

An Approach to Population and Biological Modeling for Pre and Post Calculus Students

Sharon Brown and Chris Dugaw

Dept. of Mathematics Humboldt State University

Abstract

Mathematical modeling and other quantitative analyses are becoming an ever more important part of biological research, and it is important to provide future biologists and mathematicians with a basic understanding of these methods. This minicourse will outline important topics in biological and population modeling that can be covered in calculus or pre-calculus based courses. The material will be presented in such a way that the audience could incorporate topics into an existing standard course or to develop a full course on modeling. We will cover the basics of model development, analysis, and interpretation using data, graphical, and symbolic approaches. We also provide a framework for using projects to get students to think more independently and deeply about modeling and to train students to communicate about mathematics.

Email Contact:

Brown: slb25@humboldt.edu

Dugaw: dugaw@humboldt.edu

Precalculus

- I. Intro to Modeling (*pg. 6-9*)
 - a. What is a model (*pg. 6*)
 - Definition
 - Who uses models?
 - When do you use models?
 - What can you model?
 - b. Why model? (*pg. 6*)
 - What questions can models answer?
 - What decisions can be made from model results?
 - c. Building a Model (*pg. 6*)
 - d. Modeling Approaches (*pg. 9*)
 - i. Empirical vs. Mathematical
 - ii. Deterministic vs. Stochastic
 - iii. Discrete vs. Continuous
 - iv. Linear vs. Nonlinear (Linearity) (Basic functions in Precalculus)
- II. Components of a Model
 - a. Variables and Parameters (independent and dependent variables – precalculus)
 - b. Functions and Equations (function notation)
 - c. Units and Dimensions (units, conversions)
- III. Graphs and Interpretation (precalculus graphing, basic functions)
- IV. Empirical Models (*pg. 9-12*)
 - a. Linear Models (*pg. 9*)
 - i. Regression in Excel/ TI Calc
 - ii. Plots and residuals plots in excel (i.e. check for deviation from linearity)
 - iii. Slope and intercept are parameters (linear equations in precalculus)
 - b. Non-linear models (*pg. 9*) (*Worksheet 1, pg. 12*)
 - i. Exponential: log-linear plots
 - ii. Power: log-log plot
 - iii. Connect to exponential/log rules from Precalculus.
 - iv. Special plots in excel (TI Calc)
 - v. Discuss Parameters
 - vi. Applications in Population Growth / Allometric Models
- V. Discrete Models (*pg. 13-41*)
 - a. Development (*pg. 17*)
 - i. Introduction to problem
 - ii. Assumptions (*Worksheet 2, pg. 18*)
 - iii. Translation to equations
 1. define variables (include units)
 2. define parameters (include units)
 3. create equations according to assumptions
 - iv. Check equations
 1. meets assumptions

- 2. units check
- 3. behaves reasonably?
- b. Solutions (**pg. 19**)
 - i. Numerically find t vs. $N(t)$ by iteratively solving for $N(t)$
(**Worksheet 3, pg. 21**)
 - ii. Cobwebbing; to get qualitative behavior (**Exercises, pg. 24-29**)
(**Worksheet 4, pg. 30**)
 - iii. Explicit solutions for simple difference equations
- c. Equilibriums (**pg. 31**)
 - i. Introduction, heuristic definition
 - ii. Numerically (**Worksheet 5, pg. 33**)
 - iii. Graphically
 - iv. Algebraically (**Exercises, pg. 35**)
- d. Stability (**pg. 36**)
 - i. Numerically; stable and unstable (**Exercises, pg. 37**) (**Worksheet, pg. 38**)
 - ii. Graphically with cobwebbing (**Exercises, pg. 39**)
 - iii. Slope idea; $-1 < \text{slope} < 1$ (**Worksheet, pg. 40, 41**)
- e. Interpreting results
 - i. Stable and unstable equilibrium for populations
 - ii. Stable zero equilibrium
 - iii. Unstable zero equilibrium
- f. Complex Dynamics
 - i. Logistic equation
 - ii. Bifurcation; change of stability with parameter change
 - iii. Periodic solutions
- g. Two species models (**pg. 42**)
 - i. Equations, numerical and graphical (excel) representation, equilibria.
 - 1. Predator/prey
 - 2. Host/parasite
 - 3. Competition
- h. Direction Fields (dfield Matlab and Web applet)
 - i. Simple single species idea of movement.
 - ii. Function graph and basic qualitative representation of solutions, equilibria.
- VI. Posters and Projects (**pg. 54-58**)

Calculus

- I. Intro to Modeling
 - a. What is a model
 - b. Why model?
 - c. Basic Approaches
 - i. Empirical vs. Mathematical
 - ii. Discrete vs. Continuous
 - 1. Connect Discrete Models with sequences
 - 2. Continuous models have instantaneous rates of change (derivatives)
- II. Building a Model
 - a. Variables and Parameters
 - b. Functions and Equations
 - c. Units and Dimensions
- III. Graphs and Interpretation
- IV. Empirical Models (*pg. 43*)
 - a. Linear Models
 - i. Multivariate regression
 - ii. Derive regression formulas from minimization problem
 - iii. Linear algebra – least squares and projections
 - b. Non-linear models
 - i. Polynomial regression
 - ii. Exponential and Power Functions
 - c. Continuous Random Variable Models
 - i. Connects with integration
 - ii. Mean and Variance formulas
- V. Continuous Models (*pg. 44-53*)
 - a. Development
 - i. Exponential
 - ii. Logistic as a modification of exponential
 - iii. Predator/Prey
 - iv. Compartmental Models
 - 1. SIR
 - 2. Scuba Computers (nitrogen absorption)
 - 3. Drug Absorption
 - b. One dependant variable (*pg. 47-49*)
 - i. Equilibriums
 - ii. Stability
 - 1. Application of Taylor series
 - 2. When does linear stability analysis break down?
 - iii. Direction Fields (dfield Matlab and Web applet)
 - iv. Interpreting results
 - v. More Examples
 - 1. Von Bertalanffy
 - 2. Biochemical examples.

- c. Two dependant variables (**pg. 50-53**)
 - i. Phase Planes
 - 1. Connect with parametric equations
 - 2. Numerical: pplane matlab and web applet
 - ii. Equilibria
 - iii. Stability
 - 1. Multivariate Taylor Series
 - 2. Linear Algebra Connection
 - iv. Nullcline analysis (**Worksheet 8, pg. 52**)
 - v. Limit cycles – Numerical only
 - 1. Predator Prey
 - 2. Biochemical oscillations
 - d. Higher Dimensions
 - i. Reduction to lower dimension (SIR)
 - ii. Chaos in Three Species Food Chain (Klebanof and Hastings)
Matlab model?
- VI. Discrete Models
- a. Development
 - b. Equilibriums ($N_{t+1}=N_t$ not $N_{t+1}=0$!)
 - c. Stability
 - i. Taylor Series
 - ii. Connect to continuous $\log(\lambda) = r$
 - d. Interpreting results
 - e. More Examples
 - f. Complex Dynamics
 - i. Two cycles, composition of functions $f(f(x))=x$
 - ii. Stability Chain Rule
 - iii. N -cycles $f^n(x)=x$
 - iv. Mathematica as tool for finding cycles
 - v. Matlab software for Logistic Map
 - g. Two species models
 - i. Nicholson-Bailey
 - ii. Excel/Matlab programs
- VII. Posters and Projects (**pg. 54-58**)

Precalculus Material

Intro to Mathematical Modeling

What is a Mathematical Model?

Definition: A **mathematical model** is an abstract representation of a real world situation that uses mathematical language to describe the behavior of a system. Mathematical models are used particularly in the natural sciences and engineering disciplines (such as physics, biology, and electrical engineering) but also in the social sciences (such as economics, sociology and political science); physicists, engineers, computer scientists, and economists use mathematical models most extensively.

http://en.wikipedia.org/wiki/Mathematical_model

Why Model?

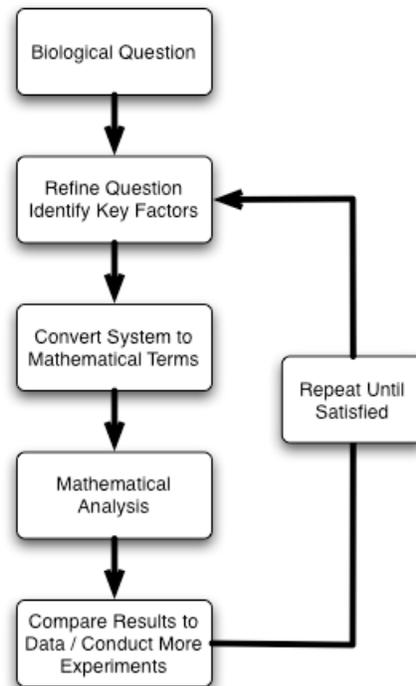
To learn more about a system that is not well understood, is hard to study, or is difficult to measure. A model can help focus experiments by showing what the important quantities to measure are, or create new questions. Sometimes an incorrect model can be the most valuable. For example the exponential growth model for populations is not an accurate model overall, but it introduced one of the most important questions in ecology “What are the factors that limit populations to prevent exponential growth?”

Building a Model

Mathematical model building starts with a real world situation or system that we want to better understand. The goal is to build as precise of a mathematical description of the situation as possible, balancing the systems details with mathematical difficulty, to enables us to better understand the original real world situation.

A mathematical model usually describes a system by a set of variables and a set of equations that establish relationships between the variables. The values of the variables can be practically anything for example; real or integer numbers, Boolean values or strings. The variables represent some properties of the system, for example, measured system outputs often in the form of signals, timing data, counters, population numbers or

density, event occurrence (yes/no). The actual model is the set of functions that describe the relations between the different variables.



Model Building Process

There are many steps to model building but it can be broken down generally into the following basic steps:

- Someone poses a question about a real world system. Usually this question is not something that can be answered purely by observations. Such as “What may be causing the decline of a particular species?”, “What is the most important age class for the survival of the sea turtle?”, “What biological factors play the strongest role in the spread of an invasive plant?”, “How quickly is the invasive species spreading and what is the best management strategy?”
- Next an attempt to make the problem as precise as possible is needed. In this step it is important to identify and select those concepts to be considered as basic in the study and to define them carefully. Usually there is consultation between the expert in the field and the mathematician during this phase of the process. The

purpose is to eliminate unnecessary information and to simplify the information that is retained as much as possible. This step consists of identifying the important basic factors, idealizing those factors to simplify the model and approximating the idealizations.

- The third step is to look at this idealized representation of the real world situation and attempt to identify the process at work and explain it mathematically. The goal is an expression or expressions of the entire situation in symbolic terms. This is the process of **mathematical modeling**. Much of the value of the study hinges on this step because an inappropriate identification between the real world and a mathematical structure is unlikely to lead to useful results. There may be several mathematical models for the same real situation. The model to be used is the one that best fits the question being studied.
- The resulting mathematical system is studied using appropriate mathematical ideas and techniques. Motivation for the mathematical study is not to produce new mathematics, but instead to produce new information about the situation being studied. The important contribution of the study may well be the recognition of the relationship between known mathematical results and the situation being studied.
- The next step in the model-building process is the comparison of the results produced on the basis of the mathematical work with the real world. The interpretation of your results and how they relate to the original real world situation. Frequently the agreement between prediction and observations is less than desirable, at least on the first attempt. At this stage you should examine your model and critique what has worked and what needs improvement.
- Usually the modeling building process goes through several iterations, each a refinement of the preceding model until finally an acceptable model is found.

<http://www.indiana.edu/~hmathmod/index.html>

Modeling Approaches

There are many different approaches to modeling and we will discuss a few of the main types here. Sometimes you are simply interested in describing a set of data with a simple function. We refer to this type of model as an *empirical model*. In contrast a *mathematical model* is a mathematical construct that describes how the fundamental components of a system interact and can be used to make predictions.

Mathematical models fall into two main categories. A well defined *deterministic model* is a model that has only one solution for a given set of parameters, while a *stochastic model* is a model that incorporates random elements, and therefore can only be used to make statements about the probability of certain outcomes. Stochastic modeling is a difficult subject and is beyond the scope of a precalculus or calculus based course.

Another important decision to be made is to determine how you will model time. A *continuous time* model represents time as a continuum of real numbers. This is appropriate for systems where change is occurring in an uninterrupted way. A *discrete time* model represents the time as a sequence of integers. This type of model is good for systems where change occurs at isolated times, for instance modeling insects that reproduce once per year.

Empirical Models

Linear Models

Linear Regression is a technique for fitting a linear model to data that is commonly covered in a precalculus course. Numerous examples of the use of linear regression in biology exist (cf. §1.2 of Greenwell *et al.* 2003, Fetta 2003), and software such as Excel and graphing calculators can readily perform linear regressions. (For a great tutorial on excel see: <http://phoenix.phys.clemson.edu/tutorials/excel/>)

Nonlinear Models

Many biological phenomena are poorly described by a linear model. Sometimes this is apparent from the raw data, but often times it is necessary to look for trends in a

residual plot. A common simple approach is to use logarithms to transform a nonlinear problem to a linear problem. This is an excellent way to show the utility of logarithmic functions and their properties.

Exponential Model

$$P(t) = Ce^{rt}$$

Taking the natural log of both sides and applying log rules yields:

$$\ln(P) = \ln(C) + rt$$

Plotting the natural logarithm of the dependent variable versus the independent variable yields a straight line with slope r and a vertical intercept equal to $\ln(C)$. It may be illuminating to tell students to let $y = \ln(P)$ and $b = \ln(C)$. Another approach is to have students fit an exponential model to data using linear regression on the natural logarithm of the output versus the input data (no logarithm applied to it). From the linear regression they can determine the best slope value and the best intercept value, which will then correspond to the r and C values for the exponential model. On the web you can find special paper called *semi log paper* for plotting data for an exponential model by hand. On this paper if the model data fits an exponential equation the data will look linear. Students may have experience using this paper in their science classes.

Examples of exponential models can be found in any applied calculus text, e.g. *Adler, Hoffman & Bradley*, and *Greenwell et al.*

Allometric Models (Power Laws)

$$A(t) = Ct^n$$

Taking the logarithm (with any base) of both sides and applying logarithmic rules yields:

$$\log(A) = \log(C) + n \log(t)$$

Plotting the logarithm of the dependent variable versus the logarithm of the independent variable yields a straight line with slope n and vertical intercept $\ln(C)$. Again it may be illuminating to tell students to let $y=\ln(A)$, $x=\ln(t)$ and $b=\ln(C)$. Students can fit an Allometric model using linear regression on the logarithm of the output data and the logarithm of the input data. Also, you can get special paper called *log-log paper* for plotting such data by hand. For examples of Allometric Models see *Hoffman and Bradley* pp. 93-95 or *Greenwell et al.* pp. 100-101.

Examples:

1. Basal metabolic rate: The rate at which animals consume energy while resting is called their Basal metabolic rate (bmr). An empirical model for the bmr of animals M is:

$$M=70w^{3/4}$$

where M is measured in kilocalories/day and w is measured in kg.

(*Hoffman & Bradley* p.93-95)

2. Swimming Velocity: The swimming velocity of a marine organism (in cm/sec) of length l (in cm) is given by:

$$v = 2.69 l^{1.86}$$

(*Greenwell et al.* p. 215)

Worksheet 1

Nonlinear Empirical Models

1. The weight of a fish called the monkeyface prickleback depends on its length. We will use the following table to determine the function that relates the weight of the fish to its length.

Weight (w) in g	Length (l) in cm	$\ln(w)$	$\ln(l)$
1.38	5	.322	1.61
147	25	4.99	3.22
575	40	6.35	3.69
1865	60	7.53	4.09

- a) Calculate the slopes between points on the graphs of w vs. l , $\ln(w)$ vs. l , and $\ln(w)$ vs. $\ln(l)$ to decide which model best describes the relationship: linear, exponential or Allometric. Remember linear functions should have the same slope between any two points.

- b) Find an equation that approximately gives the relationship between w and l .

Discrete models

Examples of Single species Linear Models

1. Cell Division: Population of cells that divide synchronously, with each producing a daughter cells, $a > 0$. M_0 is the initial number of cells, and each successive generation is labeled with a numerical subscript, e.g. M_n = number of cells in the n^{th} generation.

$$M_{n+1} = aM_n$$

(Leah Edelstein-Keshet, pg. 6)

2. Insect Population: An insect with multiple stages of life can be modeled using difference equations for each stage, then bringing those stages together in a single difference equation.

Example: The Poplar gall aphid. Adult female aphids produce galls on the leaves of poplars. All the progeny of a single aphid are contained in one gall. Some fraction of the progeny will emerge and survive to adulthood. Although many factors actually determine the likelihood of surviving and reproducing, for simplicity we look at a model that assumes all parameters are constant (independent of outside forces or effects). Define the following variables and parameters;

a_n = number of adult female aphids in the n th generation,

p_n = number of progeny in the n th generation,

m = fractional mortality of the young aphids,

f = number of progeny per female aphid,

r = ratio of female aphids to total adult aphids.

If each adult female produces f progeny then the number of progeny next generation would be given by;

$$p_{n+1} = fa_n.$$

Of these, the fraction $(1-m)$ survives to adulthood, of which only the fraction r of them are female. Thus the number of adult female aphids is given by;

$$a_{n+1} = r(1-m)p_{n+1}.$$

Now using the equation for p_{n+1} , we can write the adult difference equation in terms of a only, given by;

$$a_{n+1} = fr(1-m)a_n.$$

(Leah Edelstein-Keshet, pg. 7, 8)

3. The Malthusian Model: Assuming geometric growth of the population.

$$P_{n+1} = \lambda P_n$$

where λ is referred to as the finite growth rate of the population, calculated as the birth rate minus the death rate (λ is not an instantaneous rate).

(E. Allman and J Rhodes, pg. 2, 3)

Examples of Single species Nonlinear Models

1. Quadratic Growth Model: (“logistic growth model”); Density dependent population growth. (more commonly used in continuous time differential models to model populations with a carrying capacity). The parameter r is the growth rate at low population and the $(1-P_n)$ term is a density dependent growth term.

$$P_{n+1} = r(1-P_n)P_n$$

where $0 < r < 4$, and $0 < P_0 < 1$.

2. The Beverton-Holt model, often used in population ecology and genetics:

$$x_{n+1} = \frac{a}{b + x_n} x_n$$

where $b < a$. The parameter a represents a carrying capacity and b is a half saturation value for the population.

(Lamberson and Allen)

3. Ricker Model, used in fish population models,

$$p_{n+1} = re^{-ap_n} p_n$$

where $r > 1$, and a usually satisfies $a > 0.1$. The parameter r is the intrinsic growth rate, and a is a factor that determines the degree of sensitivity of the population to over crowding.

An equivalent version of this model, sometimes referred to as the “discrete logistic model” is,

$$N_{n+1} = N_n e^{R_0 \left(1 - \frac{N_n}{K}\right)}$$

where $R_0 > 0$, $K > 0$.

(Lamberson and Allen, E. Allman and J. Rhodes, pg. 33-36)

4. Gompertz Model for tumor growth.

$$v_{n+1} = r v_n \ln \left(\frac{K}{v_n} \right)$$

where $1 < r$, and $10 < K$. The parameter r represents the growth rate of the tumor.

(Lamberson and Allen)

5. Palmer Tree Model used to model tree growth.

$$v_{n+1} = r e^{c/v_n} v_n$$

where $0 < r < 1$ and $1 < c$. The term $r e^{c/v_n}$ is a measure of the growth term as v_n increases the growth rate is reduced.

(Lamberson and Allen)

6. Insect population model due to Hassel and May.

$$P_{n+1} = r e^{\left(1 - \frac{P_n}{K}\right)} P_n$$

where $1 < r$, and $10 < K$. The parameter r is an intrinsic growth rate term and K is a carrying capacity term.

(Lamberson and Allen)

7. Competition for resources among individuals in the same population. This model has similar carrying capacity characteristics as the continuous logistic growth model.

$$P_{n+1} = \frac{\lambda P_n}{(1 + aP_n)^\beta}$$

where $a > 0, \lambda > 0, \beta > 0$.

(*E. Allman and J. Rhodes, pg. 36*)

Discrete Model Development

Assumptions

One of the most common assumptions in building a population model for species is that each generation of a population grows in relation to the previous generation population sizes. The simplest form of this is to assume that the population size in the next generation is dependent only on the population size of the present generation. Many species population models use some form of this assumption to model the growth of populations. The growth rate term of the model will describe how the present population affects the growth of the population for the future. Such models have the general form

$$P_{n+1} = R(P_n) P_n$$

where $R(P_n)$ represent the growth rate from generation n to generation $n+1$.

In the following model

$$P_{n+1} = r(1-P_n)P_n$$

the growth rate term is given by

$$R(P_n) = r(1-P_n).$$

By examining the growth rate term we can determine some of the assumptions about the growth of this population.

Discrete Model Solutions

Numerical Solutions

Quite often in modeling we are interested in the characteristics that the model predicts given a particular set of values for parameters and an initial condition for our model. The explicit solution would yield these characteristics but it is most often quite difficult if not impossible to find. One of the beautiful things about discrete population equations is how well they are suited for a calculator or computer. One of the first things we will do is to examine a particular model and look at the sequence of values it produces as part of its solution by iterating the function. Let us look at the Beverton-Holt model:

$$x_{n+1} = \frac{a}{b + x_n} x_n, \quad b < a.$$

Assume that we start with an initial population of $x_0 = 5$ and parameter values of $a = 3$, $b = 2$. Then the model is

$$x_{n+1} = \frac{3}{2 + x_n} x_n.$$

Plugging in the initial condition for x and evaluating the model equation will give the value for x_1 . Now using x_1 as the input and evaluating the model equation will give the value for x_2 . Continuing we would then get the following sequence of values for the iteration of the model equation.

$$x_1 = \frac{3}{2 + 5} 5 = 2.14286$$

$$x_2 = \frac{3}{2 + 2.14286} 2.14286 = 1.55172$$

$$x_3 = \frac{3}{2 + 1.55172} 1.55172 = 1.31068$$

⋮

Numerical solutions with a graphing calculator

This iteration of the solution points can be done on the TI Calculator by entering

$$3/(2+\text{ans}(1))*\text{ans}(1),$$

After our first calculation using the initial condition, where ans(1) is just above the (-) key and is found by pushing 2nd (-). Once this is in the command line then you can continue to press ENTER and each successive entry is the next iteration in the solution.

Worksheet 3

Numerical Solutions to Discrete Model Using a Calculator

Consider the Beverton – Holt equation:

$$x_{n+1} = \frac{a}{b + x_n} x_n, \quad b < a$$

with $a = 3$, $b = 2$ and initial condition $x_0 = 5$.

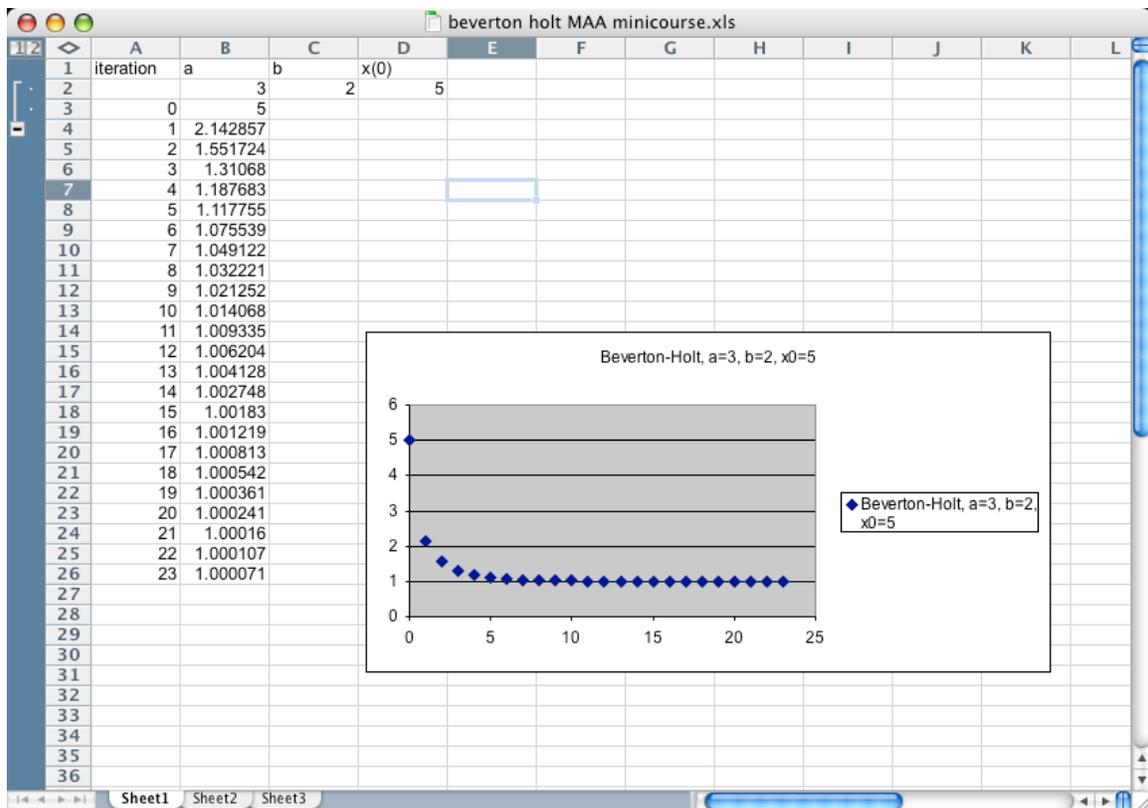
Please answer the following questions

1. Use your graphing calculator to find the values of x_n . What values do the solution points take on? (Give the first 10 values).
2. What appears to happen to the solution?
3. Can you explain what this may mean? What might this mean biologically?
4. Try another initial point. Does this change the outcome?
5. Try a different value for a , keeping in mind that $b < a$. Does this change the outcome?
6. What happens if you let $b < 0$? Would this make sense biologically?
7. Can you decide what a and b might represent biologically?
8. Can you find a value for x_0 such that all future values of $x_i = x_0$, $i = 1, 2, 3 \dots$? What might be a good name for this value of x_0 ?

Graphical Solutions Using Excel

Quite often it is nice to be able to graphically look at what our solution is doing. This gives us a picture of what the populations are doing as time goes on. To do this we would need to graph the population at each generation or time (along the vertical axis) versus the generation number or time value (along the horizontal axis).

Excel is an excellent tool to generate solution points and to graph the solution versus its iteration number. The following is a demonstration of these calculations and the corresponding graph for the original parameter and initial condition values.



Excel Window

To generate the iterative values of the solution to the given Beverton – Holt equation in Excel we first want to designate cells for our parameter and initial condition values. If you look at the above table generated in Excel you see that the parameter and initial condition variables are listed in their own cells and the corresponding values are listed below these cells. Allowing a cell to be dedicated to these values will enable us to

be able to change the values easily and have the iterated answers and graph be updated simultaneously for the new values.

In the cell to the right of iteration 1 the formula for the model was placed into the Excel spread sheet using the given values of a , b , and x_0 . The formula looks like the following;

$$=(B2/(C2+B3))*B3.$$

To make sure that the values that need to stay constant for each application of the formula do not change, place a \$ sign in front of the row and column entry for those terms in the model formula. As you can see from the given formula and the example spreadsheet given above, the values for the parameters a and b are being held constant. B2 is the position of the value of a (Bth column, 2nd row) and C2 is the position of the value of b (Cth column, 2nd row) and B3 is the position of the initial condition, x_0 . We want the formula to update the initial condition value, replacing it with the new x_1 value. This updating can be accomplished by using the click and drag property of Excel to copy the formula down a column to be applied to as many cells as you wish.

The corresponding solution graph for this model is also given above. The solution is to a discrete problem and thus should not be a continuous curve but a series of discrete points. To produce the solution to the problem you need to select the iterative column and the solution value column, click on the graphing tool box button, and select scatter plot. Choose the sub plot with no connecting lines between the points. Then press next. The next page should have the data range be the highlighted cells on you Excel sheet and the series in: Columns, selected. Once this is set then press next. At this point you can now title the graph, and give names to the axis. Then once again press next, and now you choose if you wan the graph to show up on the same sheet as your data and to be moved around as an object or if you want it on its own sheet. And then you are done. Once the graph is connected to the data, you can go back in and change the parameter values in the Excel sheet and the iterative solution values and the graph of the solution will be updated automatically. This allows you to easily and quickly see the effects of the initial condition and parameter value changes on the model without any additional work.

Worksheet idea:

Have the students examine the behavior of the model by changing each of the parameters values one at a time. Determine what effect that parameter has on the behavior of the solutions. Describe what they observe in a concise, way in writing using graphs only to demonstrate what they have explained in writing. Be sure to have them not replace written explanations with graphs, but support their written explanations with well-chosen graphs.

Cobwebbing

Cobwebbing is a graphical method to help determine the qualitative behavior of a solution to a discrete dynamical system of one variable. This method translates the iterative process of using the answer from the previous step as the input for the next step in a graphical way. Looking for a moment at a general discrete single variable model of the form $P_{n+1} = f(P_n)$ and calling P_{n+1} the output value and P_n the input value at step n , then at step $n+1$, the output value would be P_{n+2} , and P_{n+1} will have become the new input value. This switch that P_{n+1} made from being an output value in one step to an input value in the next step is what the cobwebbing method is based on. Basically what has occurred is a value on the vertical axis has now become the next value on the horizontal axis if we were to graph each successive step against the next.

Exercises

Recall the quadratic discrete model:

$$P_{n+1} = r(1-P_n)P_n$$

with $r = 2$ and $P_0 = 0.1$

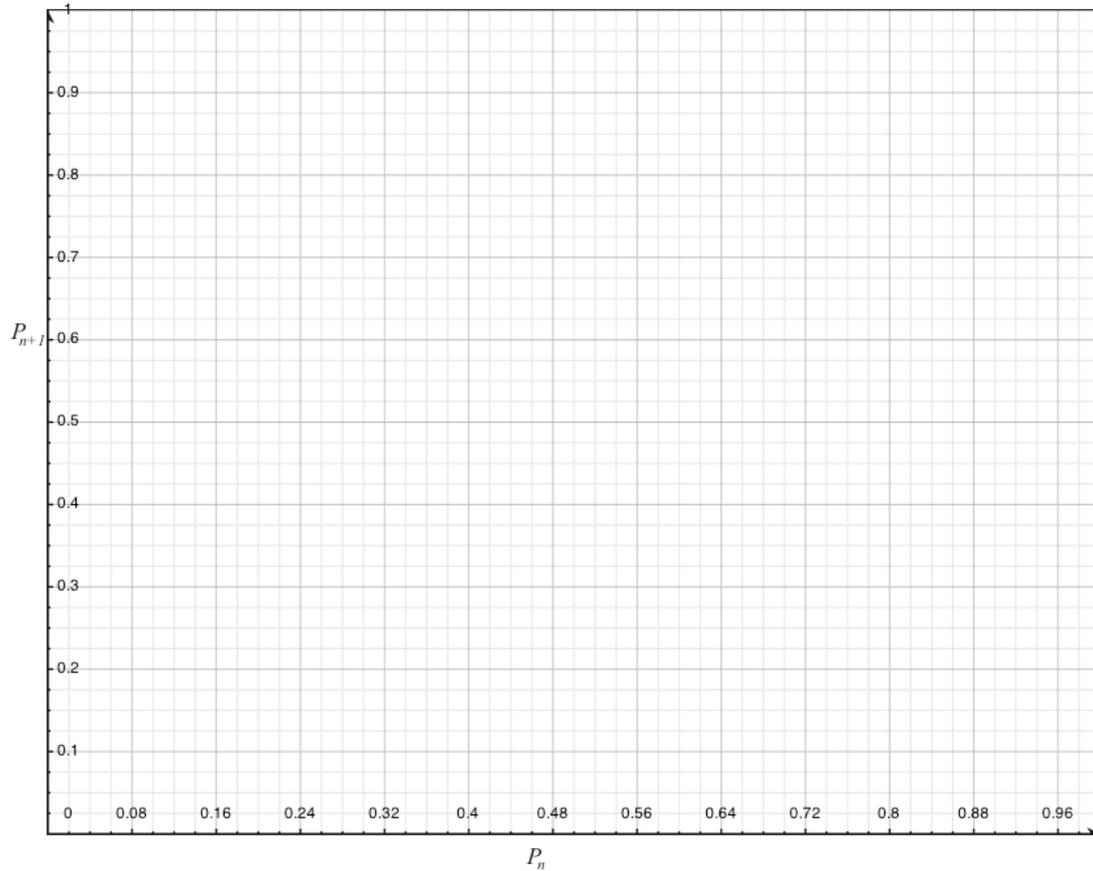
Find the first 8 iterations of the solution, e.g. find P_1 through P_8 using a calculator, keeping track of the ordered pairs, (P_n, P_{n+1}) . I'll do the first couple for you to get you started then you fill in the rest of the table.

$$P_{n+1} = 2(1-P_n)P_n, P_0 = 0.1$$

Input	Output	Ordered Pair (P_n, P_{n+1})
$P_0 = 0.1$	$P_1 = 2(1-0.1)0.1$ $P_1 = 0.18$	$(P_0, P_1) = (0.1, 0.18)$
$P_1 = 0.18$	$P_2 = 2(1-0.18)0.18$ $P_2 = 0.2952$	$(P_1, P_2) = (0.18, 0.2952)$

Now graph each of these ordered pairs on a coordinate plane where the vertical axis is the P_{n+1} axis and the horizontal axis is the P_n axis. Make sure your graph is large enough with a lot of room in between integer values so that you can graph accurately.

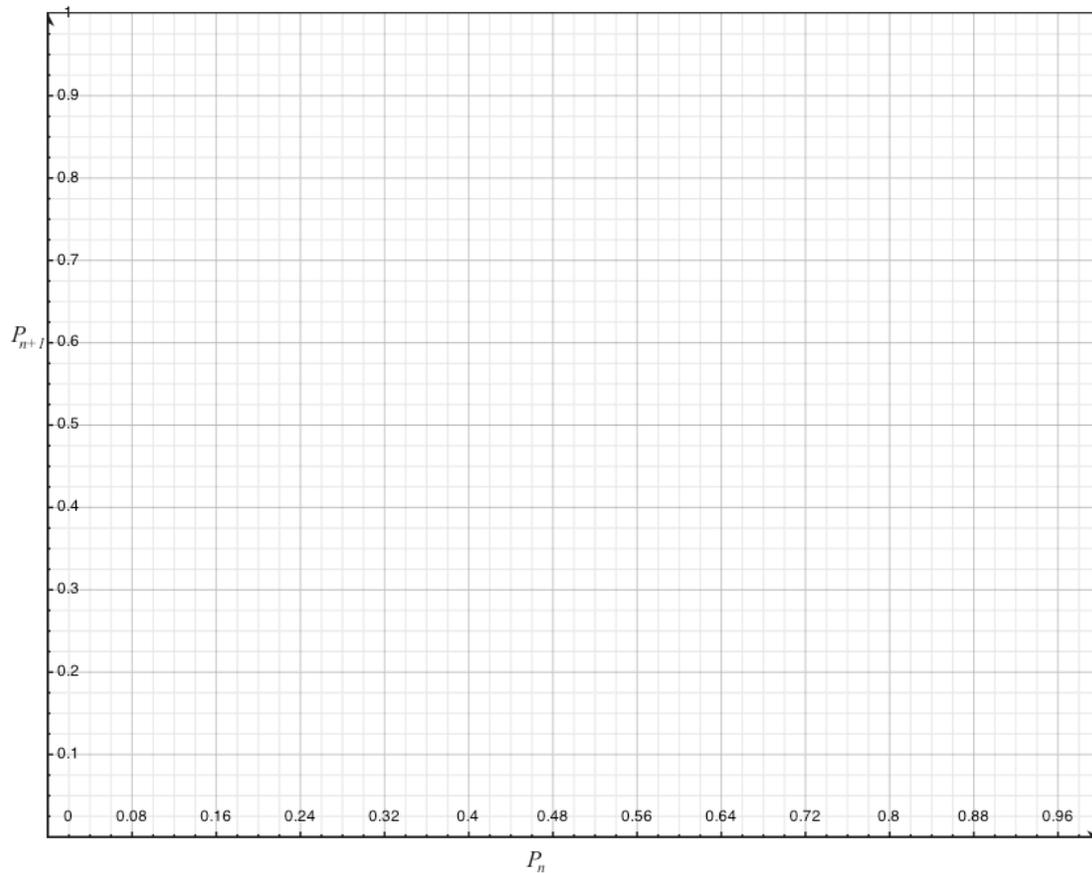
Graph P_{n+1} vs. P_n



Now on this same graph, draw the continuous function $f(P) = 2(1 - P) P$, assume for this function that $P_n = P$. If you have been careful it should be the case that each of your data points lie on the graph of $f(P)$. So we see that one way to find the iteration values of the discrete function is to draw the continuous function $f(P)$ where $f(P_n) = P_{n+1}$, and then finding the point on the function where a vertical line going through the initial value will intersect the function. This point should have the first coordinate equal to the initial value and the second coordinate equal to P_1 . To find the next iterative solution value we could then find the point on the function where a vertical line through the P_1 value on the horizontal axis intersects the function. Again the first coordinate of this second point is P_1 and the second coordinate would be P_2 . In this way we could find each of the iterative values that we wish as long as our graph was detailed enough. However this can become a rather tedious process of moving the second coordinate value of a point to the

horizontal axis and then drawing the vertical line from that value to the function to find the next point, and thus the next iterative value of the solution. A quicker way to do this method graphically would be to determine a fast way to transform the output of one step into the input of the next step. This is analogous to switching a y value into an x value. To do this we need one more line on our graph. Lets start over with a clean slate and graph our $f(P) = 2(1-P)P$ function and also on the same set of axis graph the identity line, the line along which the input and output values are equal ($y = x$ line). Still label the axis P_{n+1} and P_n .

Graph $f(P) = 2(1-P)P$ and the identity line. Be as accurate as possible with your graph.



Now that we have that graphed find the initial condition, $P_0 = 0.1$ on the horizontal axis and draw a vertical line from that value to the function.

What should be the value of this output at this point?

Go find that value on the horizontal axis and again draw a vertical line from that value to the function. So far we have not done anything new, but now for something different. Go back to the previous point on the function, the point that corresponds to our initial conditions as the input, now draw a horizontal line from that point to the identity line.

What do you notice about the point on the identity line that you just hit and the vertical line associated with your second point on the function?

If you have done this correctly you should see that the vertical line and the point on the identity line have the same input value. In other words, by moving over horizontally from our first point on the function to the identity line what we have accomplished is to convert the output of that first point into an input value. If you were to draw a vertical line from the point on the identity line to the function, the point where the vertical line intersects the function would be the next order pair for our solution set. Continuing this process of alternating vertical moves to the function curve and horizontal moves to the identity line will produce successive values for our iterative solution. This is the process of cobwebbing.

Worksheet 4

Cobwebbing

1. Create cobweb graphs for the quadratic difference equation for each r value, $r = 2, 2.5, 3, 3.5$ with $P_0 = 0.1$.
2. For each graph in question (1) above, describe what the behavior of the solution is. Are the solution values increasing, decreasing, cycling or acting strange in some way? If you were to continue cobwebbing for a long time would the solution approach a single value or multiple values?
3. If you were to change the initial condition would this change how the solution behaved? Is there a range of initial condition values that gives the same kind of solution behavior?
4. What do you notice about the point where the function intersects the identity line?
5. What would happen if you chose the initial condition equal to the value at this intersection? What would the iterative values look like in this case?
6. Choose $r = 2.5, P_0 = 0.1, 0.3, 0.5, 0.8$ and cobweb. Now convert the information from the cobwebbing diagrams to a qualitative picture about the solution over time given the different initial conditions. Graph the solution iterations versus the iteration number for each initial condition.

Equilibria

An equilibrium point of a discrete model is defined as the value of the state variable that satisfies the following conditions:

$$P = f(P) \text{ where,}$$
$$P_{n+1} = f(P_n)$$

An equilibrium point can be found a number of ways mathematically; numerically, graphically and algebraically. We will be looking at finding the equilibrium of a model in each of these ways.

Numerically

Let's look at the Ricker model for fish populations and determine the equilibrium point for that model. The Ricker model is;

$$P_{n+1} = re^{-aP_n} P_n, \quad r > 1, \quad a > 0.1$$

First we will try and determine the equilibrium for this model numerically. We need to set the parameter values to be able to numerically solve look for the equilibrium of the model; let $r = 2$, and $a = 0.5$. Now let $P_0 = 10$ and iterate on the calculator or using Excel to see what the solution does. If you iterate a few times you should get the following table of values;

Iteration - n	P_n
0	10
1	0.202138
2	0.548121
3	1.25019
4	2.00734
5	2.20726
6	2.19624
7	2.19732
8	2.19721
9	2.19723
10	2.19722
11	2.19722

We see that by the 11th iteration that the values start repeating, this implies that the input and output values are equal and we have found a value that satisfies

$$P = f(P),$$

our equilibrium condition. The difficulty with this method is that it may miss some of the equilibrium values, in particular it will miss those equilibrium that are what we call unstable. This type of equilibrium has the characteristic that the solution will move away from that value as you continue to iterate, no matter how close (but not equal) your initial condition is to that equilibrium value. We will discuss stability issues more thoroughly in a future worksheet. The nice thing about this method is that if our equilibrium is stable, the iteration approaches the equilibrium value, and we can get a nice numerical approximation of the equilibrium value. We can also see how the value of the equilibrium point may vary as we change parameter values.

Worksheet 5

Equilibria of Discrete Models Numerically

Recall the Ricker Model for population growth:

$$P_{n+1} = re^{-aP_n}P_n, \quad r > 1, \quad a > 0.1$$

1. Using the above Ricker model, keeping the same value for a and P_0 ($a = 0.5$, $P_0 = 10$), determine if the equilibrium value is dependent on the value of r by varying the r value and seeing what happens to the equilibrium value (recall $r > 1$).
2. Again, using the Ricker model, keeping $r = 2$, $P_0 = 10$, vary a and determine the effects on the equilibrium value ($a > 0.1$).
3. Now fix the values of $r = 2$, $a = 0.1$, and vary P_0 . Determine the effects on the equilibrium value.

Equilibria of Discrete Models Graphically

The condition for an equilibrium point is that the input of the difference equation is equal to the output of the difference equation, or said another way, there is no change in the system for an equilibrium input value. Graphically to determine an equilibrium point we will look for the points of intersection for the function $f(P)$ and the identity line, graphed on the axis P_{n+1} versus P_n . The intersection of these graphs will be points that satisfy

$$P_{n+1} = f(P_n)$$

and

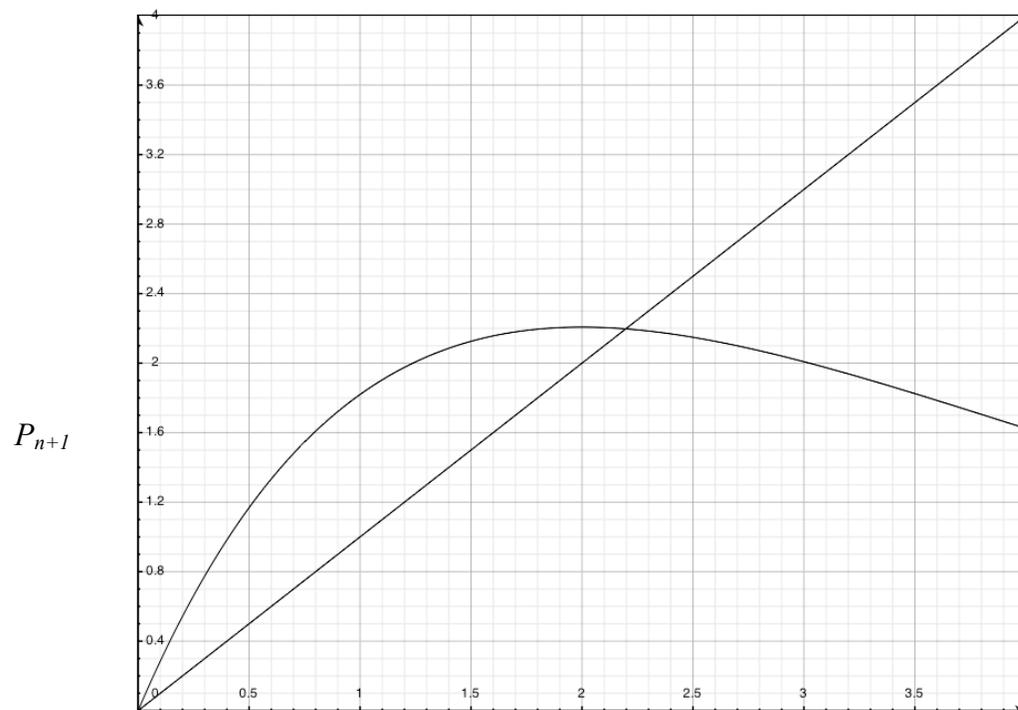
$$P_{n+1} = P_n.$$

Thus the outcome is equal to the input at these points on the model equation.

Again let us look at the Ricker model with the first set of parameter values. In this case we do not need to have an initial condition given to determine the equilibrium. From our graph of

$$P_{n+1} = 3e^{-0.5P_n} P_n$$

$$P_{n+1} = P_n$$



P_n

We see that there are two points of intersection, only one of which we were able to determine numerically. The second point is the origin, this point we were unable to figure out using the numerical method because this point is unstable. The graphical method allows us to determine how many equilibria we should be able to find, and combined with cobwebbing it will help us to determine stability. However each result we get is dependent on what parameter values are being used. The equilibria will change as we change the parameter values. We need a more general way of determining equilibria without setting parameter values ahead of time. That brings us to the algebraic method of determining equilibria.

Equilibria of Discrete Models Algebraically

To determine equilibria algebraically we must solve the problem of

$$\begin{aligned}P_{n+1} &= re^{-aP_n} P_n \\P_{n+1} &= P_n\end{aligned}$$

Let $P_{n+1} = P_n = P$ and solve

$$\begin{aligned}P &= re^{-aP} P \\P - re^{-aP} P &= 0 \\P(1 - re^{-aP}) &= 0 \\P = 0 \text{ and } P &= \frac{1}{a} \ln(r)\end{aligned}$$

Thus there are two equilibria $P = 0$ and $P = \frac{1}{a} \ln(r)$.

Exercises

1. For the following models first find the general equilibria algebraically for non-specified parameter values and then determine the equilibrium value for the given parameter values.
 - a. Beverton – Holt used for population ecology and genetics

$$x_{n+1} = \frac{a}{b + x_n} x_n$$

let $b = 4$ and $a = 10$.

b. Gompertz Model for tumor growth

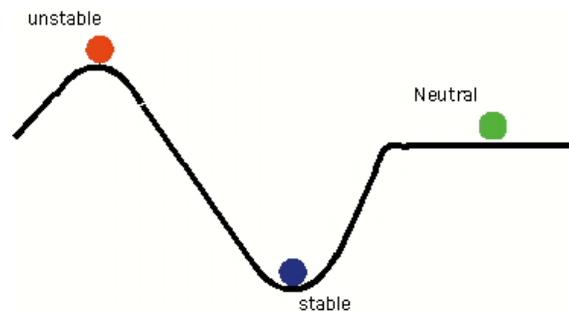
$$v_{n+1} = rv_n \ln\left(\frac{K}{v_n}\right)$$

let $r = 3$, and $K = 125$.

2. In reference to each of the models presented in the above problem discuss how varying one parameter at a time will affect the value of the equilibrium point. What are possible biological interpretations for the meaning of each of the parameters in light of what the models are typically used to represent?

Stability of Equilibrium Points

An equilibrium point for a model is considered asymptotically stable if solutions that start near the equilibrium point always stay near the point and actually approach the point as time goes on. An unstable equilibrium point will be a point that if you start near that equilibrium point the solution will continually move away from that equilibrium point. Heuristically these can be expressed respectively in terms of standing in a valley or standing on top of a hill. A stable equilibrium point is like standing in a valley and placing a ball near you, in a smooth valley if you place a ball near you the ball will role down and approach you. It may oscillate from side to side around you, but those oscillations are decreasing and the ball is actually getting closer and closer to you. On the other hand an unstable equilibrium point is like standing on top of a hill, if you place a ball near you, the ball will begin to roll away from you always getting farther and farther away.



Stability Diagram

(Taken from: http://eesc.columbia.edu/courses/eesc/climate/lectures/atm_phys.html)

There are two very simple ways to test stability of equilibrium in a single discrete model, and a third method that eventually leads to an analytical test for stability of equilibrium points.

Stability of Equilibrium Points Numerically:

As previously mentioned with a numerical approach we need to fix the parameter values and start with a given initial condition. First choose which equilibrium point you want to test the stability of, and then choose an initial condition that is near that point, not so far away that you have another equilibrium point between your initial condition and the equilibrium point you are testing.

Exercises

1. What would you expect the behavior of the solution to be if the equilibrium point you are testing is unstable?
2. What would you expect the behavior of the solution to be if the equilibrium point you are testing is stable?

Worksheet 6

Stability of Equilibrium Points Numerically

Let's look at an example and try to determine the stability of the equilibria. From the previous worksheet on Equilibria we looked at the Ricker model

$$P_{n+1} = re^{-aP_n} P_n$$

and determined that the equilibrium for this model is $P = 0$ and $P = \frac{1}{a} \ln(r)$.

1. Let $r = 2$ and $a = 0.5$, determine the equilibrium values.
2. Starting testing the stability of the equilibrium $P = 0$, choose $P_0 = 0.1$ and iterate to find the solution. What is the behavior of the solution? Would you say this equilibrium is stable or unstable?
3. Now test the stability of the second equilibrium point $P = 1.38629$, choose $P_0 = 1.3$ and iterate to find the solution. What is the behavior of the solution? Would you say this equilibrium is stable or unstable?
4. Now try $P_0 = 1.4$ and answer the same questions.

Stability of Equilibrium Points Graphically

To graphically determine the stability of an equilibrium point you use the cobwebbing technique of iterating the solution. You must be able to graph the discrete function defining the model and the identity line. Then choose an initial point near the equilibria you are testing and cobweb from that point. If the solution moves away from the equilibrium then the equilibrium is unstable, if the cobwebbed solution moves toward the equilibrium then the solution is stable. The difficulty of this is that it may be difficult to get accurate results for certain parameter ranges where the dynamics of the system is complex. Such as in the logistic, or quadratic model near the values of r where the model produces stable periodic cycles, or chaotic behavior.

Exercise

1. For the Beverton – Holt model and the Gompertz model given on the Equilibrium worksheet graph each modeling function for the given parameter values and cobweb to determine the stability of the equilibria.

Second Graphical approach:

The second means for looking at the stability of an equilibrium point is to examine, or determine the slope of a tangent line to the model function at the equilibrium point. If the tangent line has a slope between -1 and 1 then the equilibrium point will be stable, if on the other hand the slope is less than -1 or greater than 1 , then the equilibrium point is unstable. This analysis leads directly to the linearization ideas for determining stability about an equilibrium point.

Worksheet 7

Graphical Approach to Determining Stability of Equilibria

For each of the following models do the given exercises.

- a. Beverton – Holt used for population ecology and genetics

$$x_{n+1} = \frac{a}{b + x_n} x_n$$

let $b = 4$ and $a = 10$.

- b. Gompertz Model for tumor growth

$$v_{n+1} = rv_n \ln\left(\frac{K}{v_n}\right)$$

let $r = 3$, and $K = 125$.

1. Graph the model function and the identity line for each of the given models. On this graph draw a line for each equilibrium point that just touches the model function at the equilibrium point and runs parallel to the graph at that point. It should be the case that if you were to zoom into the graph and the line at the equilibrium point you would have a hard time telling them apart. This type of line is called a tangent line to the graph at the equilibrium point. Now estimate the slope of each of the lines. Is it the case that the equilibrium points that are stable have a tangent line with a slope that is between -1 and 1? Why do you think this would be an indication that the equilibrium point is stable? (Hint it has something to do with how the solution would act near that point given that the slope is between -1 and 1).

2. Given the Quadratic model

$$P_{n+1} = r(1 - P_n)P_n$$

What is the effects on the graph of the model function $f(P) = r(1-P)P$ as you vary r from 0 to 4? Now look at the graph of this function along with the identity line and a tangent line drawn at the non-zero equilibrium point. As you vary r what happens to the slope of the tangent line to the function at the equilibrium point? What can you say about the stability of the second equilibrium point as r varies?

3. Using a numerical method determine the stability of the non-zero equilibrium point when $r = 3$? What is the behavior of the solution at this point? Use cobwebbing to demonstrate what you found out with the numerical method.

Examples of Two species models

1. Predator-Prey model. Let N_t be the population of the prey at time t , and P_t be the population of predator at time t . The model for a discrete Lotka-Volterra predator-prey model is;

$$\begin{aligned}N_{t+1} &= N_t(1 + r - rP_t) \\ P_{t+1} &= P_t(1 + s - sqP_t + sN_t)\end{aligned}$$

where r is a growth term for the prey and s is a growth term for the predator population. The parameter q represents an intra-specific competition for the predator population. Both populations in this model have a density dependent growth term in the absence of the other species.

(Lamberson and Allen, pg. 55)

2. Nicholson-Bailey Host-Parasitoid Model. In a host-parasitoid system, we usually have two insect species with one, the parasitoid, laying its eggs on or in the second species, the host. These eggs hatch and the resulting larvae live at the expense of the host, usually killing it.

Let N_t be the host species population at time t and P_t be the parasitoid population at time t . The Nicholson-Bailey model is given by;

$$\begin{aligned}N_{t+1} &= \lambda N_t e^{-\alpha P_t} \\ P_{t+1} &= c N_t (1 - e^{-\alpha P_t})\end{aligned}$$

where λ and c are growth terms for the Host and Parasitoid populations respectively and α has to do with the Poisson probability of an event occurring per unit time.

(Lamberson and Allen, pg. 62)

Calculus Material

The material on model building and development are the same as in the precalculus section, so we will not repeat them here.

Empirical Models

Linear Models (See precalculus section)

Linear Regression is a technique for fitting a linear model to data. The output variable can be a linear function of one or more input variables. Linear regression involves finding the set of parameters that minimize the sum of squared errors. Multivariable calculus students can follow the derivation of this method. This is a very common technique and an abundance of examples exist. Derivations and exercises can be found in *Hoffman & Bradley* section 7.4 and *Neuhauser* section 12.7.

Nonlinear Models (See precalculus section)

It may be appropriate to have calculus students apply the method of least squares to log-transformed data after learning the technique of least squares.

Continuous Random Variables

A continuous random variable is a random number taken from the real numbers. Associated with every continuous random variable is a probability density function $f_X(x)$. The probability that the random variable X lies in an interval (a,b) is equal to:

$$\int_a^b f_X(x)dx$$

The study of continuous random variables is a natural application of the definite integral. Many applied calculus texts have chapters on this topic, e.g. *Adler, Hoffman & Bradley*, and *Neuhauser*.

Continuous Single Species Models

1. Exponential Growth: $P(t)$ is the population at time t , r is the intrinsic growth rate of the population:

$$\frac{dP}{dt} = rP(t)$$

(Edelstein-Keshet, pg. 117, 212)

2. Logistic Growth: $P(t)$ is the population as time t , r is the intrinsic growth rate, K is the carrying capacity of the environment:

$$\frac{dP}{dt} = rP(t) \left(1 - \frac{P(t)}{K} \right)$$

(Cullen, pg. 381-389, Edelstein-Keshet pg. 119, 212)

3. Allee Effect: This can be used if there is a minimum threshold value for which, if the population is below this value it will die off, and if it is above this value it will approach an equilibrium population level. $P(t)$ is the fraction of the population at time t , a is the fraction of the population threshold value, and r is the intrinsic growth rate of the population. The population fraction is the ratio of the population to the maximum population. The model takes the form;

$$\frac{dP}{dt} = rP(P - a)(1 - P).$$

(Edelstein-Keshet, pg. 215)

4. Gompertz Growth Curve – model for the growth of tumors: $V(t)$ is the volume of the tumor at time t , the growth rate is directly proportional to the size of the tumor, where the constant of proportionality is an exponential decay function, $k > 0$, and $a > 0$;

$$\frac{dV}{dt} = ke^{-at}V(t).$$

(Cullen, pg 366)

5. Von Bertalanffy Growth Model: The rate of growth in length of a fish is directly proportional to the length yet to be achieved, where $L(t)$ is the length of the fish at time t , $K > 0$, is the proportionality constant and L_{∞} is the maximal length the fish can achieve:

$$\frac{dL}{dt} = K(L_{\infty} - L(t))$$

(Cullen, pg. 373-380)

6. Distribution of a drug in the tissue: If a fixed dose y_0 of a drug is injected into the bloodstream, the drug will eventually make its way into organ(s) where it is destroyed through metabolism and/or excretion. The compartment model for the bloodstream predicts a simple exponential decay. Thus the drug leaves the bloodstream at the rate $I(t) = y_0\lambda_1 e^{-\lambda_1 t}$. This function serves as the input rate for the organ thus if $y(t)$ is the amount of drug in the organ, then the rate of change of the amount of drug in the organ is given by;

$$\frac{dy}{dt} = -\lambda_2 y(t) + y_0\lambda_1 e^{-\lambda_1 t}.$$

It is assumed that there is no drug in the organ initially and $\lambda_1 > 0$, and $\lambda_2 > 0$.

(Cullen, pg.403)

Continuous Two or more “Species” Models

Examples

1. Predator- prey model: Lotka -Volterra model for predator – prey. Let $N(t)$ be the prey population at time t and $P(t)$ be the predator population at time t , then:

$$\begin{aligned}\frac{dN}{dt} &= aN(t) - bN(t)P(t) \\ \frac{dP}{dt} &= -cP(t) + dN(t)P(t)\end{aligned}$$

where a , b , c and d are all positive constant. The parameters a and c are the intrinsic growth rate of the prey and predator respectively. The parameter b represents the probability of an encounter between a predator and a prey which results in a kill for the predator. The parameter d represents the nutritional value of a prey to contribute to the reproduction health of the predator.

(Edelstein-Keshet, pg 218, see pg 223 for variation for both the prey and predator equation)

2. Competition: A competition model would be similar to the above predator prey model except in the absence of one species the other would have positive exponential growth, and each interaction results in a negative effect on both populations. The model equations would have the form;

$$\frac{dN}{dt} = aN(t) - bN(t)P(t)$$

$$\frac{dP}{dt} = cP(t) - dN(t)P(t)$$

A more realistic version of this would allow some density dependence on the growth of a population in the absence of the other species, e.g.;

$$\frac{dN}{dt} = aN(t)\left(1 - \frac{N(t)}{K_N}\right) - bN(t)P(t)$$

$$\frac{dP}{dt} = cP(t)\left(1 - \frac{P(t)}{K_P}\right) - dN(t)P(t)$$

(Edelstein-Keshet, pg 224)

3. SIR models:

Epidemic model:

$x(t)$ = susceptible population at time t

$y(t)$ = infected population at time t

$z(t)$ = post-infected population at time t

N = total population fixed.

$$x(t) + y(t) + z(t) = N$$

$$x'(t) = -k_1x(t)y(t)$$

$$y'(t) = (k_1x(t) - k_2)y(t)$$

$$z'(t) = k_2y(t)$$

(UMAP Model 73, Epidemics, Brindell Horelick and Sinan Koont, Edelstein-Keshet, pg. 245, further development of variations of this model also in Edelstein-Keshet pgs. 242-256)

4. Scuba diving:

$$\frac{dp}{dt} = k(p_e - p(t))$$

where k is a constant related to the ability of the tissue to depressurize, p_e is the ambient external pressure at a certain depth and p is the pressure at time t . This is calculated for ranges of depths, where each initial condition is determined from the previous depths calculations.

(UMAP, Module 767, *The Mathematics of Scuba Diving*, D. R. Westbrook)

One Dependent Variable (Single Species)

In this section we consider models of the form:

$$\frac{dx}{dt} = f(x)$$

Equilibria

Equilibria occur when the derivative is zero, i.e. $f(x)=0$.

Stability Analysis

Stability analysis of one-dimensional ODEs is a standard method found in many applied calculus texts (e.g. see *Adler* section 5.3, *Neuhauser* section 8.2). We analyze the stability of an equilibrium by taking the Taylor Series expansion of the function f about the equilibrium x^* and ignoring all 2nd order and higher terms. So

$$\frac{dx}{dt} \approx f(x^*) + f'(x^*)(x - x^*)$$

Notice that since x^* is an equilibrium $f(x^*)=0$, and then let $X=x-x^*$ (the perturbation from the equilibrium point x^*). Noting that $dX/dt=dx/dt$, we get

$$\frac{dX}{dt} \approx f'(x^*)X$$

this has the solution

$$X(t) = X_0 e^{f'(x^*)t}.$$

So the perturbation X grow if $f'(x^*)>0$ and shrink if $f'(x^*)<0$. Thus an equilibrium is stable if the derivative of f at the equilibrium is negative and unstable if it is positive.

Direction Fields

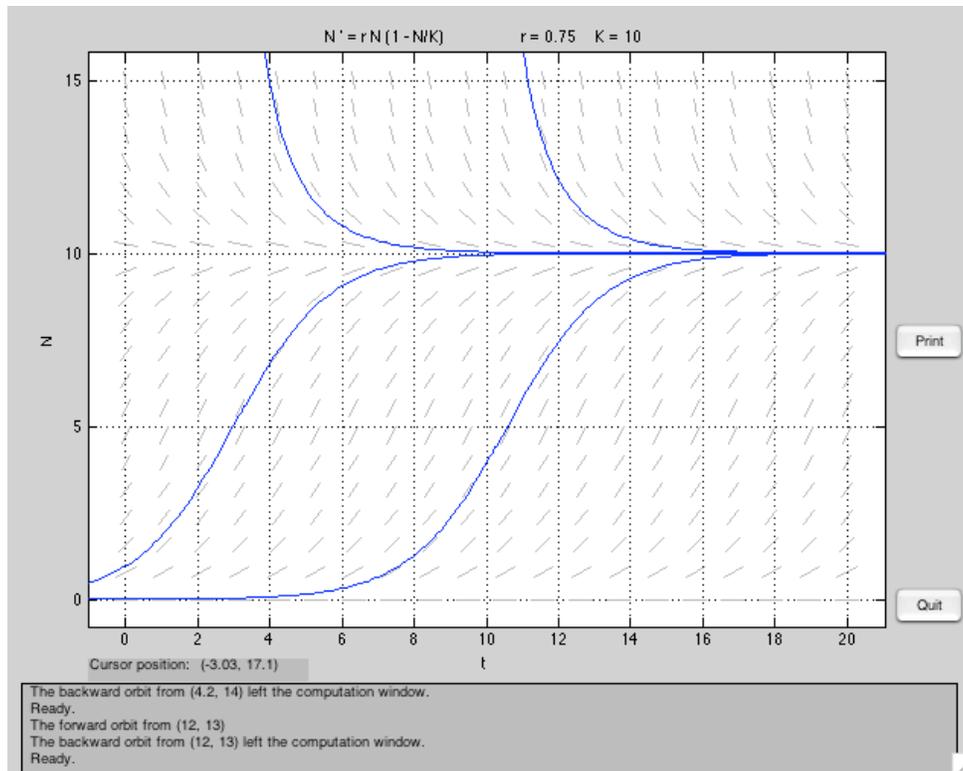
The differential equation gives a formula for the slope of the graph of the solution x versus t . To obtain a direction field you simply draw a short line segment for each location in the (t, x) -plane. The slope of the line segment at a point (t, x) is $f(x)$. The best software for graphing direction fields and solutions is **dfield** written by John Polking. It is available at: <http://math.rice.edu/~dfield/>

Example

Logistic Growth

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

Using **dfield** with $r=0.75$ $K=10$ the direction field looks like:



dfield output

Phase Lines

Phase Lines are a simple way to summarize the dynamics of one-dimensional differential equations.

To draw a phase line you can follow these steps:

- Draw a vertical x - number line.
- Find the equilibrium points (the values of x such that $f(x) = 0$), and mark them on the line with an open circle.
- Find all intervals of x -values for which $f(x) > 0$, and draw arrows pointing up in these intervals.
- Find all intervals of x -values for which $f(x) < 0$, and draw arrows pointing down in these intervals.
- Equilibrium points that have arrows pointing to them from above and below will be approached as $t \rightarrow \infty$. Fill in the circle for these equilibria, these are stable

Example

Logistic Growth

The equilibria of this differential equation are the solutions to:

$$0 = rN\left(1 - \frac{N}{K}\right)$$

Those solutions are $N = 0$ and $N = K$. We also see that $dN/dt > 0$ when $0 < N < K$ and $dN/dt < 0$ when $N < 0$ or $N > K$. This information can be used to draw the phase line.



Phase line for $\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$

Compare this to the direction field for the Logistic Growth model shown above.

Two Dependent Variables (Two Species)

In this section we consider a system of two autonomous differential equations, which have the form:

$$\begin{aligned}\frac{dx}{dt} &= f(x, y) \\ \frac{dy}{dt} &= g(x, y)\end{aligned}$$

Phase Planes

Phase planes are the most natural way to visualize systems of two nonlinear differential equations. A system of two differential equations involves three variables, two dependent and one independent, but we can graph solutions parametrically in the 2-dimensional *phase plane* if we treat the independent variable as the parameter.

The differential equations define a vector field in the phase plane where the vectors are tangent at every point to the parametric representation of a solution. The best software for graphing phase planes and solutions is **pplane** written by John Polking. It is available at: <http://math.rice.edu/~dfield/>

Equilibria

The equilibria are the points where dx/dt and dy/dt are both zero, and can be found by solving the system

$$\begin{aligned}0 &= f(x, y) \\ 0 &= g(x, y)\end{aligned}$$

Like before these equilibria can be stable or unstable.

Stability Analysis

The stability analysis of two dimensional systems requires an understanding of elementary linear algebra, but these topics can be covered in an applied course, e.g. *Neuhauser*, and *Bittinger et. al.* We analyze the stability of an equilibrium by taking the Taylor Series expansion of the functions f and g about the equilibrium and ignoring all 2nd order and higher terms. So

$$\begin{aligned}\frac{dx}{dt} &\approx f(x^*, y^*) + \frac{\partial f}{\partial x}(x^*, y^*)(x - x^*) + \frac{\partial f}{\partial y}(x^*, y^*)(y - y^*) \\ \frac{dy}{dt} &\approx g(x^*, y^*) + \frac{\partial g}{\partial x}(x^*, y^*)(x - x^*) + \frac{\partial g}{\partial y}(x^*, y^*)(y - y^*)\end{aligned}$$

Notice that since (x^*, y^*) is an equilibrium so $f(x^*, y^*)=0$ and $g(x^*, y^*)=0$, and then let $X=x-x^*$ and $Y=y-y^*$. Noting that $dX/dt=dx/dt$ and $dY/dt=dy/dt$, we get

$$\begin{aligned}\frac{dX}{dt} &= \frac{\partial f}{\partial x}(x^*, y^*)X + \frac{\partial f}{\partial y}(x^*, y^*)Y \\ \frac{dY}{dt} &= \frac{\partial g}{\partial x}(x^*, y^*)X + \frac{\partial g}{\partial y}(x^*, y^*)Y\end{aligned}$$

This linear system is stable if the all of the eigenvalues of the Jacobian Matrix (below) have negative real part, and unstable if one or more have a positive real part. The stability of the $(0,0)$ equilibrium point for this linear system coincides to the stability of the (x^*, y^*) equilibrium for the nonlinear system.

$$\begin{pmatrix} \frac{\partial f}{\partial x}(x^*, y^*) & \frac{\partial f}{\partial y}(x^*, y^*) \\ \frac{\partial g}{\partial x}(x^*, y^*) & \frac{\partial g}{\partial y}(x^*, y^*) \end{pmatrix}$$

Nullcline Analysis

Stability analysis can be cumbersome and only gives reference to the behavior of the system near the equilibrium points. Nullcline analysis can give a better understanding of the global dynamics. A nullcline is a curve or a line where one of the derivatives is zero, i.e. $f(x,y) = 0$, or $g(x,y) = 0$. The intersections of the nullclines corresponding to $dx/dt = 0$ with nullclines corresponding to $dy/dt = 0$ give equilibrium points. In addition to determining the equilibrium points, the nullclines divide the phase plane into regions where the derivatives have the same sign. Nullclines can be graphed using pplane.

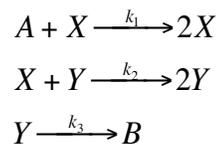
Worksheet 8

Limit cycles are periodic solutions to a system of ODE, which appear as a closed loop in the phase plane. Limit cycles can be stable or unstable. Poincare sections are the standard analytic technique for analyzing limit cycles, but are beyond the scope of a Calculus level course. We recommend studying limit cycles numerically with **pplane**.

Examples

Predator Prey: See the preceding worksheet.

Biochemical Oscillations: Consider the following chemical reactions:



where A and B are held at constant concentration. Assuming mass-action the differential for the concentrations of the chemicals are:

$$\begin{aligned}\frac{dx}{dt} &= k_1ax - k_2xy \\ \frac{dy}{dt} &= k_2xy - k_3y\end{aligned}$$

(From *Edelstein-Keshet* p.303; for more complex biologically explicit models see: *Fall et al.* and *Keener and Sneyd*)

Discrete Models

We again refer you to the precalculus material for this section.

Projects

Projects: the following is taken from a class that has projects as part of the course grade.

Project Assignment

You will complete one project for the course, worth 15% of your course grade. You will choose which one project to complete. The paper for the project is due Monday, March 26th and the poster is due Monday, April 16th.

Guidelines:

Due Dates:

First Rough Draft of the paper	Monday	March 5
Second Rough Draft of paper	Tuesday	March 20
Final Paper Due	Monday	March 26
Rough Draft of Poster	Friday	April 6
Poster Due	Monday	April 16
Individual Group Eval. Due	Thursday	April 19
Evaluation of Poster Due	Friday	April 20

You will turn in a complete, polished paper. Grammar and writing style are an important part of the paper evaluation. Your paper must be at least 5 pages typed. You may use Microsoft Word or Scientific Workplace (for Windows 95 or NT) for the equations and write up. You can obtain a disk to download Scientific Workplace version 3.0 from me.

You must also provide a poster of your work. Look at the Web site <http://www.ncsu.edu/project/posters/NewSite/> for help. You are expected to evaluate your own group poster as well as those of your classmates.

Format for the Paper

Begin by **describing the problem you are solving**. You may quote the description directly from the text, or you may paraphrase or enhance it. The person reading your report should not need the textbook to understand your problem or solution.

Next, **write your objectives in solving this problem**. Be sure to state what skills from the course you will be applying to the problem.

Now **use the texts questions as a guide in producing a solution to the problem**. It is a good idea to have subsections of your report for each question. You can list the question as the heading for the subsection, or you can incorporate the question into your discussion as you go about solving the problem.

If you are presenting a project from the book out of chapters 12-15 you must also include a description of an extension of the problem, or an application of the mathematics. This extension needs to be introduced, discussed and solved.

Finally, **summarize what you learned from solving the problem**. Make sure you state clearly how you have met your objectives! It is appropriate to address new things that you have learned while completing this project, either about mathematics or about the situation your project addresses. Part of your score reflects the **insight** you demonstrate about your topic.

Grading – Project:

The total project is worth 100 points as follows:

- 40 points for the group paper:

 - 15 points for the mathematics

 - 15 points for readability, grammar and organization.

- 40 points for the poster:

 - 50 points for the poster (graded by students)

 - See the Poster Score Sheet for grading criteria

- 10 points poster evaluation

 - 10 points for completing and entering poster evaluations and comments for each poster including your own by the due date.

- 10 points flex for group evaluation:

 - 10 points determined by the group evaluation participation scores given to you by your group members and yourself.

Paper Scoring Rubric

Projects will be scored in each of the following areas. Total points divided by 4 will give your overall score on the project. You may bring your project to my office hours before the due date if you would like preliminary feedback. **I will only grade projects that are professional quality.**

Category	4	3	2	1
Description of the project and the mathematical issues that it addresses	The purpose of the project is clearly presented. Mathematical concepts are correctly addressed.	The project is not as clearly stated, or not all mathematical issues are addressed.	The report displays only cursory attention to a description of the project and its mathematical content.	The project is not well-defined.
Solution to the problem	The math employed to solve the problem is complete and correct.	There are some errors in the mathematics, though largely the math is correct.	There are many errors in the mathematics, though there is also substantial correct mathematics.	The report is riddled with mathematical errors.
Insight gained from doing the project	The report displays a thoughtful reaction to the ideas addressed in the project.	The report displays the student has given some thought to a reaction to the ideas addressed in the project.	The report displays cursory attention to providing reactions to the material.	The report does not include reactions to the material.
Grammar, style and presentation	Excellent	Few errors	Several errors	Poorly written

Letter grades will be assigned according to the following minimums:

Minimum score	Letter grade
3.75	A
3	B
2	C
1.75	D

Poster Scoring Rubric

Evaluate each poster in each of the following categories on a scale of 0 (unacceptable) to 4 (high achievement). Total points divided by the number of categories (8) will give the overall score on the poster.

Appearance

- Readability (consider text size, neatness of writing, clarity of writing and descriptions, grammar)
- Visual Pleasantness (consider colors, graphs, white space, whether it is cluttered.)

Organization

- Flow (consider if it concepts flow well together, should include Introduction, Body and Conclusion: and Author Identification)
- Main Points (are main points easy to find, are the sections easily discernible?)

Content

- Description (is the project well-described?)
- Solution (is the mathematical solution present with enough, but not too much detail?)
- Insight (does the poster display insight about the purpose of the project or to applications of mathematics?)
- Depth of Connections (Does the poster make connections to broader ideas, skill form this class, and did the poster tie all of the big ideas together?)

Write at least one constructive overall comment (required):

Peer Review

Person Being Evaluated: _____

(Rate the person 5 if you strongly believe the statement is true, rate the person 1 if you strongly disagree with the statement)

This person met all expectations for working within this group:

Strongly Disagree 1 2 3 4 5 Strongly Agree

This person was present at all group meetings both in class and outside of class:

Strongly Disagree 1 2 3 4 5 Strongly Agree

This person did his/her fair share of work on the project:

Strongly Disagree 1 2 3 4 5 Strongly Agree

This person displayed a positive and helpful attitude:

Strongly Disagree 1 2 3 4 5 Strongly Agree

If 100% is the total work put into the paper and poster combined, what percentage of the work was performed by this group member?

Comments: (required)

Evaluator (Your name) _____

References

http://en.wikipedia.org/wiki/Mathematical_model

<http://www.indiana.edu/~hmathmod/index.html>

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Lamberson, Roland H. and Allen, David L., *Building and Analyzing Dynamic Models in Ecology and Resource Management*, preprint

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UMAP References

UMAP stands for Undergraduate Mathematics and Its Applications. This part of the COMAP (Consortium for Mathematics and Its Applications) organization. This organization has a number of wonderful things to offer for application of mathematics, we have compiled some of the UMAP Modules that relate to biological model here. This is not an exhaustive list, if you would like to see more you can visit the site, however you must be a member to download most of their modules. Here is the web address

<http://www.comap.com/>

UMAP Modules:

Precalculus:

The Lotka-Volterra Predator-Prey Model, James Morrow, **Module 675**,

This module describes and analyzes qualitatively a simplified version of the predator-prey model attributed to Lotka and Volterra. Deductions are made concerning the size of populations based on information about their percentage growth rates. The module describes a nonstandard and stimulating way of illustrating the power and utility of combining geometry and algebra.

The Hardy-Weinberg Equilibrium, Steven Kolmes, Kevin Mitchell, **Module 735**,

Using elementary probability, this unit shows how genotypes in a population reach an equilibrium in a single generation, under appropriate conditions. Real data illustrate this concept, and conditions are examined that may keep a population from attaining an equilibrium.

The Species – Area Relation, Kevin Mitchell, James Ryan, **Module 768**

This unit examines the fundamental ecological relationship that as the area A of a region increases, so does the number of different species S encountered. We begin by motivating why power curves $S = cA^z$ are often used to model this

relationship. Using logarithms, we show how a model curve can be fit to species-area data sets. WE present various interpretations and uses of the constants c and z , and show how the model has been used by researchers to describe species loss resulting from deforestation. Real data sets are used extensively throughout the unit. Descriptions of student field projects are included.

Game Theory Models of Animal Behavior, Kevin Mitchell, James Ryan, **Module 783**

This unit is an introduction to elementary game theory and some of its applications to evolutionary biology. The concepts of an evolutionary stable strategy (ESS) is defined and its consequences are explored in several two- and three-person games. References are made throughout to examples of contests between animals in the wild. The unit concludes with a detailed application of this theory to male elephants and their mating strategies, using data from research studies.

Calculus

The Mathematics of Scuba Diving, D. R. Westbrook, **Module 767**

Exponential Solutions of differential equations are used to construct decompression schedules of divers for various duration and various depths

Using Original Sources to Teach the Logistic Equation, Bonnie Shulman, **Module 766**

This Module uses original data, diagrams, and texts from three original sources to develop the logistic model of growth in natural systems with limited resources. The logistic differential equation and the familiar S-shaped logistic curve have applications in solving problems in ecology, biology, chemistry, and economics. The module illustrates with concrete examples how mathematics develops, and it provides insights into the assumptions that drive the modeling process.

The Spread of Forest Fires, Emily E. Puckette, **Module 792**

We create a simple discrete probabilistic model for spread of a forest fire. We examine the conditions for which the fire will either die out or spread indefinitely, identifying and bounding a critical value for the probability of transmission of the fire to an immediately adjacent location.

Population Growth and the Logistic Curve, Brindell Horelick, Sinan Koont, Sheldon F. Gottlieb, **Module 68**

Resilience of Grassland Ecosystems, Kevin Cooper, Ray Huffaker, Thomas Lofaro, **Module 775**

This Module introduces students to the state-and-transition theory explaining the succession of plant species on grassland and to the concept of successional thresholds partitioning plant states into those gravitating toward socially desirable or socially undesirable plant compositions over time. Students are shown how the state-and-transition theory is formulated in the mathematical ecology literature as a system of two autonomous differential equations, and how a successional threshold is defined by the stable manifold to an interior saddle-point equilibrium. A series of exercises directs students toward a qualitative phase-plane solution of the system and an analytical approximation of the stable manifold. Students also gain experience working with the numerical phase-plane plotter Dynasys, which can be downloaded from the World Wide Web. A discussion section applies the approximated stable manifold to the real-world problem of controlling livestock numbers on public grazing land to reestablish more socially desirable plant varieties. The Module is within the capabilities of students having had basic calculus and introductory course in differential equations covering phase-plane solutions.

Differential Growth, Huxley's Allometric Formula, and Sigmoid Growth, Roger V. Jean, **Module 635**,

Differential growth refers to the changes in proportions, morphological or chemical, following the increase in size, inside single species or between adults of

related species. In many cases differential growth is controlled by the Allometric formula $Y = nX^m$, establishing a correlation of growth between the variables X and Y found in many sectors of biology, from embryology, taxonomy, and paleontology to ecology and zoology. This entirely empirical formula arises, as we will see, in a variety of equivalent forms. The exercises will show that it is related to the logistic formulae of absolute growth representing S-shape curves. The great appeal of the Allometric formula comes mostly from its simplicity, from the frequency with which it arises and from its close relation to Thompson's famous Theory of Transformations, of which we will say a few words. This formula is the most versatile mathematical expression for intra- or interspecies comparisons.

The Ricker Salmon Model, Raymond N. Greenwell, Ho Kuen Ng, **Module 653**,

A difference equation model describing the dynamics of a salmon population was developed by W. E. Ricker in 1954. This unit derives the model, shows how it can be modified, and introduces the concept of maximum sustainable yield. It also shows how difference equations may lead to periodic and chaotic behavior, and a computer program enables one to explore the periods and chaos. The technique of dynamic programming is introduced to show how to maximize the income from fishing over a finite period.

Compartment Models in Biology, Ron Barnes, **Module 676**

This module introduces compartment models and their applications.

Fire Control and Land Management in the Chaparral, William B. Gearhart, John G. Pierce, **Module 687**

Catastrophic wildfires are an ever-present danger in chaparral wilderness areas. This module develops a Markov-chain model that can be used to evaluate strategies for chaparral land management and fire control. The model is applied to determine an optimal prescribed-burning policy.

Information Theory and Biological Diversity, Steven Kolmes, Kevin Mitchell, **Module 705**

Discusses and derives the key properties of one measure of diversity, the entropy function, and illustrates its use by ecologists and animal behaviorists.

A Blood Cell Population Model, Dynamical Diseases, and Chaos, William B. Gearhart, Mario Martelli, **Module 708**

This Module gives an introduction to the modeling of blood cell populations and the role of modeling in the study of dynamical diseases of the blood.

Of Mites and Models: A Temperature-Dependent Model of a Mite Predator-Prey Interaction, John B. Collings, David J. Wollkind, **Module 764**

We analyze the qualitative behavior of a model for a mite predator-prey interaction. This model is based on a simple system of differential equations, and the model parameters are assigned values determined for a specific interaction between two species of mites. Several of these parameters are functions of temperature, and temperature is treated as a bifurcation parameter in the analysis of the model. It is shown that, depending on the temperature value, the model exhibits a stable fixed point, a stable limit cycle, or both (bistability). The model is used to illustrate population outbreaks.

Immunological and Epidemiological HIV/AIDS Modeling, Paul A. Isihara et al., **Module 791**

This Module applies ordinary differential equations to both immunological and epidemiological aspects of HIV/AIDS modeling. For each aspect, we introduce a basic system that describes the growth of HIV/AIDS in the absence of countermeasures. We then explain how the basic model can be modified to predict the effectiveness of intervention programs to counter the spread of HIV/AIDS.

The Spread of Forest Fires, Emily E. Puckette, **Module 792**

We create a simple discrete probabilistic model for spread of a forest fire. We examine the conditions for which the fire will either die out or spread indefinitely, identifying and bounding a critical value for the probability of transmission of the fire to an immediately adjacent location.