BIOLOGY 1240: BIOLOGY LABORATORY
SPRING SEMESTER — 2001

HOLLING DISC EQUATION
LAB INSTRUCTOR TEACHING GUIDE

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DISC EQUATION LAB:
INSTRUCTOR GUIDE

Introduction

This guide is intended to give help to biology lab instructors in the Holling Disc Equation lab exercises.

The philosophy of the labs is to use group learning and problem-based teaching techniques so that students discover simple mathematical models of predation. This is new to biological lab courses and no one knows how to do this best. We hypothesize that WWW-based activities in the lab in which students are prompted to complete a series of small problems interspersed with instructor guidance will be effective. Our goal is test this pedagogical hypothesis.

The basic organization of the labs will be: Instructor guided discussion; then lab bench group work; then instructor guided discussion; lab bench work; and so on. The instructor should actively circulate among the students during their activities to check on their progress.

Overall Objectives of the Disc Equation Lab

We want the students to learn (1) General: The relation of data curves and equations that describe them; (2) General: How to use equations and data to estimate biologically meaningful parameters; (3) Specific: the concepts of handling time and predation rates; (4) Specific: the relationship between the equation for the Type I foraging and Type II foraging.

Structure of These Notes

Each section is written to **follow** the lab activity. The notes include *Learning Objectives* and *Discussion Points*. Learning objectives are the concepts the students should have before moving to the next step. The Discussion points are suggestions on how to get the class to understand the learning objectives.

A Predator's Functional Response

Learning Objectives

The purpose of this section of the student hand-out is primarily to set the stage and provide all students with basic vocabulary and a picture of the relationship between prey density and predation rate.

Discussion Points

Biological Examples

Based on the introduction that the students were to have read, test their understanding by asking the following questions. The answers are possibilities, you probably will have better examples. Feel free to use your favorite organism, especially if it is an example of either Type I or III. Most animals are Type II.

What type of functional response would the following organisms have?

1. Barnacles filtering small particles from the water.
   Answer: Type I because they have a huge gut capacity compared to a single meal and have a very short handling time (a term the students haven't heard yet).
2. Small Zooplankton (e.g., Daphnia) filtering small particles from water.
   Answer: Type II because they have a small gut (gets filled up and the zooplankter can't consume more until some is digested) and they have a longer handling time.
3. Lions on wildebeest
   Answer: Type III (?) because wildebeest will not form large noticeable herds until they reach moderately high population levels. At every low population levels, lions can not find wildebeest, but herds are easy to spot.

Relation of Curves to Each Other

Ask the class: What is similar or dissimilar about the curves?

We're looking for the idea that Type I and Type II are similar because the slope of Type II looks to be constantly decreasing, while the slope of Type I is constant.

The relation of Type II and Type III is more subtle. The mathematical relationship will be noted below. At this point just mention that these two curves look similar at high prey density, but different at low prey density.

The Holling Disc Equation

Learning Objectives

1. General: the relation between the functonal response curve and the equation. This is important.
2. How the Type II equation is derived.
3. Some simple algebraic manipulations.

Discussion and Approaches

Equations for Type I

Notation for Type I:

$$
\begin{aligned}
N &= \text{density of prey}(units = \#)\\
a' &= \text{attack rate constant or searching efficiency}(units = 1/time)\\
T_{\text{tot}} &= \text{total time spent}(units = time)\\
P_e &= \text{number of prey eaten by a single predator during a period of time searching}(units = \#)
\end{aligned}
$$

There is some disagreement about terminology. The above statement of the Type I response states that the response is linear for all prey densities. With that definition, the equation for Type I is:

$$P_e = a'NT_{\text{tot}} \tag{1}$$

In words, this is: "The total number of prey eaten by a single predator in T_{tot} time units is the attack rate (probability of attacking a single prey) in a unit of time times the number of prey that can be attacked, times the number of time units."

You should not simply write this equation on the board. The students can supply if for you. Give them some hints: Scenario: Hamburges hidden in the room; if the probability of attacking a single hamburger in 1 hour is 0.1, how many hamburgers are attacked in 1 hour if there are 20 hamburgers hidden? How many if I search for 6 hours?

Equations for Type II

Notation for Type II:

$$
\begin{aligned}
N &= \text{density of prey}(units = \#)\\
a' &= \text{attack rate constant or searching efficiency}(units = 1/time)\\
T_{\text{tot}} &= \text{total time spent}(units = time)\\
T_s &= \text{total search time for all prey}(units = time)\\
T_h &= \text{handling time per prey item}(units = time/prey)\\
P_e &= \text{number of prey eaten by a single predator during a period of time searching}(units = \#)
\end{aligned}
$$

The units were not supplied to the students. Before going on, ask them to supply the units. At various points later, ask them to check the units (as indicated below).

P_e increases with the time available for searching (T_s), the prey density (N), and with the searching efficiency or attack rate of the predator (a').

$$P_e = a'T_sN \tag{2}$$

Question for Students: Are the units correct? Answer: Yes. left-hand-side = #, right-hand-side $= t^{-1} \cdot t \cdot \# = \#$

To achieve generality, we need to continue to reduce the predation process to more fundamental terms. We begin by removing the T_s term in the following way.

The time available for searching will be less than the total time, T_{tot}, because of time spent handling prey. Hence, if T_h is the handling time of each prey item, then the product $T_h P_e$ is the total time spent handling all prey consumed during the foraging bout:

$$T_s = T_{\text{tot}} - T_h P_e \tag{3}$$

Substituting this into equation 1 we have:

$$P_e = a'(T_{\text{tot}} - T_h P_e)N \tag{4}$$

Rearranging, the equation gives us the Holling Disc Equation itself:

$$P_e = a'NT_{\text{tot}} - a'T_h P_e N \tag{5}$$

$$P_e(1 + a'T_h N) = a'NT_{\text{tot}} \tag{6}$$

$$P_e = \frac{a'NT_{\text{tot}}}{1 + a'T_h N} \tag{7}$$

Are the units correct? Answer: Yes. Denominator is unitless, as is $a'T_{\text{tot}}$. This leaves N with units of # in numerator.

The Relation between the curve and the equation

The problem you should discuss with the students is: Does the equation have the shape of the Type II curve?

Some minimal criteria:

1. The curve intersects the origin: Is the equation 0 when $N = 0$?
   Answer: Yes, just substitute $N = 0$ in to the equation.
2. The slope of the Type II curve near $N = 0$ is very close to the slope of the Type I curve: Is the equation slope like that of the Type I equation?
   Answer: Simplify the Type II equation to:

   $$y = \frac{Ax}{1 + Bx} = A\frac{x}{1 + Bx} \tag{8}$$

   where $A = a'T_{\text{tot}}$ and $B = a'T_h$ from the Type II curve.
   Give a numerical example for $x \approx 0.0$, say $x = 0.001$.
   Ask the class: What is the value of

   $$\frac{0.001}{1 + B(0.001)}? \tag{9}$$

   The answer is: if B is small, then the fraction will be about $0.001/1.0 = 0.001$.
   So

   $$y \approx A(0.001) \tag{10}$$

   or what we would get from the Type I straight line.
   You can repeat this argument for any value of B. If B is large, then we just have make our x smaller, say $x = 0.000001$. In other words, when B is large, the Type II equation departs from the Type I equation at smaller x, compared to when B is small.

3. The graph of Type II indicates that its value is constant when the prey density is very, very large: Is the value of the equation constant as $N \to \infty$?
Answer: Again focus on

$$y = \frac{Ax}{1+Bx} = A\frac{x}{1+Bx} \tag{11}$$

We ask: how does

$$\frac{x}{1+Bx} \tag{12}$$

behave as $x \to \infty$?
Just looking at it is hard to tell. The argument is easier if we remove the B from in front of x: Divide the top and bottom by B:

$$\frac{x}{1+Bx} = \frac{\frac{1}{B}x}{\frac{1}{B}+x} = \frac{1}{B}\left(\frac{1}{\frac{1}{B}+x}\right) \tag{13}$$

Now ask the question: What happens to

$$\frac{x}{\frac{1}{B}+x} \tag{14}$$

as $x \to \infty$?
Answer: It goes to 1.0 when $x \gg 1/B$.
Even if $1/B$ is large, we can make x even larger (approaching infinity) and so in the limit the denominator will approach the numerator and the ratio will approach 1.0.
So, finally does the equation approach a constant at high prey density as our curve requires?
Answer: We have

$$y = A\frac{x}{1+Bx} \tag{15}$$

$$= A\frac{1}{B}\left[\frac{x}{\frac{1}{B}+x}\right] \tag{16}$$

The last term on the right in brackets as we just showed goes to 1.0 as x increases, so

$$y \to \frac{A}{B} \qquad \text{as } x \to \infty. \tag{17}$$

Optional or Left as Exercise

If we write our Type II equation as:

$$\frac{P_e}{T_{\text{tot}}} = \frac{a'N}{1+a'T_hN} \tag{18}$$

to what value does P_e/T_{tot} go as $N \to \infty$?
Answer:
Divide the top and bottom of the right-hand-side by $a'T_h$ and use the above logic to let $N \to \infty$:

$$\frac{P_e}{T_{\text{tot}}} = \frac{(a'N)/(a'T_h)}{\frac{1}{a'T_h}+N} = \frac{1}{T_h}\left[\frac{N}{\frac{1}{a'T_h}+N}\right] \tag{19}$$

or

$$\frac{P_e}{T_{\text{tot}}} = \frac{1}{T_h} \qquad \text{as } N \to \infty \tag{20}$$

In other words, the maximum predation rate ($P_{e,\max}/T_{\text{tot}}$) is equal to one over the handling time.

Experiments for Type II, I, and III Foragers

These pages and activities are self-explanatory and do not involve detailed discussion from the instructor, other than explaining how to do the experiments.

Learning Objectives

The general objectives are to collect quantitative data that can be used in conjunction with an equation. Specifically, we want the students to learn how predators relate to the density of their prey. In future weeks, they will be using real predators and prey. [**Not in 1240 Spring 2001**]

Cautions for the Experiments

1. In the non-patchy experiments, it is important that the discs be randomly distributed over the board.
2. Discs should not be replaced in the same general area from which they were removed.
3. The predator is really hungry, so the student foragers should hunt as rapidly as possible.
4. The groups should force the predator to deposit the prey in the containers so that handling time is incorporated.

Discussion

After the students have performed the experiments and before you help them analyze their data, it is useful to make them think a little about the equations.

How does the Type I equation relate to the Type II equation?

Answer: Let T_h in Type II go to 0 and it reduces to the Type I.

How does the Type III equation relate to the Type II equation?

Answer: In Type III, the attack rate is a function of N, instead of being constant in Type II. The simplest function is straight line:

$$a' = b'N \tag{21}$$

so

$$P_e = \frac{b'T_{\text{tot}}N^2}{1 + b'T_hN^2} \tag{22}$$

This curve has a sigmoid shape as we drew earlier. Other authors use slightly different equations.

Estimating a'

Learning Objectives

This is the second major learning objective that we want the students to experience. We want to re-inforce in the students how to use data to estimate parameters in an equation.

Discussion Points

To motivate this material, say something like this to the class: "We now want to see how accurately our equation (or model) fits our experimental data. In order to do this, we must have values for all the constants (or parameters) in the equation. We've already measured T_h directly with the stop watches, but we do not know a'."

Write the Type II equation on the board and ask the question: How can we estimate a'?

The following is obsolete since the students have seen the derivation both in the lab recitation and in the hand-out.

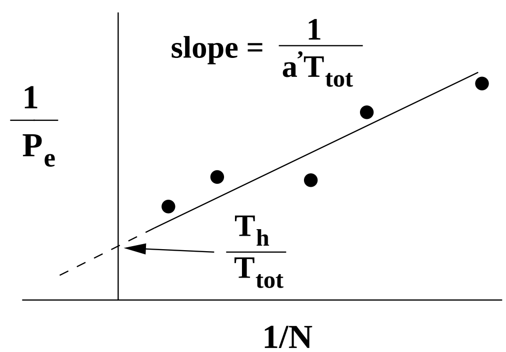
The students may suggest that we somehow solve for a'. This is a reasonable idea, and one that you should discuss. Here are two related responses:

"Okay, that might work. Let's assume we could re-arrange the Type II equation and isolate a' on one side of the equal sign. This new equation would contain on the other side of the equal sign the variables and constants N, P_e, T_h, and T_{tot}. The last two are constants that we know. But what value of N and P_e should we use? We have several. Will we get different values of a'? (Yes). Which one is correct? This is a problem and we'd like to use all the data to get one value."

A second related problem is the fact that we did replicates. This means we have different P_e for the same N which means we would again get different a' values, even for the same N. This is an even bigger problem.

We need another approach. The algebra is relatively straightforward, but the students will need to be led through it. Walk them through the algebra as presented in their handout.

After everyone understands the algebra, get the class to volunteer the graph of the curve:



1. Show them how it works for their data. Point out that this approach solves the problems with the other approaches mentioned above.
2. Mention to them that the intercept contains T_h and so we can check our stop watch estimates by using the intercept to get T_h.
3. Mention that this manipulation is a particular case of data transformation, which is used in many examples of quantitative biology. Other examples that they have seen are: (a) subtracting a constant (osmosis lab and photosynthesis lab) and (b) logarithms (Beer's Law and photosynthesis).
4. Using the computers, each student should be able to do the following:

(a) Create a spreadsheet and enter the class data

(b) Graph the class data, make a graph title, and put labels on the axes

(c) Make columns of the inverse transformations

(d) Graph the transformed data with a trendline (linear regression)

(e) Compare the original data with the results of the regression. This involves:

   i. Create a column of N values that range from 0 to 260 in units of 10 (these are the x axis values).

   ii. Create a second column that is the y axis obtained by evaluating the Type II equation using the parameters (a' and T_h) estimated from the linear regression.
   This is done with an Excel equation that looks like:
   `=(0.099*B4)/(1+(0.099)*(4.3)*B4`
   where `B4` is the cell of the first N value made in Step 4(e)i above, 0.099 is students' value for a' and 4.3 is the students' value for T_h.

   iii. Make a graph of the two columns just generated

   iv. Add the original data to the graph. This is done by adding a second data series that is the original data.

Holling Disc Equation: Solved Problems

1. Estimate the Type II Holling Disc Equation parameters (constants) for the following data. Assume that $T_{\text{tot}} = 1 day$. Include the units on your estimates.

N	10	25	50	100	180	200
P_e	0.6	1.5	2.3	3.5	3.8	3.95

Answer: Transform the data to inverses:

$1/N$	0.10	0.04	0.02	0.01	0.0056	0.005
$1/P_e$	1.67	0.667	0.435	0.286	0.263	0.253

Either by hand or using a spreadsheet, graph these points with the x axis as $1/N$ and the y axis as $1/P_e$. Estimate the slope and intercept either by eye or using a spreadsheet. For these data you should get: Slope = 14.902, Intercept = 0.1466.

The intercept is T_h/T_{tot} so $T_h = \text{Intercept} \cdot (1 \text{ day}) = \boxed{0.1466 \text{ day}}$. Note the units.

The slope is $1/((a')(T_{\text{tot}}))$ so $a' = (1/((14.902)(1)) = \boxed{0.067/\text{day}}$.

2. Using the above coefficients, what is the maximum capture rate (when prey are extremely common, dense)?

Answer: Maximum $= \boxed{1/T_h = 6.82}$. Does this make sense given the original data? Check that it does.

3. If $a' = 0.01$, $T_h = 0.5$ and $T_{\text{tot}} = 1.0$ at what density of prey will the predation rate be 1/2 of the maximum predation rate?

Answer:

$$\frac{P_e}{T_{\text{tot}}} = \frac{a'N}{1 + a'T_hN} = \frac{1}{2T_h}$$

because $1/T_h$ is the maximum rate. So, solving for N from the last equality:

$$\begin{aligned} a'N &= \frac{1}{2T_h}(1 + a'T_hN)) = \frac{1}{2T_h} + \frac{a'N}{2} \\ a'N - \frac{a'N}{2} &= \frac{a'N}{2} = \frac{1}{2T_h} \\ N &= \frac{1}{a'T_h} \end{aligned}$$

Substituting the given values: $\boxed{N = 1/(0.01 \cdot 0.5) = 200}$.