5-2020

The Marshmallow Lab: A Project-Based Approach to Understanding Functional Responses

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THE MARSHMALLOW LAB: A PROJECT-BASED APPROACH TO UNDERSTANDING FUNCTIONAL RESPONSES

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Mathematics

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Logan, Utah

2020

ABSTRACT

The Marshmallow Lab: A project-based approach to understanding functional responses

by

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In this paper, a short sequence of lessons aiming to improve students' understanding of Holling's type II functional response equation is proposed. The lessons incorporate experience with an artificial predator-prey system, first employed by C.S. Holling in his classic "disc experiment", which is also reproduced via individual-based computer simulations. This experience gives students the opportunity to gather different sets of data to model and interpret. The independent components in the lesson plan (mathematical, experimental, and computational) engage students in various modeling activities to meet multiple learning objectives. Our classroom trials indicate that the proposed instructional activities are effective for increasing students' awareness of the mechanisms inducing the emergence of nonlinear effects in predator-prey scenarios.

(45 pages)

PUBLIC ABSTRACT

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This paper presents a three-part lesson plan to improve student's understanding of Holling's type II functional reponse model. This model describes the interaction between a predator and how much it is able to consume given a constant number of prey. According to the model, while increased avaliability of prey allows predators to consume portionately more prey for low values, after some number of prey, predators will only be able to capture a limited number of prey even as the prey continues to increase. This phenomenon is known as saturation. Holling first develop this important ecological theory through his "disc experiment" which used an artifical predator-prey system. As students progress through this lesson they will attend a lecture based on the mathematical theory underlying the model, participate in a hands-on replication of Holling's disc experiment using marshmallows, and then reiterate the experiment using a computer program that simulates the functional response phenomena. Throughout this lesson, students will gain important experiences in mathematical modeling and a deeper understanding of saturation.

ACKNOWLEDGMENTS

Thank you to Dr. Luis Gordillo and Dr. Brynja Kohler for their kind and encouraging mentorship throughout this project from celebrations in success to a global pandemic. I am also grateful to Leoncio Rodriguez-Quinones for his listening ear in troubleshooting my model program and in navigating graduate school.

I would also like to thank Matt Lewis for running additional lab trials to give more breadth to our collected data.

Melissa Pulley

CONTENTS

LIST OF TABLES

Table Page

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

1.1 Mathematical modeling in applied mathematics education

Mathematical modeling is used to solve countless problems in the real world [1, 5, 6]. Employing a simple model, users can study a complex, authentic scenario to explore possibilities and solutions, develop conceptual framework, make predictions, and generate explanations [14]. Modeling allows students to strengthen connections between pure and applied math, giving meaning to mathematical theory by creating connections to the real world [6].

In learning, particularly in mathematics, there are many levels at which learning can or should be achieved, dependent on the goals of a course, unit, or lesson [3]. Some objectives simply require a transfer of knowledge (i.e. simple knowledge tasks such as memorizing a formula or definition), while others may benefit from a construction (i.e. learning a proof, or building a model) [15]. In recent applied mathematics education, there are many calls for project-based learning opportunities. Project-based learning is grounded in constructivist learning theory, where participants investigate authentic problems and construct knowledge through a process or project as opposed to traditional learning via only classroom lecture [7]. This learning model allows students to move from teacher-centered to student centered learning as they engage in "minds-on" and "hands-on" activities [14].

Mathematical modeling lends itself well to a project-based learning approach as students engage in the nonlinear mathematization process and study of real world problems [6]. The process to create these models tends to be open-ended and messy, without one clear solution [15]. Through modeling experiences, students learn to appreciate the assumptions that allow mathematical analysis to be applied, but also recognize that initial assumptions must often be revisited and revised [6]. Even if a student's attempt ultimately did not work

out (whether due to student error, insufficient data, etc.), the experience allows them to recognize imperfections in data or flawed modeling assumptions [9].

Mathematical modeling also provides experiences that transitions well into solving problems in other scenarios [14]. Particularly in upper secondary and undergraduate level courses, mathematical modeling is an integral part of a student's mathematics general education that allows students to unite mathematics with other disciplines [5, 15]. Since not every student who takes a college mathematics course venture to become an applied mathematician, content and teaching of these course should be revised to give students the appropriate training that will transition into their eventual careers [15]. Incorporating project-based mathematical modeling opportunities allows students to enhance problem solving skills in other academic and career settings [14].

With the increasing presence of mathematical biology as a important discipline, mathematicians and biologists find themselves more frequently collaborating, resulting in the need to cross train students in knowledge and skills including biology, statistics, modeling, computation, technical writing, and presentation skills [5]. While students in these disciplines require more intentionally interdisciplinary learning opportunities, relatively few initiatives to collaboratively teach mathematics and biology have been developed, where most mathematical and biological models are presented disjointly [14]. Offering interdisciplinary project-based learning opportunities will allow students to engage in modeling within and beyond freshman level algebra and calculus, and to cohesively learn mathematics and biology [14].

Although the presence of project-based mathematical modeling in mathematical biology is limited, there are some notable example. At Utah State University, mathematical biology faculty and students have developed the Laboratory Experiences in Mathematical Biology (LEMB) initiative at `https://digitalcommons.usu.edu/lemb/`. This initiative includes a series of comprehensive laboratories and materials to ease inclusion of the laboratory experiences in the classroom. In the "Brine Shrimp LEMB", students track movement of brine shrimp in a petri dish to determine if they move in a random walk, exposing

students to diffusion, PDE models, and parameter estimation [15]. Another example in LEMB initiative is the "Coffee Thermocline LEMB". In this lab, students create a layered system of coffee and milk to serve as a physical model for temperature gradients in lakes or the atmosphere, allowing students to collect temperature data and develop a suitable mathematical model [2].

Other examples in literature include, Greer and Palin's mathematical modeling experience in light of recent pH1N1 campus outbreaks. In this example, students in a differential equations course and in an epidemiology course met together four times over the course a semester to create a model based on campus outbreak data. Students with different backgrounds in mathematics and biology were encouraged to share their expertise to build and revise the model. While this project was not designed to be replicated, it suggests the power of engaging students in developing models for current events [9]. An additional mathematical modeling in microbiology course, "Microbes Count", was created by Jungck where mathematical modeling and use of online interactive models is embedded within many of the different course unit, efficiently layering both mathematics and biology in a single course [14].

Mathematical biologists have also cited the need for increased mathematical modeling opportunities by creating a framework to quantify student achievement and learning in these activities. Diaz-Eaton et al. have developed the "Rule of Five" for this purpose [5]. In this framework, the authors outline five types of modeling representations: experiential, numerical, visual, symbolic, and verbal. A modeling activity is a task that causes a student to move from one modeling representation to another. This recent work will allow modeling experiences in mathematical biology to be better united.

1.2 Holling's functional response model

In the series of papers [11–13], C.S. Holling established the principles upon which our understanding of the relationship between predation rate and prey density lies. He successfully argued how individual predator responses in the consumption of prey to changes in prey density are fundamental for the description of predator-prey systems and their

population regulation. These responses are known today as *functional responses*, a term first introduced by M.E. Solomon in [19]. At the time, Holling presented a classification of responses, currently known as types I, II, and III, which is found in virtually any textbook of theoretical ecology. Their incorporation into mathematical predator-prey modeling provides a "more realistic" rate of predation, due to the emergence of limited attack capacity in the predators [16, 20].

One of Holling's prime goals was to exhibit the basic mechanisms that must operate in any predatory situation, leaving secondary elements, i.e. characteristics to each system, initially aside [4]. This is particularly clear in [12], where he presents his famous reductionist framework (for the type II) based on an artificial predator-prey situation that explains the basic response. Holling's experiment used sandpaper discs on a table as prey and a blindfolded individual participated as a predator, who executed searches by tapping with their finger on the table. This simple experience made transparent the fundamental components of predation that Holling had previously studied with great detail in natural scenarios [11].

The functional response is understood as a predator's consumption rate per unit of area, which depends on the density of the prey. The idea can be introduced by asking the students to think about natural mechanisms that might generate changes on the rate of predation, and how this could potentially affect the population of prey, followed by the representation of some function $F(R)$ that plays the key role in the regulation of the prey population. In other words, if $G(R)$ represents some law of growth for the prey population and if there are M identical predators present then

$$\frac{dR}{dt} = G(R) - MF(R). \tag{1.1}$$

The type II response model is derived completely from mechanistic considerations by assuming only two activities for the predator: (i) searching for prey and (ii) prey handling (including possible killing, eating, and digesting). The model is obtained by considering averages of the variables involved. First, define the total time of observation, T, as the sum of the time used by the predator in searching and the total handling time spent on the

captured prey. Then, writing T_s for the former, defining T_h as the time used in handling one prey, and assuming there were C prey captured, the product CT_h gives the total handling time with

$$T = T_s + CT_h. \tag{1.2}$$

It becomes natural to assume that the average number of resource units captured is proportional to the (constant) prey density, and the time used in searching,

$$C = aRT_s = aR(T - CT_h),$$

from which

$$\frac{C}{T} = \frac{aR}{1 + aRT_h}. \tag{1.3}$$

The left hand side of (1.3) is an average rate of prey consumption per predator per unit of area, i.e. the function $F(R)$ mentioned before. The constant a must have dimension $[\text{time}]^{-1}$, and represents the average rate of successful encounters of one predator with prey, sometimes called "attack rate". The saturation level is given the horizontal line at $1/T_h$.

Although it is not possible to find the detailed path C.S. Holling followed in developing such a deep understanding of the driving mechanisms of predation, the intimate relation to his laboratory and field experience is unquestionable. It is also clear that his papers [11–13] are in agreement with the goals of modern pedagogy in applied mathematics: reasoning inductively, finding patterns in data, applying mathematics to empirical contexts, and communicating the results clearly [3, 15]. Thus, in this work, a lesson plan framework is described to allow students to encounter Holling's theory from different perspectives with particular interest in individual-based simulations.

CHAPTER 2
METHODS

This lesson plan includes three components that provide students insight into Holling's steps to discover the fundamental components of predation. The three parts include: (T) theory, the mathematical theory developed by Holling, (E) the experiment, similar to Holling's "disk experiment", and (S) the individual-based computer simulations. These components are designed to be presented to students in three different sessions. Content derived in (T) and (E) were developed through study of Holling's methodoligies [11–13]. (S) is developed through extension of Holling's work using stochastic modeling tools to replicate the experiment.

Detailed materials for the lesson plan components (including computer codes, data collection sheets, etc.) are available at `https://digitalcommons.usu.edu/lemb/` under the name *The Marshmallow Lab*, as part of the "Laboratory Experiences in Mathematical Biology (LEMB)" initiative and in Appendix C.

2.1 Trial locations

Variations of this lesson have been tested with diverse groups of students that mix undergraduate and graduate, mathematics and biology majors, as well as in groups of senior high school students. This report includes results obtained after implementing the lesson in an introductory nonlinear dynamics course at a land-grant university and in a survey of mathematics course aimed at first/second-year mathematics majors at a private college in the spring 2019 semester. In general, the analysis of students' written work, reports, and verbal comments after their experience with the lesson plan revealed a notable increase in understanding of the predation and saturation phenomena.

At the land-grant institution, student were engaged in lesson sequence of (T), then (E), and finally (S) in three 50-minute meetings, looking for changes in the students' un-

derstanding after each piece. At the private college, the (T) and (E) were condensed to fit into one, 60-minute class period. The simulation portion (S) of the activity was assigned for homework. In the final ten minutes of each meeting, students were given a brief assessment questionnaire:

1. What is your biological interpretation of the "saturation phenomenon"? How does it emerge? Can you name other examples where saturation appears?

2. What are the assumptions for the type II curve? Are they in accordance with your experiment?

3. Is Holling's equation realistic enough to be used for modeling real scenarios? Which other assumptions would you like to include? Do you think the type II functional response would be a good model in your new scenario?

4. Which kind of changes in the curve profiles would you expect as you modify the parameters? Can you give biological interpretations of the observed changes?

For future use, the order of the components is also able to be customized to achieve alternative classroom objectives. For instance, the chronological order (following Holling) would run first (E) or (S) and then ask the students to develop their own theoretical ideas based on the observations; at the end, (T) would be presented giving students the opportunity to compare their modeling ideas with Holling's. In contrast, a additional sequence could run (T) followed by either (E) or (S) could help the students in testing their understanding of the predation mechanisms represented in the theory (the type II equation) and challenge the assumptions made for the model.

2.2 Lesson plan components

2.2.1 (T): Theory

In this section, instructors should prepare a lecture of Holling's functional response model. This component should a detailed description of the function and its parameters, a,

the attack rate, and T_h, the handling time, as well as the model's underlying assumptions. Instructors may also offer a brief description of Holling's original "disc experiment".

Fitting a Type II Functional Response Curve to Data

To fit the type II functional response curve, assuming that data on the number of prey consumed by one predator as function of prey density is available, the goal is to find the estimates for the parameters a and T_h in equation (1.3). Nonlinear regression is an efficient tool for approximating these values, but our assumption that this lesson would be imparted to students that have no previous knowledge of regression might leave the instructor with at least a couple of options: (i) use the nonlinear regression command included in MATLAB as a black-box or (ii) take, for instance, the reciprocal of equation (1.3),

$$\frac{1}{C} = \frac{1 + aRT_h}{aRT} = \frac{1}{aT}\frac{1}{R} + \frac{T_h}{T}, \tag{2.1}$$

which is of the form $y = \alpha x + \beta$ with $\alpha = 1/aT$ and $\beta = T_h/T$, and finally, use least squares to find α and β. The transformation of (1.3) into (2.1) is known as the *Lineweaver-Burk transformation*, which appeared in the study of enzyme kinetics, [17]. Unfortunately, this procedure is prone to errors but it is worth asking the students for its consideration with the possibility of a further discussion topic. There are other equivalent transformations of (1.3) that lead to the use of least squares for estimating a and T_h but again, given the availability of computer power for carrying nonlinear regression, a deeper discussion on the most convenient fitting methods would be, at least initially, out of scope for this lesson plan. However, the curious students can be encouraged to look at [8, 10], for instance. The presentation of least squares to the students can be made minimal: assuming m observations of some quantity, say $(x_1, y_1), \cdots, (x_m, y_m)$, where the x_i's are the values of the independent variable and the y_i's the measured values of the quantity of interest, we fit a straight line as follows:

1. Define the matrices

$$A' = \begin{bmatrix} 1 & 1 & \cdots & 1 \\ x_1 & x_2 & \cdots & x_m \end{bmatrix} \qquad \text{and} \qquad y' = \begin{bmatrix} y_1 & y_2 & \cdots & y_m \end{bmatrix},$$

   where $'$ represents the transpose of a matrix

2. Compute the product $B = A'y$, which is a matrix of size 2×1

3. Define $\theta' = [\alpha \quad \beta]$ and solve the so called Normal equations

$$A'A\theta = B$$

   for θ.

From the results and equations for α and β, parameters can be determined a and T_h. Matlab code for this process and the nonlinear regression with corresponding plots can be found in appendix B

In the framework of the “Rule-of-Five”, running the marshmallow lab allows students to experience many different approaches to modeling [5]. In part (T), students are presented with the theoretical background of the functional response model. Students are given the functional response equation and are taught to interpret the model's parameters (symbolic $\rightarrow$ verbal). This modeling activity is only achieved when part (T) is performed first in the sequence of the lab.

2.2.2 (E): Experiment

For this component, students will participate in a interactive laboratory experience to replicate Holling's “disc experiment”. A student will play the role of predator, which consumes on marshmallows, while keeping their density constant and other students keep time and record data. The most convenient way of running the experiment is in teams of four students. Student A performs the role of *predator*, student C the one maintains a constant density of marshmallows constant during the trial by adding marshmallows when

one has been eaten, and students B and D track of total time, handling time, and number of marshmallows consumed.

Lab materials

- Masking tape
- Two stopwatches
- A bag of mini-marshmallows. They are easy to chew and swallow, and have mild taste.
- A blindfold

Set up and run of one trial

1. Delimit a rectangular area on a desk using the masking tape. Student A sits at the desk making sure that every point on the rectangle is at comfortable reach with her/his arm.

2. Blindfold student A and instruct her/him to search for prey by tapping a fingertip randomly around on the area: no sliding and no search patterns for search within the marked area. Student A must perform quick searches. When the student A finds a marshmallow, she picks it up and eats it. After swallowing the search continues. The consumption must be done quickly too.

3. Student B starts a stopwatch while giving a signal, by shouting *go!* or *start!*, and student A begins the search.

4. When the predator encounters a marshmallow, student D starts her stopwatch. As soon as student A's finger is back tapping Person D stops the handling time stopwatch and updates the counter of eaten marshmallows. For handling time, the accumulated time spent in each marshmallow is recorded.

5. Student C replaces new marshmallows in the rectangle each time that one is eaten. The position for the new marshmallow must be random, so the predator does not learn where food can be found with certainty.

6. Student B shouts *stop!* after 90 seconds have elapsed since the start and A stops the search.

In part (E), students are able to achieve several different types modeling activities as they progress through the section. Referring to the "Rule-of-Five" framework [5], many aspects of modeling appear naturally. As the students recreate the functional response mechanism in their varying roles with marshmallows, they record the handling time and numbers of marshmallows captured in each run for varying constant densities of marshmallows (experimental → numerical). At this stage, students may also examine their data to locate potential occurrences of the saturation phenomena (numerical → verbal). Now, using their gathered data, students use regression to fit parameters of the functional response model equation (verbal → numerical). Now, using the data and fitted parameters, students plot a graph as a visual representation of the saturation phenomena (numerical → visual). Students are also able to identify the saturation visually as the curve flattens (visual → verbal).

One of the problems in the execution of part (E) might be the short duration of the class. In our experience, a course with meeting time of fifty minutes may use thirty five minutes for data collection and more or less the rest of the time for answering the questionnaire. However, in this short time we were able to collect data of only two trials for each density value, for five density values. Furthermore, there might be unaccounted factors influencing the data collection process in (E), namely the predator starts to dislike the marshmallows' flavor and slows the handling time or it gets tired and the searching is not as quick as in the initial trials, or the times are incorrectly recorded. As consequence, the data collected might induce awful fitting results if the Lineweaver-Burk transformation is used. This issue can be resolved by reproducing the disc experiment in the computer in part (S).

2.2.3 (S): Individual-based simulations

Using NetLogo, a popular agent-based programming language freely available at https://ccl.northwestern.edu/netlogo/, a program was developed to simulate the experiment. In the program, the predator performs searching by moving with a random walk and each time it founds a prey (white squares) it stops searching for a fixed amount of handling time, adjustable on the interface. Prey density can also be modified and the simulated data appears in a small window. Figure 2.1 shows a screen shot of what the students see when running the program.

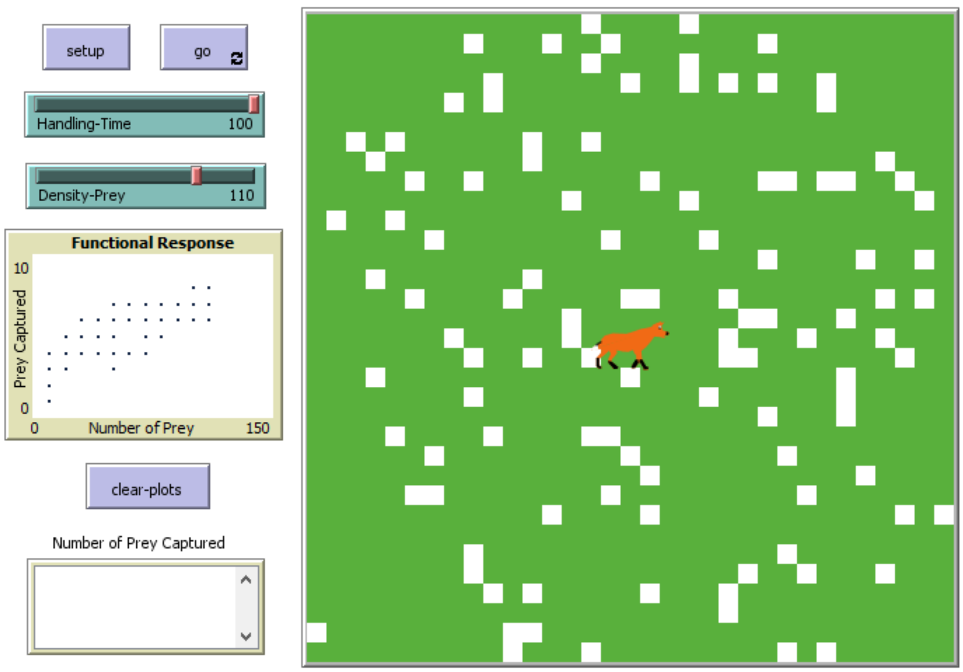

Fig. 2.1: A screen shot of the NetLogo program. The students can play changing the handling time and the density of prey (slides). The data is captured and retained on the screen with the legend "Functional Response" on top, where they can appreciate the emergence of the nonlinear effects (saturation).

In part (S), students are able to reiterate many of the modeling activities in the "Rule of Five" framework [5] that they completed in part (E). However, students are able to manipulate settings on the NetLogo program. While in part (E), students had less control over parameters such the handling time, the simulation allows students to easily adjust to

handling time as well as the density of prey (symbolic → experimental).

If instructors to follow a alternate sequence of parts, they may achieve different learning objectives. For example, if part (E) or (S) were completed first, students would be able to write their own equations based on their own observations and graphs before taking a closer look at the established theory (visual and/or experiential → symbolic).

2.3 Learning objectives

Stated learning objectives convey the pedagogical value of this lesson and help the instructor with tracking student progress. Each objective is labeled according to the intended learning level associated with our aims [3, 15]. Table 2.1 contains the learning objectives that inform our analysis of the student questionnaires and written reports.

	Learning Level	**Learning Objective**
1.	Construct a Concept	The student identifies examples where saturation occurs.
2.	Discover a Relationship	The student explains the relationship of prey density, handling time, and predator consumption rate.
3.	Comprehension and Communication	The student explains the emergence of a saturation phenomenon in Holling's Type II function response model by interpreting the equation and its graph, identifying variables and assumptions, and by describing how parameters impact the shape of the curve.
4.	Algorithmic Skill	Given a data set, the student parameterizes a mathematical model using linear and nonlinear regression techniques.
5.	Application	The student decides what assumptions could be added to the model to make it more realistic.
6.	Creative Thinking	The student generates novel connections between biological and mathematical formulations of saturation phenomena.
7.	Appreciation	The student gains appreciation for how the appropriate modeling assumptions are included and interpreted in the mathematical modeling process.
8.	Willingness to Try	Given an the interactive agent-based model simulation, the student demonstrates a willingness-to-try as they engage in parameter value experimentation to better understand the functional response model.

Table 2.1: The marshmallow lab learning objectives. Objectives 1-6 are in the cognitive domain and objectives 7 and 8 are in the affective domain.

CHAPTER 3

RESULTS

After testing the contents of this lesson in various settings, it is clear that this experience allowed students to widely increase their understanding of the functional response model. The students were also tasked with writing a final report discussing their findings from each component of the lab. Samples of students' data and fitted functional response curves are given in Figure 3.1. To illustrate student understanding of the functional response and achievement of learning objectives in Table **??** through the modeling activities in this experience, quotes from student final reports and questionnaires are included.

In the questionnaire, students were first asked to identify examples of saturation aside from the occurrence in the functional response model. As students progressed through the components, they were able to understand and to cite a wide variety of simple and complex occurrences of saturation such as dissolution of sugar/salt in water, the amount a human can eat before feeling satisfied, supply and demand, and ability to process information over time. This reveals student achievement for objective 1, a conceptual understanding of saturation phenomena.

In sections (E) and (S), students were able to achieve objectives 2 and 3. Through required modeling reports, students explain their understanding of the theoretical model and the connections to their experimental results. In this way, their comprehension of the functional response model is assessed.

Initially, it is not often clear to students from the symbolic representation that the saturation effect is imposed by the handling time. Several students expressed the belief that the saturation was caused by "physically, how much a predator could eat." As the classes moved beyond theory, one student noted that after "actually [seeing] the cyber-fox move and wait when prey was caught ... I [understood] that the fox was limited by its handling time". The student later noted that "I can study a model all day, but somehow

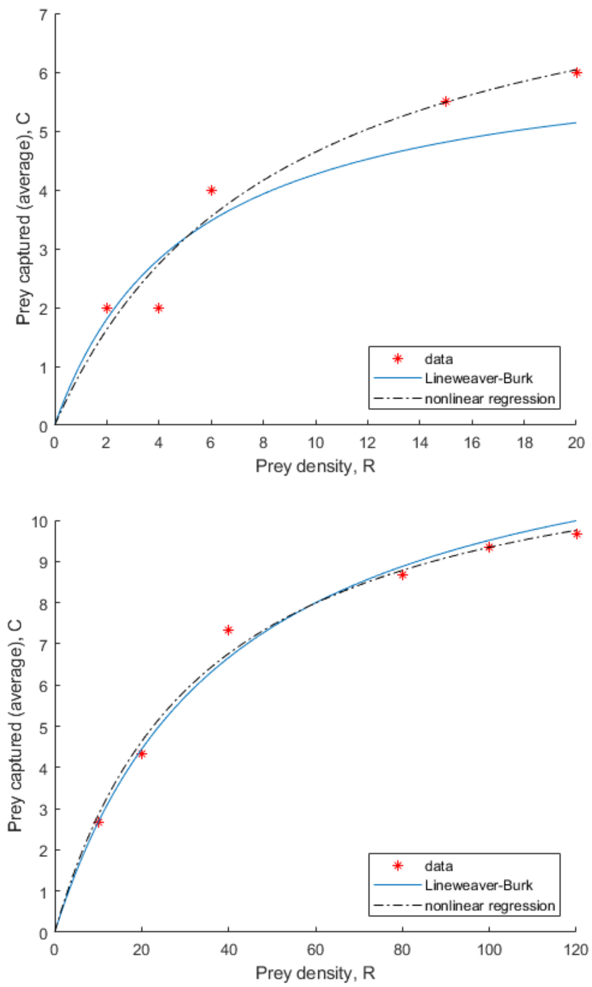

Fig. 3.1: Averages of data obtained by students in a classroom following the sequence (T)(E)(S). **Top:** Data collected using the marshmallow experiment (E). Two different procedures were used to fit the model to the averaged data, the Lineweaver-Burk transformation (continuous) and nonlinear regression (dash-dots). The session duration might impose time constraints, limiting the data obtained. However, as observed in this example (two observations per density value), the emergence of the nonlinear effects (saturation) is still evident. **Bottom:** Data collected using computer simulations. Although NetLogo allows running trials in parallel at an amazing speed, we asked the students to run three trials per density value and then average.

having actual experimental numbers and data point helps my understanding." Another student noted that, as data is collected "at some point, although the [density of] prey is still increasing the amount a predator eats will level out." The student then attributes the leveling out of consumption of prey as density of prey increased through each trial to the fact that a "predator can only eat so much in a given time, and the amount of prey [captured] becomes saturated." The experimental and visual elements of parts (E) and (S) helped students to grasp that, without considering hunger, a predator is limited simply by the duration of its handling time, resulting in saturation.

Achievment of objective 4 is assessed after both (E) and (S) by assisting students with fitting model parameters after their data is collected. Using concepts introduced in part (T), students are able to use regression techniques to compute parameter values from their data generated in (E) and (S). Each instructor may decide how much they want to emphasize this objective. If a discussion of parameter-fitting is not deemed well-fitting to the course, existing software can be used as a blackbox.

Parts (E) and (S) also increased student retention and understanding of the model's assumptions. After the presentation of the theory, students often only remembered very few of the model's assumptions, but in their final reports, students expressed understanding and suggested additional assumptions, achieving objective 5. A student noted that another factor that "could be added to the model to make it more realistic [is] a hunger variable." This student went on to note that this addition would directly diminish the predator attack rate. The student also predicted that "the time it takes to reach saturation will be less." This observation also shows achievement of objective 6, as the student attempts to not only improve the model, but to strength the connection between mathematical and biological theory. Furthermore, this shows that the repetition and use of the agent-based model invokes creative and critical thinking that leads students to ask important questions and inspire further research.

This evidence also shows growth in student understanding of the modeling process. As students progressed through this lesson, they better understand that modeling is a

simplification of what happens in real life, and gained apreciation of the appropriateness of model assumptions, illustrating further achievement in objective 7. A student noted while the functional response model assumptions are "unlikely to be true in nature... these [functional response] models have played critical roles in ecological theory." The same student continued to note that these simplified systems still allowed mathematical tools to be applied to gain critical insight of the real world scenario.

Students also demonstrated willingness-to-try (objective 8), as they continued to adjust parameters on the computer simulation to experiment and note the impact on the curve. In part (S), as interacting with the agent-based model, students often continued to run simulations with differing parameters to test the existence of the saturation phenomenon. Students who had initially hypothesized that the number of prey captured would double if the prey density doubled, were able to first-hand disprove these claims, solidfying their understanding of the functional response model.

Conclusion

Although Holling's work on functional responses was groundbreaking in ecology, its importance is often downplayed in introductory mathematical biology courses and textbooks. It is common to observe a jump into the mathematics describing population dynamics after a short introduction of Holling's classification for functional responses (type I, II, and III), without a pause to appreciate the biological processes that inspired the theory. The latter is fundamental in shaping students' deep understanding because the approach also reveals the limitations and issues subtly embedded into the equations.

Holling's artificial predator-prey experiment is one of those rare instances that can be replicated easily, it is cheap, safe, and relatively quick to mount and run. But overall, in our experience, it is inspiring and fun for students and teachers. Undoubtedly, there are various other individuals reproducing Holling's disc experiment in a classroom. The goal of this paper is to present it in the form of a structured lesson plan with three components that complement each other and reinforce students' understanding. These components can be presented in different order to develops different learning objectives. This lesson plan can

also serve as a departure point to explore and discuss further topics in more depth, including parameter estimation of models, stochastic modeling, complexity in ecological models, and project-based learning, to name a few. After this lesson is imparted, the instructor can also opt to extend the discussion into the types I and III functional responses with more detail.

There have been many calls for mathematicians to implement interdisciplinary mathematical modeling projects in courses of a level both inside and outside of mathematics [5,15]. These projects encourage students to think critically about mathematics as more than cluttered equations on paper, but a diverse set of tools with limitless applications. While other invaluable contributions to mathematical modeling and mathematical biology education are appearing, resources for these innovative projects are still limited. The"Marshmallow Lab" helps to fill this need by offering a multidimensional modeling project that allows students to understand the functional response model through diverse experiences and technology.

Funding Acknowledgement

Melissa Pulley received support from the National Science Foundation under Grant No. 1633756 and the National Institute of Food and Agriculture, United States Department of Agriculture under Grant No. 2017-67013-26566.

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APPENDICES

APPENDIX A

NetLogo code for individual-based simulations

```
globals
[
func-response
Prey-Captured
belly-capacity
]
turtles-own
[
  count-down
]
to setup
  clear-globals clear-ticks  clear-turtles clear-patches clear-drawing clear-output
  ask patches [set pcolor green]
  set Prey-Captured 0
  ask n-of Density-Prey patches [set pcolor white]
  crt 1
  [
   set shape "fox"
   set size 4
   set count-down Handling-Time
  ]
  reset-ticks
end
```

```
to go
  ask turtles
  [
    ifelse pcolor != white
    [continue]
    [stay]
  ]
  tick
  if ticks >= 900
    [
      plotxy Density-Prey Prey-Captured
      set-current-plot "Functional Response"
      output-print Prey-Captured
      stop
    ]
end

to continue
  right (random 359)
  forward 1
end

to stay
  set count-down count-down - 1
  set label count-down
  if count-down = 0
  [
    set count-down Handling-Time
```

```
    set label ""
    set pcolor green
    ask one-of patches [set pcolor white]
    set Prey-Captured Prey-Captured + 1
    continue
  ]
end

to clear-plots
  clear-all-plots
end
```

APPENDIX B

MATLAB code for fitting a type II functional response curve to data

B.1 Linear and nonlinear fitting

```
clear all
warning off
%Replace data in vector x and y with prey densities and average
   number of
%prey captured
 T=90;                    % total time
 x=1./[2 4 6 15 20]';    % densities
 y=1./[2 2 4 5.5 6]'; % avg observations

 % Least squares fit
 A=ones(5,2);
 A(:,2)=x;

 B=A'*y;
 C=A'*A;

 z=C\B;

 R=1./x;
 C=1./y;

  figure(1)
```

```
hold on
plot(R,C,'r*')

Th=z(1)*T
a=1/(z(2)*T)

w=0:0.1:20;
plot(w,a*T*w./(1+a*Th*w))


xlabel('Prey density, R')
ylabel('Prey captured, C')

% nonlinear fit

d=nlinfit(R,C,@TypeII,[0 4]);
Fit=TypeII(d,w);
plot(w,Fit,'-.k')

legend('data','least squares','nonlinear fit','Location','
    southeast')

% comparison LS vs. nonlinear fit
[a Th ;d]
```

B.2 Type II curve

```
function Pe = TypeII(d,x)

Pe=d(1)*90*x./(1+d(1)*d(2)*x);
```

APPENDIX C

Laboratory experience in mathematical biology materials

C.1 Laboratory experience in mathematical biology instructions

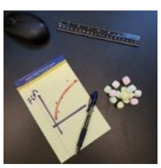
C.2 Sample student data collection sheets

Marshmallow Lab

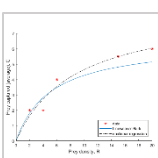
Laboratory Experiences in Mathematical Biology

Overview: In this three-part lab, students explore nonlinear effects (saturation) emerging in predator-prey scenarios through lessons in (T) theory, (E) the “disc" experiment, and (S) the computer simulations.

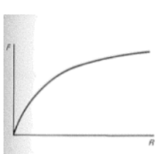
Lesson Outline: The lab consists of 3 parts: theory (T), experiment (E) and computer simulations (S). The order in which these parts are run is not considered. The students will explore the emergence of a nonlinear phenomenon through the so-called functional response in predators. The agenda presented below is aimed towards students from different academic backgrounds who have completed a course in college algebra.



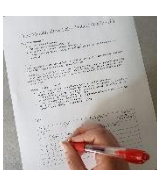
Lab Setup: Students study the functional response mechanisms of predators through theory, experimentations, and computer simulations.



Data and Examples: The recorded data by the students from the experiment and computer simulation parts of the Lab (i.e (E) and (S) parts of the lab) as well as the fitted curve is presented here.



Background and Extensions: A brief explanation of the theory of a Type II Functional Response curve is offered here for part (T).



Assessment items: The following assessment items were written to target learning objectives in the Marshmallow Lab for any course whose students have an understanding of college algebra.

Marshmallow Lab

Laboratory Experiences in Mathematical Biology

Lesson Outline: The lab consists of 3 parts: theory (T), experiment (E) and computer simulations (S). The order in which these parts are run is not considered. The students will explore the emergence of a nonlinear phenomenon through the so-called functional response in predators. The agenda presented below is aimed towards students from different academic backgrounds who have completed a course in college algebra.

Expectations:

Students form groups in order to run each of the parts mentioned above. Each student will be given a questionnaire designed to track the understanding of the functional response mechanism. Each student is expected to complete all of the following.

- Be part of a group.
- Download and install the software for agent based modeling **NetLogo**, available at https://ccl.northwestern.edu/netlogo/.
- Actively participate in each part of the lab.
- Collect the data obtained by performing parts (E) and (S) of the labs.
- Answer a questionnaire after each part has been completed.
- Present a report.

Lab Agenda:

Each of the parts that comprise the lab are completed in the classroom. The order in which the parts are run can vary, but here we present the one that has been completed in a previous run of the lab.

1. Lecture (Theory part (T)): An introductory lecture and/or reading of the basic theory and ideas of the functional response mechanism (40 min) using Background and Extensions LEMB section, followed by the students answering a set of questions (10 min).
2. Experiment part (E): This part is completed by each group. One student will play the role of predator, which preys on motionless little marshmallows. The most convenient way of running the experiment is in teams of four students. Collection of data must occur while the experiment is being run (40 min). Students answer a questionnaire (10 min).
3. Simulations part (S): Students are shown and explained how to use a software that simulates a predator-prey environment, they are asked to run different simulations varying the number of prey, while simulations are run students must collect the data obtained (40 min). Students answer a questionnaire (10 min).

Marshmallow Lab

Laboratory Experiences in Mathematical Biology

Lab Setup: Students study the functional response mechanisms of predators through theory, experimentations, and computer simulations.

Materials: Aside from LEMB materials, the materials required for each part are:

- (E): Masking tape, stopwatches, a bag of mini marshmallows (These are easy to chew and swallow and have a mild taste), a blindfold.
- (S): A laptop computer, with NetLogo installed in it. NetLogo can be download it from the link: https://ccl.northwestern.edu/netlogo/

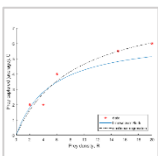
Methods: The following set up is recommended to run part (E) of the Lab. The most convenient way of running the experiment is in teams of four students. Student A acts as a predator, student C adds marshmallows as eaten to main constant density of prey in one trial. Students B and D track total time, handling time, and number of marshmallows consumed. (S) should be run similarly, with each student individually collecting data from the NetLogo program. Data Collection sheets have recommended values for handling time and prey density for both (S) and (E).

Set up and run of one trial (E):

1. Delimit a rectangular area on a desk using the masking tape. Student A sits at the desk making sure that every point on the rectangle is at comfortable reach with their arm.
2. Blindfold student A and instruct her/him to search for prey by tapping a fingertip randomly around on the area: no sliding and no search patterns for search within the marked area. Student A must perform quick searches. When the student A finds a marshmallow, she/he picks it up and eats it. After swallowing the search continues.
3. Student B starts a stopwatch while shouting “go” and student A starts the search.
4. When the predator encounters a marshmallow, student D starts their stopwatch. As soon as A’s finger is back tapping, student D stops the handling time stopwatch and updates the counter of eaten marshmallows. For handling time, the accumulated time spent in each marshmallow is recorded.
5. Student C randomly places a new marshmallow in the rectangle each time one is eaten.
6. Student B shouts ‘stop" after **90 seconds** and A stops the search.
7. Students repeat steps 2 – 6 for each given density of prey.

Marshmallow Lab

Laboratory Experiences in Mathematical Biology



Data and Examples: The recorded data by the students from the experiment and computer simulation parts of the Lab (i.e (E) and (S) parts of the lab) as well as the fitted curve is presented here.

Sample Data (E): After running part (E), students used data to create Figure 1, which shows the corresponding curve fitting using the provided MatLab Code. Two different procedures were used to fit the model to the averaged data, the Lineweaver-Burk transformation (continuous) and non-linear regression (dash-dots). Time constrains might severely limit the data obtained. However, as observed in this experience (two observations per density value), the emergence of saturation (non-linear phenomenon) is evident.

Prey density, R	Prey eaten, C				Total handling time, T^* (Sec)				Handling time/prey $T_h = Avg\ T^*/Avg\ C$
	Trial 1	Trial 2	Trial 3	Average	Trial 1	Trial 2	Trial 3	Average	
2	1	3		2	8	27		17.5	8.75
4	2	2		2	16	16		16	8
6	4	4		4	25	36		30.5	7.625
15	6	5		5.5	46	48		47	8.5454
20	6	6		6	50	53		51.5	8.583

A note of caution: If a student consumes the marshmallows quickly enough in part (E), they may need to run additional trials with higher densities of prey to achieve a saturation effect.

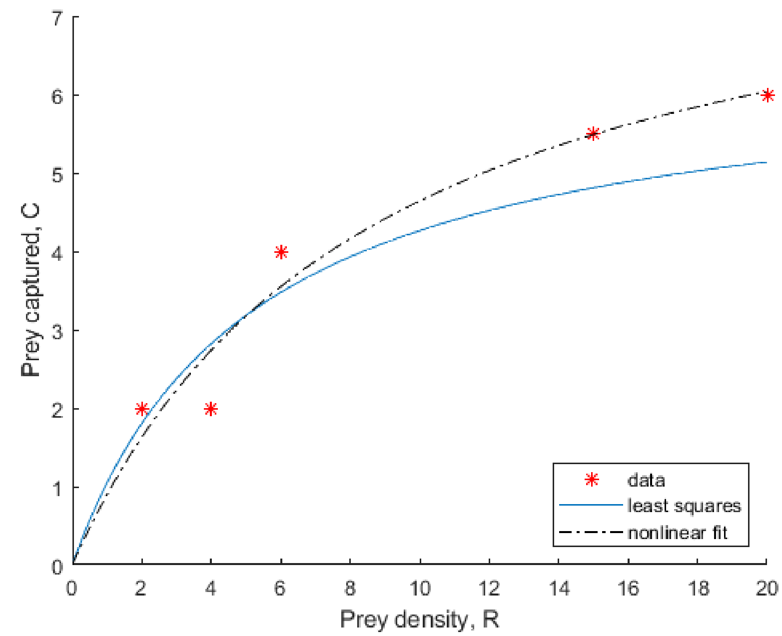


Figure 1.

Sample Data (S): After completing part (S) in NetLogo, the simulation data was similarly used to compute parameters and create Figure 2 using the same provided MatLab Code and legend from Figure 1. Students used a handling-time of 72 ticks and different varying densities of prey, but still achieved a saturation effect.

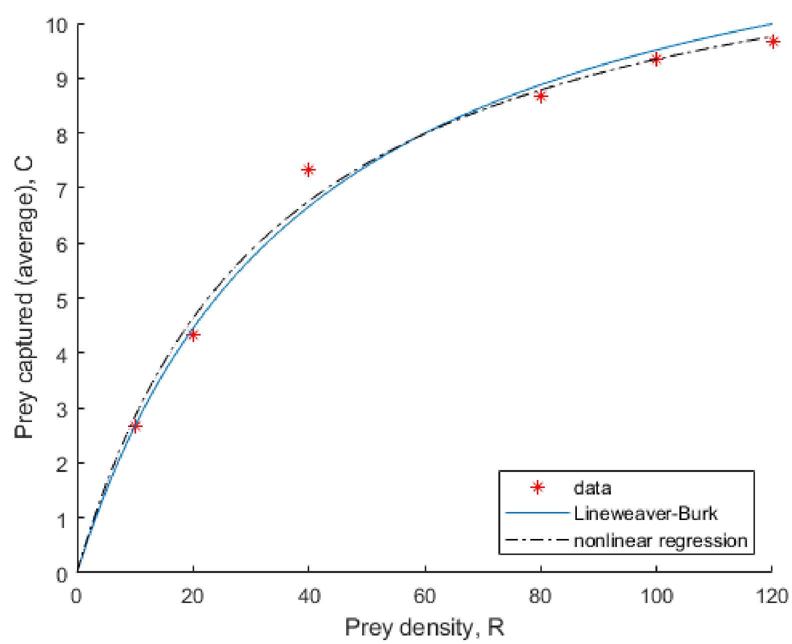
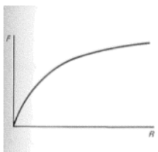


Figure 2.

Marshmallow Lab

Laboratory Experiences in Mathematical Biology



Background and Extensions: A brief explanation of the theory of a Type II Functional Response curve is offered here for part (T).

The Functional Response: The Type II Curve: The functional response is understood as a predator's consumption rate per unit of area, which depends on the density of the prey, R. The idea can be introduced by asking the students to think about natural reasons that might generate changes on the rate of predation, $\frac{dR}{dt}$. This could affect the population of prey, $F(R)$, that plays a key role in regulation of the prey population. In other words, if $G(R)$ represents some law of growth for the prey population and if there are M identical predators present then

$$\frac{dR}{dt} = G(R) - M\,F(R).$$

Then the type II response model is derived completely from mechanistic considerations, assuming two activities for the predator: (i) searching for prey and (ii) prey handling (including possible killing, eating, and digesting). The model is obtained by considering averages of the variables involved. First, define the total time of observation, T, as the sum of the time used by the predator in searching and the total handling time spent on the captured prey. Then write T_s for the former and define T_h as the time used in handling one predator. Assuming C prey captured, the product CT_h gives the total handling time

$$T = T_s + CT_h.$$

It becomes natural to assume that the average number of resource units captured is proportional to the (constant) prey density, and the time used in searching,

$$C = aRT_s = aR(T - CT_h),$$

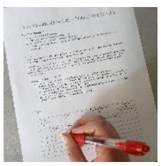
From which

$$\frac{C}{T} = \frac{aR}{1 + aRT_h}.$$

The left hand side of the equation above is an average rate of prey consumption per predator per unit of area, the function $F(R)$ above. The constant a must have dimension $[T]^{-1}$, and represents the average rate of successful encounters of one predator with prey, also known as the “attack rate". The saturation level is given the horizontal line at $1/T_h$.

Marshmallow Lab

Laboratory Experiences in Mathematical Biology



Assessment items: The following assessment items were written to target learning objectives in the Marshmallow Lab for any course whose students have an understanding of college algebra.

1. **Comprehension and Communication:** What is your interpretation of the "saturation phenomenon"? How does it emerge?

2. **Construct a Concept:** What are other examples where saturation appears?

3. **Comprehension and Communication:** What are the assumptions in the Type II curve? Are they in accordance with your experiment?

4. **Application:** Is Holling's equation realistic enough to be used for modeling real scenarios? What other assumptions would you like to include? Do you think the type II functional response would be a good model in your new scenario?

5. **Discover a Relationship:** Which kind of changes in the curve profiles would you expect as you modify the parameters? Can you give biological interpretations of the observed changes?

The Marshmallow Lab – Data Collection (E)[36]

Team assignments:

- Person A: blindfolded predator
- Person B: measures the total predation time
- Person C: keeps the density of marshmallows constant
- Person D: measures the total handling time and keeps track of the number of marshmallows consumed

Setup:

Use masking tape to delimit a rectangular area on a desk. Person A sits at the desk making sure that every point on the rectangle is at comfortable reach with her/his arm.

Blindfold Person A and instruct her/him to search for prey by tapping a fingertip randomly around on the area: no sliding and no search patterns for search within the marked area. Person A must perform quick searches. When the Person A detects a marshmallow, she picks it up and eats it. After swallowing the search continues.

Procedure for one trial:

1. Person B starts a stopwatch while shouting “go” and Person A starts the search.
2. When the predator encounters a marshmallow, Person D starts her stopwatch. As soon as Person A’s finger is back tapping Person D stops the handling time stopwatch. For handling time, the accumulated time spent in each marshmallow is recorded.
3. Person C replaces new marshmallows in the rectangle each time that one is eaten. The position for the new marshmallow must be random.
4. Person B shouts “stop” after 90 seconds and the trial ends.

Data

Prey density, R	Prey eaten, C				Total handling time, T^*				Handling time/prey $T_h = Avg\ T^* / Avg\ C$
	Trial 1	Trial 2	Trial 3	Average	Trial 1	Trial 2	Trial 3	Average	
2									
4									
6									
15									
20									

The Marshmallow Lab – Data Collection (S)[37]

What is NetLogo?

It is an agent-based programming language and integrated modeling environment.

What does our code do?

It simulates a predator searching and capturing motionless prey. The program automatically records and plots the number of preys encountered and the cumulative handling time. Each time that a prey is eaten a replacement is created with random location.

What does the program include?

The program shows a user interface that allows the user to modify the parameters relevant to the experiment. There are two buttons:

- **Setup:** Sets up the environment to run one trial
- **Go:** Starts the simulation of one trial

and two sliders:

- **Density-Prey:** Adjusts the number of prey
- **Handling-Time:** Adjusts the handling time

There is also a panel labelled **Number of Prey Captured**. Use the number showed at the end of each trial to fill out the table provided below.

Data

Prey density, R	Prey eaten, C			
	Trial 1	Trial 2	Trial 3	Average
10				
20				
40				
80				
100				
120				