

The Holling Disc Equation

Introduction

There are many examples in nature which demonstrate that predators can control the numbers of their prey. For example, predatory lampreys almost eliminated the lake trout in the Great Lakes between 1950 and 1960. Wolves kept the elk numbers in check in the Yellowstone area before humans eliminated the predator. The goal of this lab is to take a closer look at the nature of predator/prey interactions. When predators are faced with increasing local density of their prey, they often respond by changing their consumption rate. This relationship of an individual predators' rate of food consumption to prey density was termed the **functional response** by C.S. Holling in 1959. In this lab, we will repeat the method Holling used to establish the basis for the analysis of the functional response. He developed the conceptual model using blindfolded human subjects (the "predator") and 4-cm sandpaper discs (the "prey").

The Three Types of Functional Responses

Figure 1 illustrates the three general types of curves expected in various predator-prey situations.

Type I is a linear relationship, where the predator is able to keep up with increasing density of prey by eating them in direct proportion to their abundance in the environment. If they eat 10% of the prey at low density, they continue to eat 10% of them at high densities. The dotted line indicates a maximum consumption rate that some authors attach to Type I foraging.

Type II describes a situation in which the number of prey consumed per predator initially rises quickly as the density of prey increases but then levels off with further increase in prey density.

Type III resembles Type II in having an upper limit to prey consumption, but differs in that the response of predators to prey is depressed at low prey density.

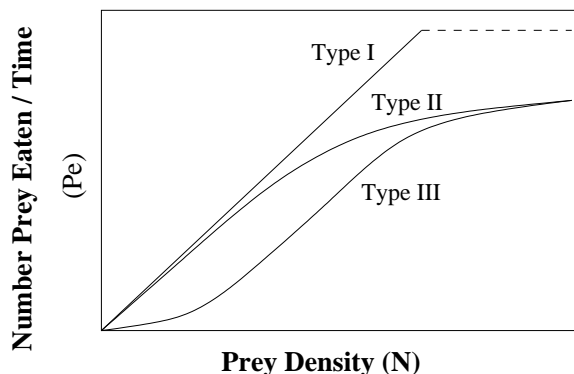


FIGURE 1: Three types of functional response relating prey density (N) and the number of prey eaten by one predator (P_e).

The Holling Disc Equation

Two factors dictate that the functional response should reach a plateau. First, the predators may become satiated (i.e., their stomach completely filled), at which point their rate of feeding is limited by the rate at which they can digest and assimilate food. Second, as the predator captures more prey, the time spent handling and eating the prey lowers the searching time. Eventually, the predator reaches the minimum time it takes to search, capture and consume. The predator cannot find prey and eat it any faster. The consumption rate cannot increase when the ability of the predator to catch and eat is at a maximum.

C.S. Holling described this relationship between search time, handling time, and consumption rate by a simple expression known as the “disc equation.” The equation was developed using blindfolded human subjects trying to find and pickup small discs of sandpaper on a flat surface. Any such task, including subduing and eating a prey item (whether a model of sandpaper disc “prey” or a real prey) requires the following measurable elements that we will incorporate into a mathematical equation following the logic of Holling:

N	=	density of prey
a'	=	attack rate or searching efficiency
T_{tot}	=	total time spent
T_s	=	total search time for all prey
T_h	=	handling time per prey item
P_e	=	number of prey eaten during a period of time searching

We make the following assumptions. 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'). This is summarized as:

$$P_e = a'T_s N \quad (1)$$

As you will see when you take the Holling Disc data for yourself, search time (T_s) decreases as prey numbers (N) increase. As a result, T_s is not a constant. Thus, this equation as written will change for each different circumstance which a predator experiences. This variability will very likely obscure the general principles of predation. 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:

$$T_s = T_{\text{tot}} - T_h P_e \quad (2)$$

Substituting this into equation 1 we have:

$$P_e = a'(T_{\text{tot}} - T_h P_e)N \quad (3)$$

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

$$P_e = \frac{a'NT_{\text{tot}}}{1 + a'T_hN} \quad (4)$$

Mini-quiz: Test your algebra skills and show how to get from equation 3 to 4. It will take three steps.

Equation 4 describes a Type II functional response, and is known as the Holling “disc equation.” It was given this moniker because Holling generated it by having a blindfolded assistant pick up (“prey upon”) small sandpaper discs placed on a table. Note that the equation describes the amount eaten during a specified period of time: T_{tot} . The density of the prey is assumed to remain constant throughout that period. In experiments, this can be guaranteed by replacing any prey that are eaten.

Holling was not content to merely show that this was a basic relation for a blind human searching for sandpaper discs. He also demonstrated that Type II curves were generated when three species of small mammals preyed upon cocoons of the sawfly in a controlled laboratory setting.

Questions

1. Equation 4 describes the curves in Figure 1a (II). Look at equation 4 above and describe what would happen to the shape of the graph T_h , got smaller and smaller and approached zero.
 2. Using simple algebraic manipulation, derive equation 4 from equation 3
 3. How would you estimate a' , the attack rate or searching efficiency?
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Today's Lab

You will now simulate several bouts of predation using one of your group as a predator and the others to keep track of handling time, total elapse time, and number of prey “consumed.” We have set up the details exactly as Holling did in his 1959 study. Work in groups of 4 or 5. At each lab bench there is a predation arena with a different density:

Bench	No. of prey discs per 9 square feet
1	256
2	173
3	90
4	30
5	10
6	4

Equipment for Each Lab Bench

- 1 predation board with sandpaper discs
- 1 count up/down timer
- 1 small plastic tub to put eaten prey into
- 1 small plastic tub with new replacement prey
- 1 blindfold

Assign members of your team to the following chores:

- 1 predator (to be blindfolded) [person a]
- 1 person to measure handling time on a stopwatch [person b]
- 1 person to monitor the 1 minute predation bout duration with a timer [person c]
- 1 person to replace “eaten” prey with a new sandpaper disc [person d]

Note: The last two assignments can be a single person.

Once you have organized yourselves with the above materials and assignments, follow the instructions on the next several pages to explore the effects of alternative predator behavior.

Type II Response

You are now ready to investigate the predation rates of a Type II forager.

Blindfold the predator and instruct him/her to search for prey by tapping a finger tip randomly around on the board. No sliding allowed, only tapping. The predator must be hungry and in a hurry. No leisurely tapping allowed. When the predator detects a piece of sandpaper, he picks it up with the thumb tack and locates the prey tub (stomach). When the predation technique has been approved by the whole group, you are ready to begin.

Here is what should happen in your group:

1. Person c [total time] start your stopwatch while shouting “go”.
2. When the predator encounters a disc, the handling time person [b] starts his or her watch.

3. The predator removes the disc and places it in a tub to the side. As soon as the predator's finger is back tapping on the board, the handling time person [b] stops the handling time stopwatch.

For handling time, you are recording the accumulated or total time spent in each activity. You do not have time to write down how much time each handling event takes. The value you record will be total handling time ($\sum T_h$, "sum of all T_h ").

4. The prey replacement person [d] puts a new disc out and tacks it securely to the board. It must be placed in a different place than the location of the preyed upon item. (or the predator will know to go right back to that spot for another snack)
5. Continue with this procedure until 60 seconds have elapsed and the time minder [person c] yells, "stop."
6. Repeat these 60-second predation bouts two more times and record the results on the supplied charts.

First record what the predation density is at your lab bench: per 9 square feet.

7. Calculate the mean of all your trials and use these numbers for the class report.

Your Group Data Type II

Trial	Prey Eaten (P_e)	Total Handling Time ($\sum T_h$)	Handling Time/Prey ($T_h = (\sum T_h)/P_e$)
1			
2			
3			
Mean			

(**Note:** *Total Handling Time* ($\sum T_h$) is the cumulative time recorded by person b.)

8. Place your mean values in the chart on the front board or overhead and then copy other student values to fill in your own chart of the complete Type II response:

CLASS DATA TYPE II

Prey Density (N)	Total Prey Consumed (P_e)	Total Handling Time ($\sum T_h$)	Handling Time/Prey ($T_h = (\sum T_h)/P_e$)
4			
10			
30			
90			
173			
256			

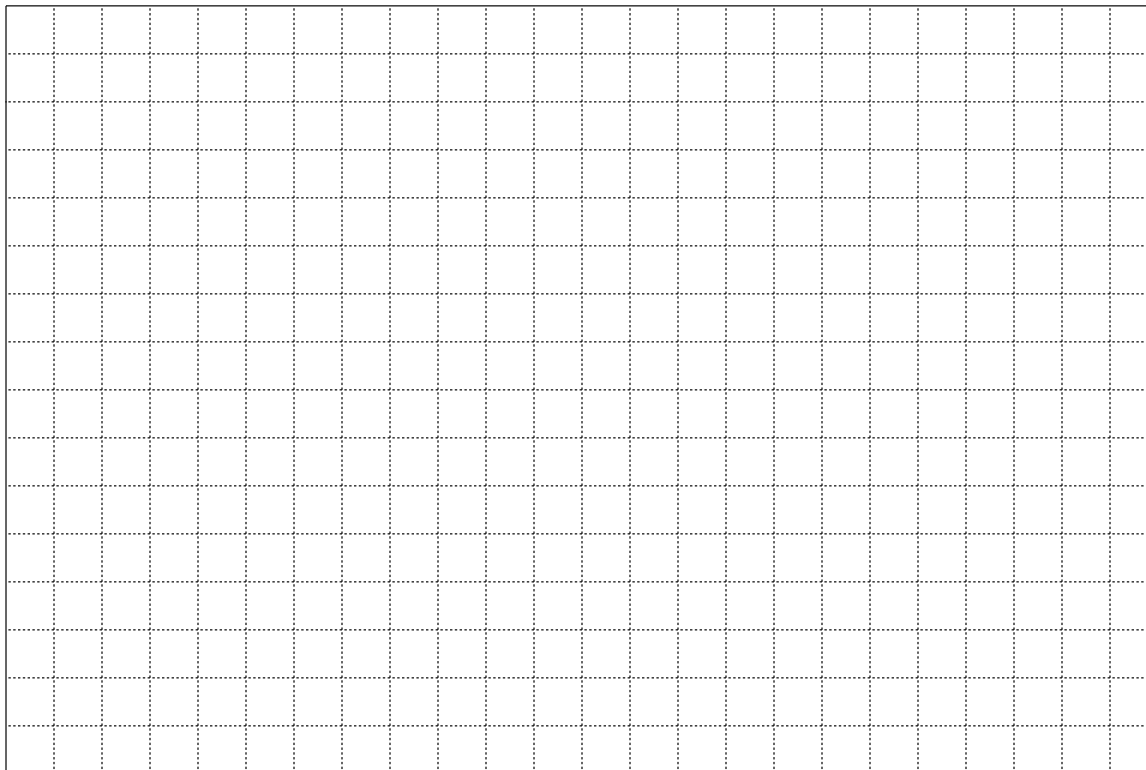


FIGURE 2: Class data for functional type II.

(**Note:** *Total Handling Time* is the cumulative time recorded by person b.)

9. Next, in Fig. 2 plot this curve: Prey eaten as a function of prey density.

When all the groups are ready, proceed to the next experiment.

Type I Response

Next, we consider a predator whose handling time is extremely short.

Recall our basic disc equation:

$$P_e = \frac{a'NT_{\text{tot}}}{1 + a'T_hN}$$

As handling time gets shorter and shorter ($T_h \rightarrow 0$), the denominator in the above equation approaches 1.0. The graph of this function (prey eaten (y axis) vs prey density (N)) becomes more like a straight line with slope a' . This is the Type I response described in Fig. 1 on an earlier page.

To simulate this predator/prey situation we try to shorten T_h as much as possible. This time, run three bouts of predation lasting one minute (as before) with the following difference in step 4.

4. As soon as the predator locates a sandpaper disc prey, the predator indicates it by stopping the tapping. At this point, the prey replacement person whisks the prey away from the spot for the predator and places it in the tub to the side. The predator continues to forage without interruption. The prey replacement person then takes a prey item from the side tub of extras and places it in a new location as before. The density of prey stays the same, as before.

NOTE: *The handling time person still times the short time between location of the disc and the time the predator starts tapping again. T_h should be shorter, but not zero, compared to the previous Type II series.*

Complete the following table.

Your Group Data Type I

Trial	Prey Eaten (P_e)	Total Handling Time ($\sum T_h$)	Handling Time/Prey ($T_h = \sum T_h/P_e$)
1			
2			
3			
Mean			

(**Note:** *Total Handling Time ($\sum T_h$) is the cumulative time recorded by person b.)*

Place your mean values in the chart on the front board or overhead and then copy other student values to fill in your own chart of the complete Type I response:

CLASS DATA TYPE I

Prey Density (N)	Total Prey Consumed (P_e)	Handling Time/Prey ($T_h = \sum T_h/P_e$)
4		
10		
30		
90		
173		
256		

When all of the data has been reported, graph the class data in Fig. 3.

Question: Can you think of a predator/prey situation in which a Type I type of functional response would be expected?

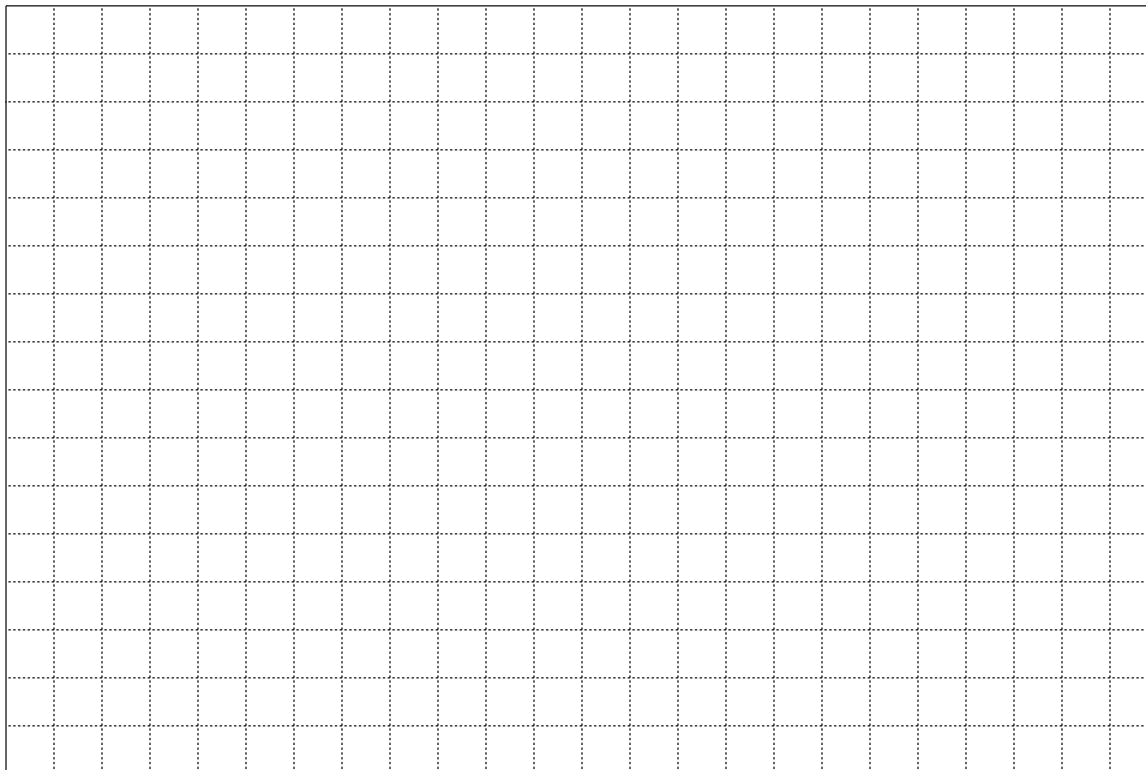


FIGURE 3: Class data for Type I functional response.

When the entire class is ready and the instructor instructs you, go on to the next experiment.

Type III Response

If the prey has a refuge in the predation arena, or the predator learns while foraging (thus, making him/her a better forager with time), the Type III curve would be expected (see Fig. 1). In this functional response, the predator does less well at low densities, but increases its foraging rate at intermediate densities. At high prey density, the predator's handling time limits its predation rate. This process results in the "S-shaped" curve in Fig. 1 above.

To simulate this, we will clump the prey. When the predator encounters a disc in a clump, he or she knows to go back to the clump. Before starting this bout, all members of the team should clump the sandpaper discs into groups. The bigger the total number of discs, the bigger each clump should be.

Use the experimental protocol for Type II foraging and complete the following table.

Your Group Data Type III

Trial	Prey Eaten (P_e)	Total Handling Time ($\sum T_h$)	Handling Time/Prey ($T_h = \sum T_h/P_e$)
1			
2			
3			
Mean			

(**Note:** *Total Handling Time* ($\sum T_h$) is the cumulative time recorded by person b.)

Place your mean values in the chart on the front board or overhead and then copy other student values to fill in your own chart of the complete Type I response:

CLASS DATA TYPE III

Prey Density (N)	Total Prey Consumed (P_e)	Handling Time/Prey (T_h/P_e)
4		
10		
30		
90		
173		
256		

When all of the data have been reported, graph the functional response in Fig. 4.

Wait for the everyone to complete the graphing at which time the instructor will help you with the next problem: *What is the attack rate for the disc eaters?*

Estimating a'

Our problem is that we want to estimate the value of a' for the Type II functional response. The equation is:

$$P_e = \frac{a'NT_{\text{tot}}}{1 + a'T_hN}$$

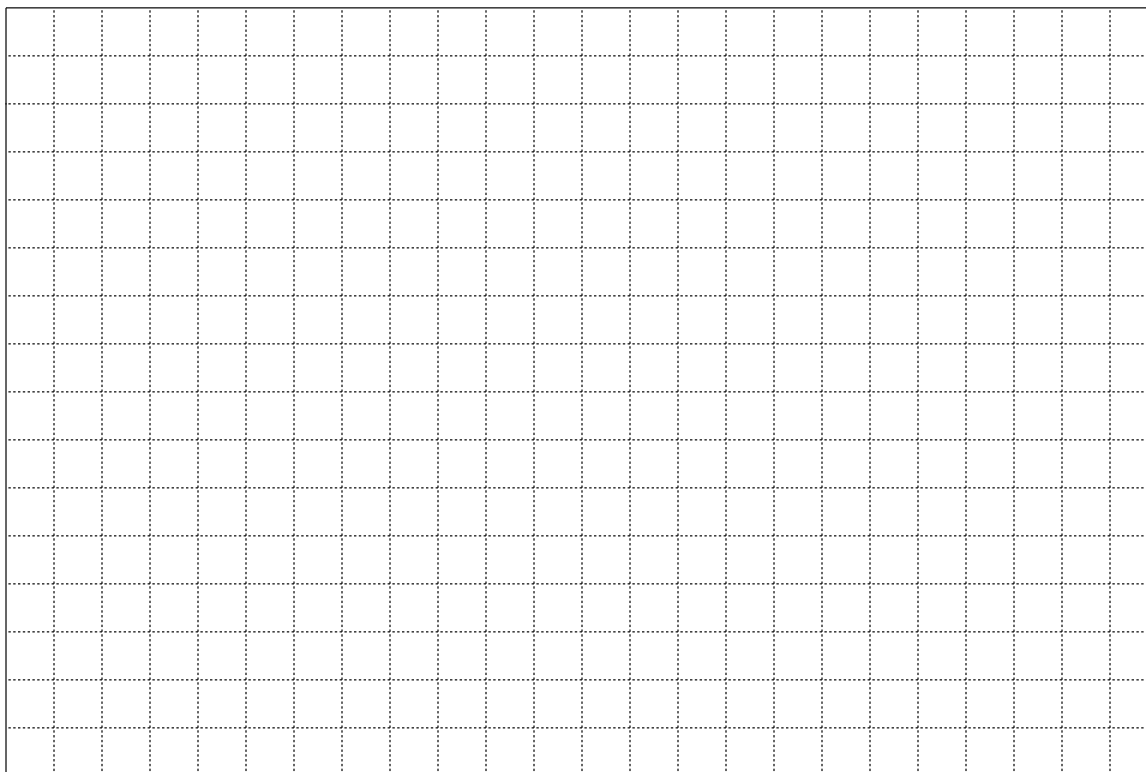


FIGURE 4: Class data for Type III functional response.

We know that this equation is not a straight line, because the equation is not in the form of a straight line:

$$y = mx + b$$

The maximum predation rate is $1/T_h$ and is the maximum value that P_e can have. Attack rate, a' in the Type II equation, determines how steeply the curve rises with increasing prey density (N).

Our experiments have given us a set of values for P_e for each value of N , but not a' . We want to estimate a' taking into account the fact that it depends on all of the prey densities we experimented with and the fact that there is statistical variation in our estimates at each particular prey density. This is why we asked you to repeat the disc experiment three times.

The General Idea

One possible idea to solve this problem is to try and convert the curvilinear Type II equation as written above into a straight line equation. Then, we might hope, we could graph our data, draw a straight line through the data points (pretty easy for humans with good eyes). Once we have a straight line, we will have estimates for the slope and the intercept. Maybe (we hope), one of these two quantities will tell us what a' is.

How do we know a scheme like this might work? Well, you might not know it, but this idea has worked in the past for quantitative biologists on different problems (e.g., Beer-Lambert Law, Newton's Cooling Law, photosynthesis equation). So, it might work again. This is how science often happens: get some experience, then apply what worked before to the new problem. If it works, great; if not, well ... it's back to the drawing board and take another approach.

But the main point is: Have courage! Try it and see if it works!

The Messy Details

We want to re-arrange the Type II equation to be a straight line. We notice that the numerator looks kind of like mx , where $x = N$ and $(a'T_{\text{tot}} = m$. But the denominator causes problems with that. So, let's simplify the denominator by taking the inverse of both sides.

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

This last equation has a lot of terms in it, but it has the form

$$y = \frac{A + B}{C} = \frac{A}{C} + \frac{B}{C}$$

So,

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

Let's now re-write this one more time to see if we have a straight line:

$$\frac{1}{P_e} = \frac{1}{a'T_{\text{tot}}} \frac{1}{N} + \frac{T_h}{T_{\text{tot}}} \tag{5}$$

Compare this with a straight line:

$$y = mx + b$$

We have a straight line when we let

$$x = \frac{1}{N}$$

$$m = \frac{1}{a'T_{\text{tot}}}$$

and

$$b = \frac{T_h}{T_{\text{tot}}}$$

So, if we plot the class data as $1/P_e$ on the y-axis against $1/N$ on the x-axis, we should have data points that appear to fall along a straight line.

In the following table, calculate the inverses required.

Prey Density	Type II		Type I		Type III	
	$1/P_e$	$1/N$	$1/P_e$	$1/N$	$1/P_e$	$1/N$
4						
10						
30						
90						
173						
256						

In the space provided in Fig. 5, graph the class data. Then draw a single, “best-fit” straight line through the data points. From the line, estimate a' and T_h .

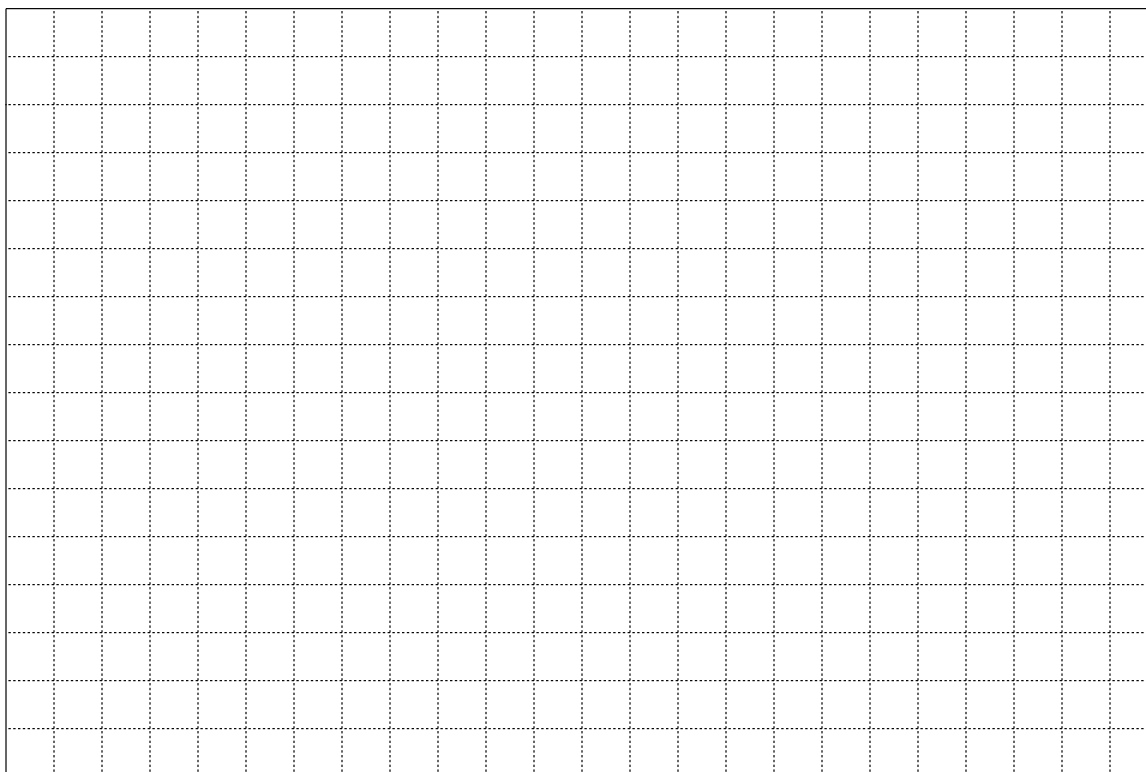


FIGURE 5: Graph and best-fit of transformed class data.

Holling Disc Equation: Solved Problems

1. Estimate the Type II Holling Disc Equation parameters (constants) for the following data. Assume that $T_{\text{tot}} = 1\text{day}$. 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: $N = 1/(0.01 \cdot 0.5) = \boxed{200}$.

Holling Disc Equation Problems

Do the following. For full credit, show all of your intermediate steps and algebra, where required.

DUE: Your lab instructor will inform you when this is due.

- Using the data below, estimate a' and T_h by transforming the data and plotting. From this plot, use your best guess to estimate the two constants.

N	2	4	8	16	32
Pe	2	3.5	7	7.5	8

- Transform the following equation into a straight line. Show your algebra steps and identify the slope and the intercept. x is the independent variable and y is the dependent variable, q and r are constants.

$$y = \frac{qx}{3q + rx}$$

- You perform a foraging experiment like the Holling disc equation in class on an organism you've never studied before. You present the predator with prey densities that increase by units of 5 (i.e., 5, 10, 15, 20, etc.) At each experiment, you observe that the predator eats exactly half of the prey available.
 - What is the equation for the functional response for this organism? [Hint: it is not Type II.]
 - What is the attack rate?
- You are the head manager of the Wasatch National Park where cougar prey on deer. Your job is to manage the deer herd so that the cougars will maintain constant numbers. Suppose that for the cougar population to stay constant, each cougar must eat on average 3.75 deer per month. Using the values below, how many deer are needed in the Park? Units are based on one month.

$$a' = 0.005 \quad T_h = 0.067 \quad (\text{about 2 days})$$

A calculator answer is not sufficient. Use the equations developed in class and use algebra to solve for the answer. Show all your algebraic steps. [The solved problems distributed by the instructor will be helpful.]