

## Principles of Ecology BIOL412001

### Laboratory 7: Predator Functional Response Due Date: 1:00 PM April 5<sup>th</sup> (Tues) or April 7<sup>th</sup> (Thurs), 2005

THE REPORT FOR THIS LABORATORY CAN BE COMPLETED AS A GROUP EFFORT. YOU MAY COMPLETE THE ASSIGNMENT IN THE SAME GROUP THAT YOU COLLECTED THE DATA WITH, OR YOU MAY CHOOSE OTHER PEOPLE TO WORK WITH OR TO COMPLETE IT BY YOURSELF – THE CHOICE IS YOURS. HOWEVER, IF YOU SUBMIT IT AS A GROUP, PAY VERY CLOSE ATTENTION TO THE REQUIREMENTS FOR SUBMITTING GROUP ASSIGNMENTS OUTLINED AT THE END OF THIS DOCUMENT.

#### **Introduction**

In this lab, we are going to test an important assumption of the Lotka-Volterra predator-prey model. Recall from lecture that with this model, any external perturbation that shifts the predator or prey populations away from their joint equilibrium point creates a state known as a neutral equilibrium. This state is where both predator and prey populations continue to oscillate forever. Any further perturbation of the system will give these population oscillations a new amplitude and duration until some other outside influence acts upon them. This state is called a neutral equilibrium because no internal forces act to restore the population to the joint equilibrium. In other words, there are no density dependent factors in the model that act to dampen out the oscillations. Continued external perturbations will cause the oscillations to increase to the point where either the prey or the predator population will die out.

The reason the Lotka-Volterra model possesses a neutral equilibrium is because of a potentially unrealistic assumption concerning how the consumption of prey by an individual predator changes as the density of prey available to it increases. The model gives the rate of change of the prey population as

$$\frac{dR}{dt} = rR - cRP.$$

Where  $R$  is the number of prey,  $P$  is the number of predators,  $r$  is the exponential growth rate of the prey population, and  $c$  is a constant representing the "capture efficiency" of the predator (if  $c$  is small, then the predator is not very good at capturing the prey, and if it is large then the predator is very good at capturing the prey). The equation above states that the total rate of prey consumption is  $cRP$ . If we divide this term by the number of predators ( $P$ ) we get the rate of prey consumption **per individual predator**, which is simply  $cR$ . In other words, prey are consumed in direct proportion to their abundance or density at a rate equal to  $c$ . So, if the number of prey were increased by a factor of 10, then the number of prey consumed by an individual predator would also increase by a factor of 10. If prey increased by a factor of 100 or 1000, then so would the number of prey consumed by an individual predator. Clearly this is unrealistic for most types of predators. Some predators, such as filter feeders, may be able to increase their prey consumption like this up to a point, but most will reach a limit at which they become satiated and cannot consume any more prey even if the prey are abundant and easy to catch. Using this logic, it should be clear that the relationship between the number of prey consumed per predator and the density of prey in the real world is not a simple linear relationship like the one given in the Lotka-Volterra model.

The relationship between the number of prey consumed by an individual predator and the density of prey available to it is called the predator **functional response**, and was first defined by C.S. Holling in 1959. The specific relationship discussed above, where prey consumed per predator is a simple linear function

of prey density, is called a type I functional response. We have already discussed the fact that a type I functional response seems logically unrealistic for most predators and is responsible for the unrealistic neutral equilibrium found in the Lotka-Volterra model. However, it can also be thought of as a testable quantitative hypothesis of how prey consumption changes with prey availability. As you will be aware, in order to test any hypothesis, we need an alternative hypothesis for comparison. The aim of this laboratory exercise is to devise an alternative quantitative hypothesis to the type I functional response that encapsulates greater biological realism, and then to compare how well these two hypotheses fit data we will collect in a study of the frightfully ferocious, but rarely seen predator *Studentius rex*. We will use least squares to compare the two hypotheses. The hypothesis with the largest sum of squares will be rejected on the grounds that it does not provide a good description of our data. We will then accept the hypothesis with the smallest sum of squares as being the better of our two choices at describing the data. This process cannot **prove** that either hypothesis is the **true** explanation of our data; only that one hypothesis is a more plausible explanation than the other. You must always remember that because the scientific method is based on experimental tests of falsifiable hypotheses, it cannot prove anything. It can only eliminate alternative hypotheses, and in doing so, accrue evidence to support the hypothesis that is retained.

### Functional Responses and Alternative Hypotheses

The type I functional response can be represented by the following equation

$$N = cR,$$

where  $N$  is the number of prey consumed by an individual predator during a specific interval of time. This is simply the equation of a straight line with the intercept equal to zero. For a predator with a type I functional response, plotting  $N$  against prey density ( $R$ ) would give a straight line with slope  $c$  and an intercept of zero (see Figure 1 below). This equation **IS** an hypothesis. It states a quantifiable relationship between prey consumed and prey density that can be tested experimentally. We will call this hypothesis our null hypothesis. Often, the term "null hypothesis" is reserved for the condition where there are no relationships in the data, or no treatment effect. However, in our situation, the equation above represents the simplest explanation of the data we will collect, and for this reason we will refer to it as our null hypothesis.

The first step in developing our alternative hypothesis is to specifically state the question we want to answer:

What is the relationship between the number of prey eaten per predator and the density of prey?

Now that we know the question we want to answer, we can start defining our hypotheses. We have already done this for our null hypothesis, by virtue of the assumptions in the Lotka-Volterra model. But we don't have a model for our alternative hypothesis yet – we have to define one ourselves. Before trying to do this, it is best to start with a verbal formulation first.

Lets start by considering what a predator does in order to catch its prey and eat it. A predator must spend time searching for its prey, and then it must capture, kill, and eat its prey. The time spent killing, manipulating, and ultimately eating the prey is called the "handling time". One prey is usually eaten at a time, so the next prey eaten by this predator will require more search time and more handling time. Given these assumptions about the interaction between individual prey and individual predators, we must now extend this to cover the question of interest. How will the number of prey eaten change when prey density increases? The time the predator spends hunting is divided into two parts: search time and handling time. It is likely that the search time per prey depends on the prey density. If more prey are present, then the

time needed to find one should decrease. So, a predator can search out more prey in a given period of time and this should increase the number of prey discovered. However, the handling time per prey will not change because it is a one-on-one interaction and prey density won't affect it. More prey discovered will result in more time spent handling them. So, as the prey density increases, less and less time should be spent on searching and more and more time on handling the prey until, at high densities of prey, a predator will spend virtually no time searching for prey and all of its hunting time will be spent handling its prey. At this point, increasing prey density will not change the number of prey caught per predator, because the search time is already at its minimum and can't be cut any more. This is a verbal formulation of our hypothesis.

Now, let's develop a numerical formulation. Let  $N$  be the number of prey consumed by a predator during a hunting session. This will be a function of the number of prey ( $R$ ), the capture efficiency of the predator ( $c$ ) and the time spent searching by the predator ( $T_s$ ):

$$N = cT_s R .$$

However, the search time is only a portion of the total time. The search time is the total time ( $T$ ) minus the time spent handling individual prey ( $T_h$ ), multiplied by the number of prey handled ( $N$ ):

$$T_s = T - T_h N .$$

Thus, as the number of prey handled increases, less and less time is available for searching. Now, substitute for the search time in the original equation:

$$N = c(T - T_h N)R .$$

Expanding this to remove parentheses and then solving for  $N$  so as to remove  $N$  from the RHS of the equation while retaining  $N$  on the LHS gives:

$$N = \frac{cRT}{1 + cRT_h} .$$

The equation above gives an asymptotic curve similar to the one labeled "type II functional response" in Figure 1 below. This equation was also formulated by C. S. Holling in 1959 and is known as his "disk equation" because he first tested it by blindfolding people in his lab and having them "prey" on disks of sandpaper placed on a desktop. In any case, we now have an explicit alternative hypothesis that we can compare to the type I functional response using least squares.

This is not the only alternative hypothesis we could have generated. Holling also generated another potential prey response with its own equation. This was a sigmoidal increase similar to the type II response, but it assumed that predators made choices between different kinds of prey depending on how dense the different prey populations were. Holling called this a type III functional response.

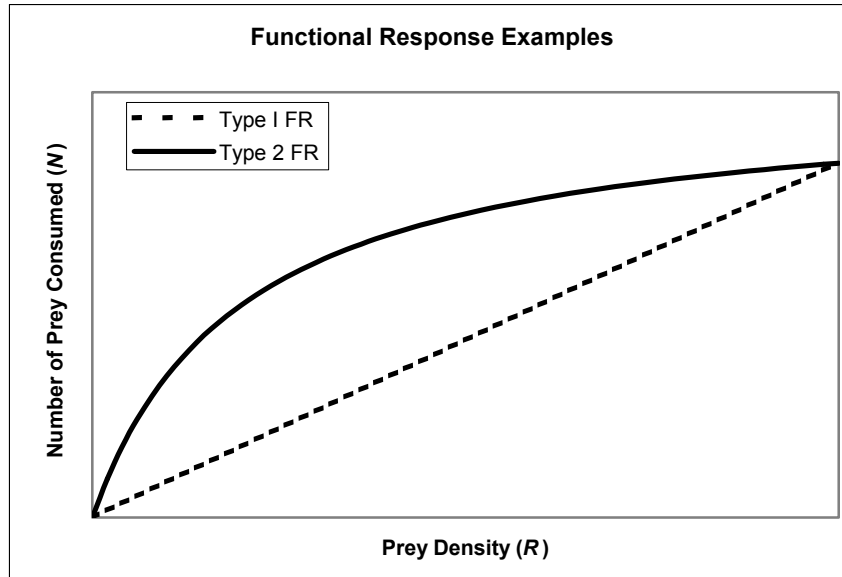


Figure 1. Example functional response curves.

### Experimental Design and Data Collection

It would be best to test our hypotheses with real predators in a field situation. Unfortunately we do not have the opportunity to do that, so we will have to use ourselves as the predators (*Studentia rex*) preying on innocent little bean seeds. We will design an experiment that conforms to the assumptions we made when we developed our hypotheses.

- 1) Get the densities of beans your group will use from your instructor.
- 2) Lay out a square 10 m on a side.
- 3) Have one person in your group disperse beans at **random** across the square. Don't hide the beans; simply let them fall on the grass as they may. Try to be as **random** as possible. There seems to be two kinds of people – regular dispersers and clumped dispersers. Very few people, if any, are random dispersers. Some people will spread the beans across the grid so that all areas get some beans. This is regular spacing, not random, and a smart predator will soon learn that the next bean is a regular distance from the last. The second type of person is characterized by the fact that they don't want to put much effort into the exercise and will simply dump beans in a couple of spots. This is a clumped or aggregated pattern, and a smart predator will soon learn that wherever one bean is found, there will be plenty of others nearby and that it should hunt-out any patch before moving to the next. Try your best to be the nonexistent random disperser by avoiding regularity or clumping.
- 4) Have someone else from your group be the predator by searching for (preying on) beans. To ensure that we conform to the model, we must have a handling time. This would normally involve the amount of time it takes to capture, kill, and consume the prey. Since we will only be capturing our prey (we won't try to kill or eat the beans), we will specify our own handling time as 5 seconds. In order for our data to be reliable, the predator will have to adhere to the following protocol: Whenever a bean is captured, the predator should stop moving and kneel or stand up (whatever is most convenient), close their eyes, and then count to five by saying to her/himself "one-one thousand, two-one thousand, three-one thousand, etc". You must close your eyes so that

you are not searching for other beans while "handling" the one you just caught. While counting, place the bean in the bag provided. This protocol is very important for the exercise, so don't cheat by using a shorter counting period or looking around for more beans while counting. You may use another member in the group to keep time for the predator. Remember, it's not a competition to see who can get the most beans. We will all be sharing the data so it's important for the entire class that this be done accurately. The predator will be allowed to hunt for 5 minutes, so someone else in the group must keep track of the total hunting time.

- 5) Record the number of beans the predator found.
- 6) All captured beans should be placed in a bag so they can be replaced in the square to restore the original density of beans in anticipation for the next predator.
- 7) Each group should repeat this procedure five times for each density of beans. Let everyone in the group be a predator at least once for each bean density. This means groups should not be greater than five.
- 8) Return to the lab and report you data for the number of beans caught by each predator for each of the initial densities of beans.

### Data Presentation and Analysis

Much of this exercise will be based on what you have already done for your analysis of the *Salvinia* experiment. You now have enough experience using XL to figure out how to conduct this analysis yourself, so I am only going to give you an outline of how to do it here. Let me know if you have any problems with it. While it may seem complicated, it really is straightforward. Give it your best shot before coming to me, but don't waste excessive time if you do run into problems.

Set your data out in an XL spreadsheet in the following way. The first column will contain values for the different densities of beans and should be labeled "*R*". The next five columns will contain the number of beans caught at each density. Remember there are five replicates for each density; hence there should be five columns of raw data for each density. Label each of these column *N*<sub>1</sub>, *N*<sub>2</sub>, *N*<sub>3</sub>, etc. In the next column, calculate the average number of beans caught for each of the different densities. Label this column "Avg. *N*" for the average number of beans caught.

We will be fitting the following two equations to our data using least squares:

$$N = cR \quad \text{Equation 1.}$$

$$N = \frac{(cRT)}{(1 + cRT_h)} \quad \text{Equation 2.}$$

Equation 1 is the equation for a type I functional response and is our null hypothesis. Equation 2 is the equation for a type II functional response and is our alternative hypothesis. In each of these equations, *N* is the average number of beans consumed at each density and corresponds to the numbers in the column labeled "Avg. *N*". *R* in the equations is simply the density of beans and corresponds to the data column labeled "*R*". In Equation 2, *T* is the total amount of time each predator was allowed to hunt for, which was 5 minutes, or 300 seconds (we have to use 300 seconds because our handling times were measured in seconds). Also in Equation 2, *T*<sub>h</sub> is the handling time, which equals 5 seconds. Looking at both equations we can now see that we have only one unknown parameter, which is *c*, the capture efficiency of the

predator. However, we do not know if  $c$  will be the same for both models. Because of this uncertainty, we need to estimate  $c$  separately for both models.

Remember from the *Salvinia* lab that we had cells to the right of our data in which we entered values for the different parameters in addition to a cell for the sum of squares. You need to create cells analogous to these for the current analysis. For each of the two models, you will need a cell for the parameter  $c$ , and a cell for the sum of squares. It doesn't matter where these cells are on your spreadsheet, but laying this spreadsheet out in a format similar to the *Salvinia* analysis will make things clear and logical. Enter an initial starting value for  $c$  for each model; the number 1 is a good starting point.

We will now enter the equations for the two hypotheses we want to compare in the two columns immediately to the right of "Avg.  $N$ ". Label these two columns "Type I FR" and "Type II FR". Look carefully at Equation 1 above to ensure that you enter it correctly into the first cell of the column labeled "Type I FR". You will have to use an absolute reference (dollar signs) for the reference to the cell containing the value of  $c$  for this equation. Once the equation is entered correctly into this cell, copy and paste it into the appropriate rows beneath it.

Equation 2 is a bit more complicated, but is nevertheless straightforward to enter into the first cell of the column labeled "Type II FR". Make sure you surround the terms in the numerator and the denominator with parentheses as indicated in Equation 2 above. You will have to use absolute references again for the cell reference pointing to the cell containing the value for  $c$  for this equation (be careful not to get confused about which cell for  $c$  you are referencing). Once entered correctly, simply copy and paste in the cells below it.

We now have to calculate the squared deviations between the actual data ( $N$ ) and the model predictions for both hypotheses (models). Remember that the squared deviations are calculated as

$$(\text{data} - \text{model prediction})^2$$

for each model separately, so you will have two columns of squared deviations – one column for the type I functional response and the other column for the type II functional response. Once you have this done, enter the summation function in the appropriate sum of squares cell to calculate the total sum of squares for each model.

Now, create a scatter plot with  $R$  (the density of beans) on the  $X$ -axis, and three data series: the average values of  $N$  (Avg.  $N$ ), and the predictions for each of the two functional response hypotheses. Make sure that the data points for  $N$  are **NOT** connected by any lines, and that the data points for each of the two hypotheses **ARE** connected by straight line segments (do not use the trend line function for these data points). This graph should look like the graph you used in the *Salvinia* analysis. Make sure you give the graph a title, label the axes and legend appropriately, etc.

You are now ready to start adjusting the values for  $c$  for both models to find the values that give you the smallest sum of squares for each model. It will be easier to do this one model at a time. Remember you can use the graph to help guide you in choosing the values for  $c$  that you will try, but you must rely on the sum of squares to tell you which values of  $c$  give you the best fit to the data. Also remember that we expect one of these models to have a smaller sum of squares than the other, we just don't know which model that will be yet.

## Exercises

Answer the following questions once you have fitted both models to the data and identified which model has the smallest sum of squares.

- 1) State the null hypothesis.
- 2) State the alternative hypothesis.
- 3) Which of these two hypotheses did you reject and why?
- 4) Does the hypothesis you retained provide a better biological explanation of the data than the hypothesis you rejected and why? If not, what might be some of the reasons for this disparity? Remember what the limitations of these hypotheses are (refer to the beginning of this handout and the text book). They provide two possible explanations of the data, but they both could be wrong.

## Before you submit your assignment, make sure you check the following items:

YOU MAY SUBMIT A GROUP ASSIGNMENT FOR THIS LAB. SEE THE DETAILS BELOW ON HOW TO DO THIS.

Make sure the layout of your spreadsheets is clear and logical, your graph showing the data and the two models is clear and labeled correctly, the answers to the exercises are in the correct order, the answers are clearly identified on the spreadsheet, and that you have used the appropriate number of decimal places in your answers (no more than 2 decimal places are required for this lab).

## GROUP ASSIGNMENTS

If you choose to work on this assignment in a group, you **MUST** follow these instructions for submitting the lab report. The completed report must be turned in **only once** by someone designated by the group.

The assignment must begin with a statement that it is a group effort with a list of everyone who contributed to it (this statement can appear on a separate worksheet at the beginning of the XL file). In addition, each of the contributors must send separate emails providing the following information:

- 1) A statement in the subject header concerning which lab assignment the email refers to.
- 2) A list of everyone who contributed to the lab assignment, including the email's author.
- 3) A statement that the author of the email contributed to the assignment, has checked the calculations for accuracy, and agrees with the conclusions reached.

No one in the group will receive any credit for the assignment unless all contributors send emails and all of the lists of contributors contain the same names. If another group or individual submits a lab that is substantially identical, then no one in either group will receive any credit for the lab. This mechanism is in place solely to prevent individuals from receiving credit for the effort of others (a word of warning – choose your lab partners wisely!). It is reasonable to expect that those who use the same data will have identical calculations (if done correctly). However, we can and do check tags in computer files that provide a complete dated history of who created and edited the file. **DO NOT SHARE YOUR FILES WITH PEOPLE OUTSIDE YOUR LAB GROUP, AND NEVER SHARE YOUR COMPUTER LOG-ON ACCOUNT WITH ANYONE ELSE. AT THE VERY LEAST, YOUR NAME WILL APPEAR IN THESE TAGS ON THEIR ASSIGNMENT, WHICH IS GROUNDS FOR BOTH INDIVIDUALS (OR GROUPS) FAILING THE ASSIGNMENT.** In addition, the spreadsheet's formatting, the wording of the conclusions, and (most significantly) the errors all act as fingerprints for the identification of a laboratory assignment. **Once again, labs that are substantially identical will not receive any credit at all.**

## **HOW TO SUBMIT YOUR ASSIGNMENT**

You will submit this assignment by emailing the XL file as an attachment to Saudat Adamson (our TA). Saudat's email address is:

sadamson@mytsu.tnstate.edu

YOU MUST USE YOUR MYTSU EMAIL ACCOUNT TO SEND THE FILE TO SAUDAT. THE REASONS FOR THIS ARE EXPLAINED IN THE COURSE SYLLABUS AND WILL NOT BE REPEATED HERE.

## **NAMING YOUR COMPUTER FILE**

To expedite the significant task of grading these assignments, we request that you adhere to the following convention when naming the computer files you send us:

Lab X YyyyZzzz.xls

Where X = the lab number, the "y's" are the first 4 letters of your last name, and the "z's" are the first 4 letters of your first name. **Please pay close attention to the spaces and the capitalization.** This may seem pedantic, but it really does help us enormously. Using this format, I would name my file for this particular lab as "Lab 7 PeteAndr.xls".

Written by Dr. P. Ganter and Dr. A. Peterson, TSU.