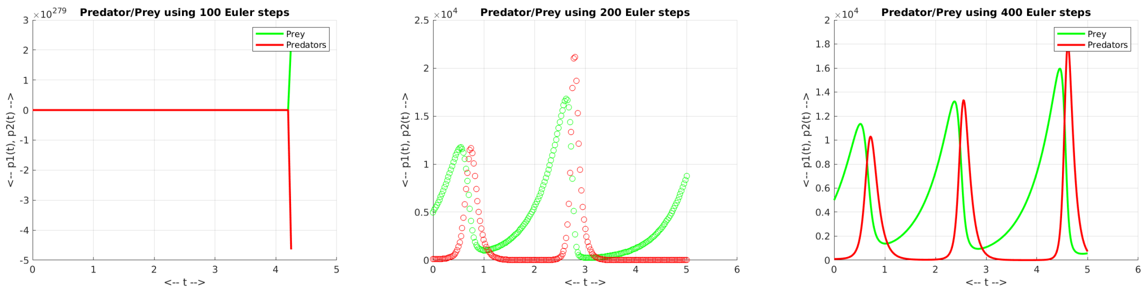
As it turns out, there is not a general solution to predator prey equations, and so our best hope is to get a reasonable approximation. We will again choose the simple approach of an Euler solver. Our Euler method now has to update two quantities, p_1 and p_2, at every time step. It's pretty easy to see the changes that are necessary in order to get this to work.

```
alpha = 2.0
beta = 0.001
gamma = 10.0
delta = 0.002

tstop = 5.0
nstep = 100

for i = 0 : n
  if ( i == 0 )
    t = 0.0
    p1 = 5000
    p2 = 100
  else
    dt = tstop / nstep
    dp1 = (   alpha - beta  * p2 ) * p1 * dt
    dp2 = ( - gamma + delta * p1 ) * p2 * dt
    t = t + dt
    p1 = p1 + dp1
    p2 = p2 + dp2
  end
  tvec(i+1) = t
  p1vec(i+1) = p1
  p2vec(i+1) = p2
end
plot ( tvec, pvec )
```

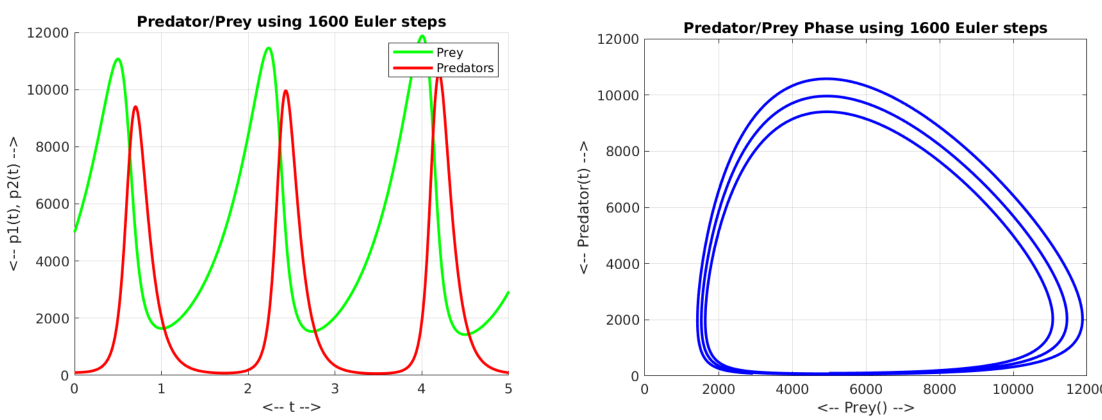
For our first guess, we used 100 Euler steps over the interval from 0 to 5 years. However, our estimate blows up, with the predator population heading to infinity, and the prey going negative. When we use 200 and then 400 steps to analyze the same time interval, a more reasonable picture appears, with both populations going through cycles that bounce a little higher each time.



Predator Prey simulations: 100, 200 and 400 Euler steps

In fact, it turns out that the populations actually will follow a fixed cycle, but we'll only be able to see this convincingly if we increase the number of Euler steps. Try 800 steps, and if necessary 1600, to see that the pictures suggest this behavior.

To see the cyclic behavior in aother way, we can make what is called a **phase plot** of the data. Instead of plotting $(t, p_1(t))$ and $)(t, p_2(t))$, we will plot $(p_1(t), p_2())$. The fact that these two quantities change together is documented by their tracing out what looks almost like a closed curve.



Population and Phase plots: 1600 Euler steps

After using a greater number of steps, we can see that the population plot is beginning to look periodic and the phase plot, although clearly making three loops, might actually form a closed curve if we tried for greater accuracy in our calculations. It turns out that there is not a simple exact formula for the solution to this predator prey problem, but it is known that, for a wide range (but not all)) of the parameters α, β, γ and δ, the exact mathematical solution is periodic, as our esimated solutions suggest.

13 The effect of growth rates

All our examples of population change can be regarded as modeling $p(t)$ using a differential equation with a growth rate g:

$$
\begin{aligned}
\frac{dp}{dt} &= r\,p(t) & g &= r \\
\frac{dp}{dt} &= r\,(1 - \frac{p(t)}{p_{max}})\,p(t) & g(t) &= r\,(1 - \frac{p(t)}{p_{max}}) \\
\frac{dp_1}{dt} &= (\alpha - \beta\,p_2(t))\,p_1(t) & g_1(p_2(t)) &= (\alpha - \beta\,p_2(t)) \\
\frac{dp_2}{dt} &= (-\gamma + \delta\,p_1(t))\,p_2(t) & g_2(p_1(t)) &= (-\gamma + \delta\,p_1(t))
\end{aligned}
$$

This suggests that we could make new population models by simply trying out different formulas for growth rates $r()$. Examples include:

$r = t$	physically unlikely
$r = \sin(t)$	modeling daily or yearly cycles
$r = 1/p(t)$	small populations surge
$r = f(t) - p(t)$	try to match some target data

A variation on the predator-prey equation would replace the exponential growth term in the prey equation by a logistic term. This would impose the condition that tere is a limited amount of grass available. This would avoid allowing the prey population to explode if all the predators die.

If a population $p(t)$ achieves and holds a constant value, we say it is *steady.* If the population is defined by a growth ODE of the form

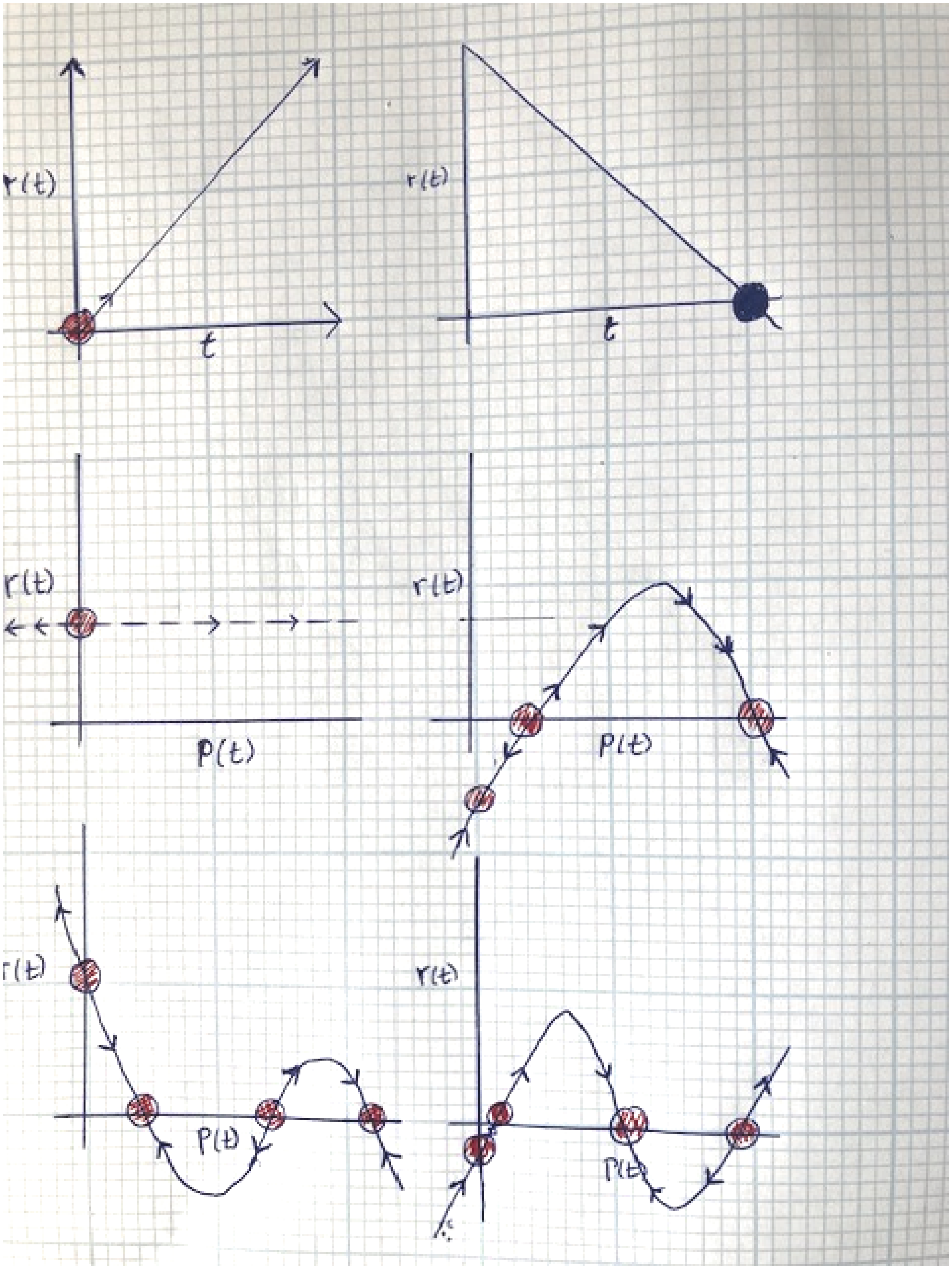
$$p'(t) = r(t, p(t)) * p(t)$$

then steady solutions can only occur if $p(t) = 0$ or the growth rate $r()$ is 0. Mathematically, a steady solution has stopped changing. But in physical systems, there can be small variations or perturbations in the quantities we measure. So for a physical system, such as a population, we would like to make a stronger statement than saying that the population has stopped changing. Instead, we would like to say that, as long as there are small enough, even small changes or measurement inaccuracies in the population will not cause a noticeable increase or decrease. In that case, we say the population value is *stable.*

In the following plots of growth rates, we ask whether there are stable solutions.

1. If $r(t) = t$, then the zero population is steady, but all positive populations are unstable; they all grow to infinity at an increasing rate. (All negative populations, if that is meaningful, decrease to negative infinity)
2. If $r(t) = max(1 - t, 0)$, then all positive populations grow, but at a slower and slower rate, until time all growth stops. So all populations become stable after that point.
3. If $r(p(t)) = c$, for some positive constant, then positive populations grow, negative populations decrease, and zero is steady, but unstable.
4. If $r(p(t)) = -p^2 + 4p - 3 = -(1 - p)(3 - p)$, the steady populations are 0, 1 and 3. Can you see why 0 and 3 are stable, but 1 is unstable?
5. If $r(p(t)) = -p^3 + 6p^2 - 11p + 6 = (1 - p)(2 - p)(3 - p)$, the steady populations are 0, 1, 2, and 3. The stable solutions are 1 and 3.
6. If $r(p(t)) = p^3 - 6p^2 + 11p - 6 = -(1 - p)(2 - p)(3 - p)$, the steady populations are 0, 1, 2, and 3. The stable solutions are 0 and 2.

From these simple examples, you might conclude that stable and unstable steady solutions will always alternate. Can you come up with a simple formula for $r(p(t))$ which has just two steady solutions, both stable? Or three?


r(t)
t
r(t)
t
r(t)
P(t)
r(t)
P(t)
r(t)
P(t)
r(t)
P(t)

Six growth-rate graphs