

1 A Few Basic Concepts

As with discrete models, continuous models have steady states and there are even methods for finding when a particular steady state is stable or not. It might surprise you to learn that these methods are almost identical to the ones you learned, but just different enough to be confusing! Proceed with caution...

2 Steady States

The notation “fixed points” is generally reserved for discrete models. With continuous models the phrases “steady states” or “equilibrium states” is preferred. Now in discrete models we found fixed points by dropping the subscripts and solving the equation for our variable. What happens now that we do not have any subscripts? Well we need to take a closer look at what a steady state means. A steady state is where there is no change in the population. I would like to point out that this does not mean there is not turn over in the population, only that the births are equal to the death and therefore the population size is neither increasing or decreasing. Back to our original questions, if there is no change in the population size then what should the derivative be? The derivative tells how our population is changing over time, and thus if there is no change our derivative should be **zero**!

2.1 Logistic Steady State

We know from our experience with the simulations of the Logistic model that there is a steady state when the population reaches the carrying capacity. We also know (though we may have to think about it for a minute) that there should also be a trivial steady state when our population is zero. How can we find these without using simulations?

To find the steady states, we need to set our derivative equal to zero and solve the equation for our variable. You may use MATLAB to do this or you may be comfortable enough to do this by hand. Just to remind you, the Logistic model we were working with is:

$$\frac{dB}{dt} = r(1 - \frac{B}{K})B$$

This means we want to solve this equation when $\frac{dB}{dt} = 0$.

$$0 = r(1 - \frac{B}{K})B$$

These can be directly plugged into a MATLAB solver, since we already have one side of the equation set to zero.

```
>> clear B r K
>> syms B r K
>> solve('r*(1-(B/K))*B', 'B')
```

We find out there are two answers (two steady states). One of these states is the trivial state $B = 0$, and the other state occurs when $B = K$, i.e. when our population is exactly equal to our carrying capacity. Now let us look at the exponential differential equation model.

2.2 Exponential Differential Equation Model Steady States

Now that you are getting more comfortable with several of the ideas and concepts behind mathematical modeling, we can look at the simulations from the exponential model and conclude that the only steady state will be the trivial one. We might as well check this by using the analysis technique we just learned. Remember we are looking to find where

$$\frac{dB}{dt} = rB$$

has the derivative equal to zero (or where there is no change in the population). This means we want to solve

$$0 = rB$$

Since parameter r is not zero then we know $B = 0$. Using MATLAB to check this answer we would need to type

```
>> clear B r
>> syms B r
>> solve('r*B', 'B')
```

which confirmed exactly what we found! We will review this process in the next section and highlight some differences between finding fixed points of discrete models and steady states of continuous models.

2.3 Fixed Points and Steady States Summary

To review, when you want to find the fixed point(s) of a discrete model you need to:

1. Drop the time subscripts off of the variables.
2. Solve for the variables.

When you want to find the steady state(s) of a continuous model you need to:

1. Set the derivative equal to zero
2. Solve for the variables.

It can be tricky to remember this distinction, so we remind you about these two methods again at the end of this lab. Note that when we know how to find steady states, we will be able to learn how to determine when the steady state is stable, unstable or undetermined.

3 Stability of Steady States

Stability still means the same thing for discrete and continuous models: “How will the population behave if we perturb it slightly?”

- Will the population return to where it was before the perturbation (stable)?
- Will the population change and give us something different than what we had before the perturbation (unstable)?

The method of actually finding the stability of each steady state in continuous models is identical to that of discrete models. However, the criteria for when a state is stable or not is vastly different. Stability for continuous models depends on the derivative of the right hand side of the equation. (Note, since we are not working with systems yet we do not need to use the Jacobian matrix, and a traditional derivative will work.) Now we will be concerned where this derivative is positive or negative and will not be working with absolute values.

- If the derivative of the right hand side of the differential equation with respect to the population variable and evaluated at the steady state is
NEGATIVE, then the steady state is **stable**.
- If the derivative of the right hand side of the differential equation with respect to the population variable and evaluated at the steady state is
POSITIVE, then the steady state is **unstable**.
- If the derivative of the right hand side of the differential equation with respect to the population variable and evaluated at the steady state is
ZERO, then we can not tell if the fixed point is stable or not
with this particular method.

Once again, this is very similar to before with a slight twist.

3.1 Stability of the Logistic Model

We just found two steady states for the Logistic Model, the trivial state $B = 0$ and the carrying capacity state $B = K$. To find the stability we need to look at the right hand side of the equation,

$$\frac{dB}{dt} = r(1 - \frac{B}{K})B$$

and then we need to take the derivative of $r(1 - \frac{B}{K})B$ with respect to the population variable B . We then evaluate the derivative at both steady states separately to see the stability of each state. Let's use MATLAB for that.

```
>> clear f B r K df
>> syms f B r K df
>> f = r*(1-(B/K))*B
```

```
>> df = diff(f, B)
>> subs(df, 'B', [0 K])
```

We find that the derivative evaluated at $B = 0$ is r , which we know is positive. This implies the trivial state is unstable and small perturbations from this state will not return the population back to $B = 0$. On the other hand, we found that the derivative evaluated at $B = K$ gives $-r$. Since this is negative, we know that the steady state $B = K$ is stable and small perturbations from this state will not cause a change in the behavior of the population. (We already suspected this from the simulation.) Why does this make sense biologically?

3.2 Stability of the Exponential Differential Equation Model

For the exponential differential equation model

$$\frac{dB}{dt} = rB,$$

we only found the trivial steady state at $B = 0$. We will also discover that the derivative of the right hand side turns out to be positive no matter where the derivative is evaluated.

```
>> clear f B r df
>> syms f B r df
>> f = r*B
>> df = diff(f, B)
>> subs(df, 'B', 0)
```

Since our derivative turned out to be positive, the trivial steady state is unstable and any perturbation to this state will cause the population to grow! Does this agree with the simulations from your previous lab?

4 Summary of One-Dimensional Discrete and Continuous Models

This table is to help you keep straight all the techniques and rules we have learned so far.

Technique	Discrete	Continuous
Equilibrium State	(Fixed Point) To find: remove subscripts and solve	(Steady State) To find: set derivative equal to zero and solve
Stability	Take derivative of right hand side and evaluate it at the particular fixed point	Take derivative of right hand side and evaluate it at the particular steady state
(Stable)	If the absolute value of the answer is LESS than 1	If the value of the answer is NEGATIVE
(Unstable)	If the absolute value of the answer is GREATER than 1	If the value of the answer is POSITIVE

You are now ready to simulate and analyze one-dimensional continuous systems using MATLAB!

5 Practice Problems

1. Find all of the steady states for the following model and then tell under what conditions is each point biologically relevant. This model incorporates a term in the form $\frac{aX}{b+X}$, traditionally known as a Michaelis-Menten kinetics term. Terms like this one are often used to describe chemical reactions or biological processes that reach a maximum level.

$$\frac{dX}{dt} = \frac{aX}{b+X} - cX$$

2. Find the stability of both the fixed points from the previous problem, remember to state the conditions needed to make the steady states stable and unstable. (Also remember any biological constraints needed!)
3. Simulate the model

$$\frac{dX}{dt} = \frac{aX}{b+X} - cX$$

to show your previous results. Start by picking parameter values that will make the non-trivial state biologically relevant and stable. Can you find any parameter values that would make the non-trivial state unstable, but still biologically relevant? Then pick parameter values that will make the trivial state unstable. Can you find any parameter values that will make the trivial state stable?

4. In a previous lab on discrete models and their long term behavior, we use a model from the book *Mathematical Models in Biology* by Leah Edelstein-Keshet:

$$X_{t+1} = -X_t^2(1 - X_t),$$

and found where this model had fixed points and where the fixed points were stable or unstable. Then we even used simulations to confirm our results. To compare discrete and continuous models, let us repeat this experiment with a similar continuous model:

$$\frac{dX}{dt} = -X^2(1 - X).$$

Now using the continuous model answer the following questions, which will give different results from before.

- (a) Find all the steady states.
- (b) Which of these states (if any) are biologically relevant?
- (c) Find the stability of each of the biologically relevant steady states.
- (d) Simulate this model starting with the following different initial conditions:
 - i. initial X value = 0
 - ii. initial X value = 0.1
 - iii. initial X value = 0.9
 - iv. initial X value = 1
 - v. initial X value = 1.1
 - vi. initial X value = 2
- (e) Do your simulation results match your stability analysis? Why or why not?
- (f) Describe the differences you find between the discrete model (previous lab work) and the continuous model.