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An Interdisciplinary Research Course in Theoretical Ecology for Young Undergraduates†

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Name of Institution	University of Nebraska-Lincoln
Size	about 24,000 students
Institution Type	large state university with PhD program
Student Demographic	recent high school graduates with high potential and interests in mathematics and biology
Department Structure	Mathematics and Biology are individual departments in the College of Arts and Sciences

Abstract

As part of an interdepartmental effort to attract promising students to research at the interface between mathematics and biology, we created a course in which groups of recent high school graduates and first-year college students conducted a research project in insect population dynamics. The students set up experiments, collected data, used the

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data to develop mathematical models, tested their models against further experiments, and prepared their results for dissemination. The course was self-contained in that the lecture portion developed the mathematical, statistical, and biological background needed for the research. A special writing component helped students learn the principles of scientific writing and presentation. The success of the course was indicated by the high quality of student work and positive feedback from the students.

10.1 Course Structure

- Weeks per term: 5-week summer session
- Classes per week/type/length: five 1-hour lecture periods each week
- Labs per week/length: five 1-hour laboratory periods each week
- Average class size: 8–14 students in one section
- Enrollment requirements: For high school students and university freshmen. Students had to apply for the program and get a recommendation from a teacher.
- Faculty/dept per class, TAs: Team-taught by one mathematics instructor and one biology instructor, with the mathematics instructor doing the quantitative portion of the lecture.
- Next course: The purpose of this course was to teach research skills. There were no related courses, but many of the students did research projects later in their program. Some students chose to take additional courses in mathematics and/or biology, including interdisciplinary courses offered by either department.
- Website: http://www.math.unl.edu/programs/rute/

10.2 Introduction

Research Skills for Theoretical Ecology (RSTE) was an interdisciplinary research-based course for beginning undergraduates that was taught at the University of Nebraska-Lincoln in a five-week summer session from 2006 through 2010. The genesis of this course is described elsewhere in this volume (Ledder and Tenhumberg, 2013). The course was intended as a recruitment and preparation tool for a subsequent extended research program; hence, we expected applicants for it to have completed one year of college, including two courses in calculus and at least one in biology.

Our initial offering of RSTE was in the summer of 2006. This first attempt at an entry-level undergraduate research program highlighted both the promise and the challenge of our course design. We found it difficult to fill the program with fully-qualified students. Financial constraints cause most of our undergraduates to plan their summer around a full-time job, while our program could pay them for only five weeks; this kept some of the most qualified students from applying. We were unable to enforce our intended prerequisites, as few biology students had taken mathematics beyond Calculus I and few mathematics students had taken even one biology course. We recruited three new high school graduates to augment the five post-freshmen. Several of the students were unable to do the mathematical work, and none had adequate scientific writing skills. Nevertheless, the research work yielded excellent experimental data that was used to estimate parameters for a mathematical model and to validate it. The students indicated that the course was well worth taking. Two of the biology students continued to do interdisciplinary research after the course, one in microbiology and one in natural resources. One student is doing PhD work in epidemiology and another in statistical modeling. Two other students are doing PhD work in other areas of mathematics.

The difficulties exposed by our pilot offering were addressed in our subsequent course planning. For recruiting, we eliminated all prerequisites and targeted talented college-bound high school graduates as our primary clientele. Our purpose changed from training students already planning a research career to offering a potential career-altering experience to students at the beginning of their college experience. Reaching students at this early stage of an academic career allowed us to influence undergraduate course selection and career plans. We changed our strategy for teaching the mathematics without lowering our expectations. We hired a teaching assistant (Mr. Adams) to teach scientific writing for 2007.

In this paper, we describe the Research Skills for Theoretical Ecology course that grew out of our initial effort and was taught in the summers of 2007 through 2010. We discuss the research plan; the assignments, activities, and teaching methods; and the outcomes and student feedback. We conclude with recommendations for similar courses at other institutions.

10.3 Student Profile

Some recruiting was done in our own freshman-level mathematics and biology courses, but most of it was done through our extensive contact list of high school mathematics teachers and through announcements sent to prospective biology majors by the Admissions Office. College-bound students in Nebraska take four years of mathematics, so it is easier for mathematics teachers than biology teachers to identify strong seniors; we also felt that ability and interest in mathematics was more critical than ability and interest in biology. Our experience showed the focus on high school mathematics to be a good decision, as nearly all of the applicants had their principal interest in biology but proved capable of doing the mathematics.

Our applicant pool remained small, but of high quality. In 2007, for example, we received eighteen applications and offered positions to sixteen students, yielding a class of fourteen. All fourteen had outstanding academic records and strong letters of support from a teacher. Our group included ten new high school graduates, all planning to major in life science areas including biology, biochemistry, pre-medicine, and pre-veterinary medicine. Six were from Nebraska's urban centers (Omaha and Lincoln), one from a small city, and three from rural high schools. Four were from Catholic high schools and six from public schools. Four were enrolled at the University of Nebraska-Lincoln (UNL) for the coming year and six were going elsewhere. We also had three current UNL students, all in mathematics, and one student about to be a (high school) senior at a highly-regarded mathematics and science academy in Illinois. There were six males and eight females. Six of the fourteen students identified scientific research as a possible career choice. The student profiles in subsequent years were similar.

10.4 Objectives and Design Principles

The goal for the course was to engage students in interdisciplinary research. By "interdisciplinary," we meant a unified whole, with experimental biology and mathematical modeling as critical and interrelated components, not biology augmented by statistical analysis, mathematics problems motivated by biology, or a loose confederation of the two. We interpreted "research" as a verb that refers to the process of generating new knowledge, not a noun that refers to work suitable for publication. We wanted our students' work to be a serious investigation of an extended open-ended problem, with conclusions supported by experimental data and mathematical models. The objectives and design principles are discussed elsewhere in this volume (Ledder and Tenhumberg, 2013); here we simply state them to provide context.

Objectives for a Research-Based Course in Theoretical Ecology:

1. Learn knowledge and skills for theoretical ecology research.
2. Conduct theoretical ecology research.
    a. Collect laboratory data on ecological problems.
    b. Use laboratory data to construct mathematical models.
    c. Use mathematical models to make predictions.
    d. Use additional laboratory experiments to test the predictions.
    e. Draw appropriate conclusions.
3. Learn scientific communication skills.
    a. Read primary literature in ecology.
    b. Write scientific research papers/posters.

Design Principles for a Research-Based Course in Theoretical Ecology:

1. The course should be about skills rather than content. Everything in it should be based on a coherent research plan.
2. The research program should be both experimental and theoretical, with a clear focus.

3. The research program needs to be devised primarily by the biologist with the mathematician's approval because the biologist needs to have the laboratory expertise for the project and the mathematician needs to be able to devise a mathematics component to complement the given biology component.
4. The course should be fully integrated: biology and mathematics, theory and experiment, laboratory and lecture.
5. An authentic research experience must lead to a research paper, although the research need not be publishable.
6. The course must be self-contained: it must provide the necessary biology background, teach the laboratory methods, build the mathematics up from a pre-calculus background, and teach scientific writing.

10.5 The Research Program

The general theme of our research program was biological pest control. Within this broad theme, the research focused on insect herbivore population dynamics, with and without predation. Our system consisted of the pea aphid *Acyrthosiphon pisum* (a widely-distributed North American insect pest), the broad bean plant *Vicia faba*, and the coccinellid (ladybird beetle) *Hippodamia convergens* (adults and larvae eat aphids).

Pea aphids are small insects that feed on the phloem of a several plant species, including the broad bean. They pass through four nymphal (immature) stages before molting to the adult stage. In the laboratory and during the summer in the field, pea aphids reproduce asexually, with offspring born live. They mature in about ten days and seldom live for more than four weeks. Their rapid life cycle makes them an excellent study species for a five-week course. Furthermore, their relatively large size and general immobility when undisturbed makes aphid handling and counting straightforward; even newborns are visible by eye. Adult coccinellids can be purchased from commercial suppliers (Carolina Biological Supply Co.) and maintained on a pea aphid diet in large chiffon-netted aluminum cages. Adult coccinellids start mating right after arrival and oviposit eggs one week later. In the lab the larvae hatch after about three days and start consuming aphids right away. The larvae go through four instars (immature stages) before pupation.

The research project combined an aphid population dynamics component with a predator-prey dynamics component, each of which required two experiments and one mathematical model. The mathematical modeling was challenging, but feasible, for good students at the high school level. Because the course lasted only five weeks, the experiments were conducted simultaneously and the models were introduced sequentially during lecture. Figure 1 indicates the logical connections among the components. Those components that appear to the left of the vertical dotted lines represent simulated experiments done with the BUGBOX models, while everything to the right represents empirical experiments on the real biological system or mathematical modeling of the biological data.

10.5.1 Aphid Population Dynamics

In the *vital rates experiment*, the students first transferred individual adult aphids in numbered 4 cm diameter clip cages fastened to bean leaves on a living plant. After 24 hours, the students removed all aphids from each cage except for one newborn. The fate of the newborn aphid could then be followed from birth to death. Each day thereafter, each clip cage was examined to record all life history events, including the days when the aphid molted to the next developmental stage (determined by observing the cast-off exoskeletons), the day of the aphid's death, and the daily number of offspring produced after the aphid becomes an adult. These data were used to determine average developmental time, fecundity, and survival rates for each stage. Because of the large variation in aphid demographic rates, we used 40–60 clip cages with one aphid each.

In conjunction with their experimental work, the students studied the density-independent population dynamics model

$$x_{t+1} = \mathbf{M}x_t, \tag{1}$$

where x_t is the population vector consisting of the six (four nymph, two adult) stages on day t. We split the adult stage into two stages because pea aphids do not reproduce in the first 1–2 days after becoming adults. $\mathbf{M}$ is a 6×6 matrix comprised of the survival, development, and fecundity rates obtained from the *vital rates experiment* data. The students used the R software package (R Development Core Team 2012)) to calculate the asymptotic population growth rate (the dominant eigenvalue of the matrix) and to simulate how the average aphid abundance changes over

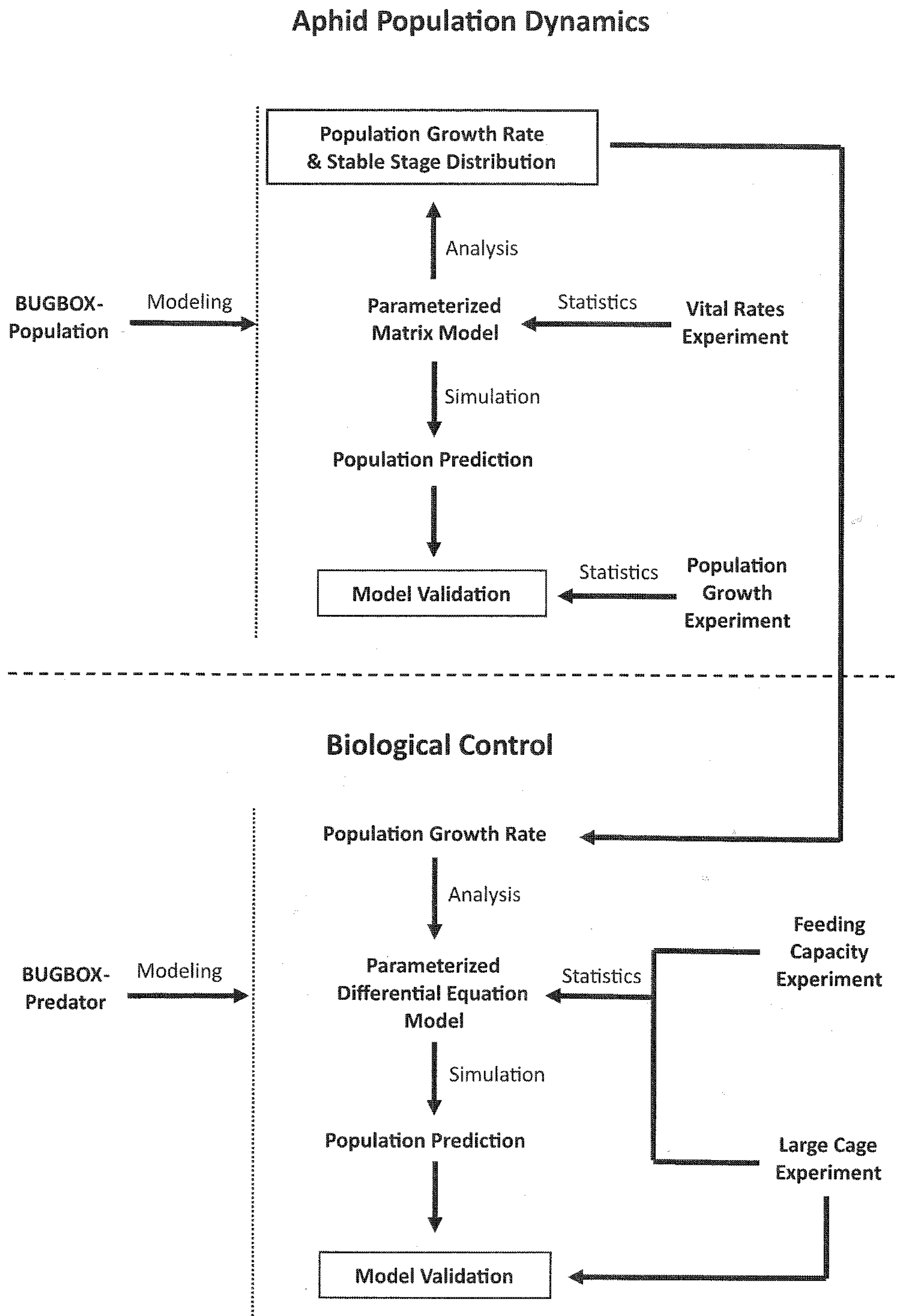

Figure 1. Schematic Representation of the Aphid Population Dynamics and Biological Control Research Plans

time. Of particular interest is the quantity N_t/N_{t-1}, the ratio of the total number of aphids on day t to the total number on day $t-1$. This ratio is sensitive to changes in the population age structure. Given enough time, it should approach a constant value, which represents the asymptotic population growth rate under ideal conditions.

The *population growth experiment* began with one adult aphid on a healthy bean plant in each of several large chiffon-netted aluminum cages (44 × 51 × 61 cm); a minimum of three cages was required. The aphid populations were counted each day for twenty days, with additional plants added as needed to prevent density-dependent mechanisms, such as reduced survival and reproduction, from influencing the population dynamics. The ratios N_t/N_{t-1} were computed from the data and compared with the ratios predicted by the model. This experiment tested the validity of the stage-structured linear model predictions.

10.5.2 Predator-Prey Dynamics

In the *feeding capacity experiment*, the students placed individual first-instar coccinellid larvae in plastic containers with an excess number of aphids. They estimated the maximum consumption in a 24-hour period by comparing the numbers of aphids at the beginning and end of the period. Each day, all remaining aphids were replaced with fresh ones. Students continued feeding the coccinellids until they either died or pupated. A similar experiment was used to determine the maximum consumption rate for adults.

The simplest feasible model for aphid population dynamics in the presence of coccinellids is

$$\frac{dx}{dt} = rx - qy, \tag{2}$$

where x is the total aphid population size, t is the time in days, y is the fixed number of coccinellids, q is the maximum predation per coccinellid per day as determined from the *feeding capacity experiment*, and the relative growth parameter r is given by

$$r = \ln \lambda, \tag{3}$$

where λ is the value at which the N_t/N_{t-1} ratio stabilizes. We tested the model (2) by adding 7–9 adult coccinellids (an average of one predator for each 60–70 aphids) to each cage at day 20 of the *population growth experiment*. The students kept counting daily for an additional 3–4 days. The daily population totals showed that the model (2) significantly overestimated the impact of the coccinellids because it does not incorporate the effect of depletion on the searching efficiency (longer search times are needed to find prey when prey density is low). A better model, using the Holling type II functional response (Holling, 1959), is

$$\frac{dx}{dt} = rx - \frac{qyx}{a + x}. \tag{4}$$

The extra parameter a, called the *semi-saturation parameter*, represents the population size at which the capture rate per predator is one half of its asymptotic maximum. In principle, we could fit a from the additional *population growth experiment* data by using nonlinear regression analysis. In practice, this was difficult to accomplish because x represents the population density rather than the actual population size. The population density is the population size divided by an appropriate measure of the habitat size. If habitat size were the volume of the cage, it would be possible to convert population counts into population densities; however, habitat size should be based on the plant surface area, which cannot easily be estimated.

10.5.3 Research Results

Each time we taught the course, we had excellent results for the aphid population dynamics component. With an initial population of one adult and no nymphs, the N_t/N_{t-1} ratio starts high. It decreases for about eight days while the population of nymphs continues to increase. Once the first nymphs mature, the proportion of reproducing adults increases, leading to an increase in the N_t/N_{t-1} ratio. It takes about two weeks of diminishing oscillations for the N_t/N_{t-1} ratio to stabilize, with the stable value very close to that predicted by the model.

Results for the *feeding capacity experiment* were mixed. Our first supply of coccinellids was infested with a parasitoid, so we got no results at all. Generally, the feeding rate increases with larval age, but with a high degree of variability. The adult feeding rate experiment showed an even larger variation among individuals. The addition of adult coccinellids to the *large cage experiment* never yielded results that agreed with either model (2) or model (4), indicating that neither is adequate.

10.6 Student Work in and Out of Class

Because we wanted to provide a research experience for students, we would have liked to have them spend all their work time on laboratory work, statistical analysis, mathematical modeling, computer simulation, and documentation.

Our course focused on these activities, but it also included activities needed to teach students the scientific background, statistical methods, mathematical models and techniques, computer programming, and scientific writing. Our class met formally for two hours on each of twenty week days (ten hours in the laboratory, four hours in biology class, eighteen hours in mathematics class, seven hours in writing class, and one hour for assessment). Outside of class, the students read biology literature; did homework, data analysis, and writing; and took turns collecting data on weekends. The class met informally in the final week, with the students working on their papers. Altogether, we expected the students to work approximately thirty hours per week for each of the five weeks, which is roughly equivalent to the workload of a 3-credit course.

10.6.1 Laboratory Class

The instructor provided the experimental design and taught the laboratory skills; the students set up the experiments and collected the data. Each student took a turn at each of the experiments, with half of the students doing laboratory work in any given day. The laboratory class became routine after the first few days of intensive instruction.

10.6.2 Biology Class

The first hour of the course consisted of a PowerPoint lecture by the biology instructor on the biology of aphids and coccinellids. The remaining three hours were used for discussion of six research and survey papers on biological pest control (Messing and Wright, 2006), aphid ecology (Hutchinson and Hogg, 1984; Sandstrom, 1996), coccinellid ecology (Obrycki et al., 2001; Wyss et al., 1999), and aphid behavior in the presence of predators (Nelson and Rosenheim, 2006). The students read these outside of class and prepared written summaries prior to a 30-minute classroom discussion with the biology instructor.

10.6.3 Mathematics Class

The students met with the mathematics instructor for one hour on each day of the first four weeks to learn the quantitative material of the course. There were three largely independent topics:

1. Mathematical models of predation, including the simple linear functional response and the Holling type II saturation response (Holling, 1959).
2. The mathematical concepts, analytical techniques, statistical analysis of laboratory data, and computer simulation for stage-structured discrete linear models (1).
3. Derivation and phase line analysis (Brauer and Castillo-Chavez, 2001) of the differential equation models (2) and (3).

10.6.4 Writing Class

Rather than giving the students a style guide for their research paper, we expected them to develop their own. This was done in the writing class with genre analysis. We began by asking the students to look for common features in the assigned articles from the course reading packet. Then we discussed scientific writing conventions and how the students were to use these in their writing. In this way, the students discovered the correct style for scientific writing rather than having it imposed as a set of rules. By the time the genre analysis was finished, the students were already beginning to write their papers. Remaining writing class sessions were used for peer responses. We asked the students to bring a portion of their writing along with author's notes (brief reflective statements about their writing that places the piece in the writing process and guides peer or instructor responses). Pairs of students then exchanged papers and responded to each other's writing as guided by the author's notes. In this way, the students were able to focus their feedback on those aspects of writing that their partners wanted to improve.

10.6.5 Mathematics Paper

The mathematics paper was on the derivation of the Holling type II functional response from data the students collected from a virtual laboratory experiment (see below). It consisted of an introduction, experimental methods and results sections, a mathematical modeling section that presented the derivation of the model in their own words, and a discussion section that described the success of the model in fitting the data and identified model assumptions that are not satisfied in the real biological system. We collected these short papers at the end of the second week, responded to them quickly, and had the students revise them.

10.6.6 Research Paper

The research paper was the culmination of the course, but writing began at the end of the second week. All the writing was done outside of class, with concentrated editing in the writing class. The students wrote the paper section by section, beginning with the experimental methods section. Each section had due dates for a first draft and a revised draft, and the final paper was due on the last day of class. The format for the paper was not specified by the instructors, but developed by the students in their writing class. The instructor helped the students discover appropriate scientific conventions for ecology papers with mixed experimental and mathematics content.

10.6.7 Homework

Most of the work the students did outside of class was directly related to their research project. The data analysis started in the mathematics class and was completed outside of class. Both the research paper and the mathematics paper were written entirely outside of class. The biological readings were done outside of class, and there was a small amount of mathematics homework necessary for understanding the mathematical methods used in the research.

10.7 Pedagogical Challenges

10.7.1 Teaching Biology

The biggest challenge in designing the biology component of the course was to find a meaningful interdisciplinary research project that could be completed within five weeks. First, we needed to find a topic students would recognize as important after only a single introductory lecture because the experiments had to start on the first day of the course. Second, we wanted an empirical model that would allow students to collect all necessary data within four weeks, allowing the final week for data analysis and presentation of the results. Third, the experimental procedures had to be sufficiently simple for students to carry out after a minimal training period, with additional instruction as needed. Fourth, the experiments had to provide data that could be incorporated into mathematical models (providing all required parameter estimates). Fifth, we wanted to find an ecological topic where we knew predictions were likely to match observations. These requirements prohibited us from creating a novel research project that could be published; rather we used aspects of Dr. Tenhumberg's published research (Tenhumberg, 1995; Tenhumberg, 2004; Tenhumberg et al., 2009; Tenhumberg, 2010).

We framed our research project in the general theme of biological pest control, a topic that our mostly rural students could immediately appreciate as important. We specifically wanted to do demographic research that would predict pest population dynamics. We chose aphids as a model species because of their short generation time (approximately 2–3 aphid generations coexist on a single plant in the field); this makes them a perfect study system for the laboratory. Aphids have distinct life history stages that make them ideally suited for a stage-structured modeling approach. Furthermore, aphids are sufficiently large that no extra equipment is required for population counts. Lastly, based on Dr. Tenhumberg's research (Tenhumberg, et al., 2009; Tenhumberg, 2010), we knew that the asymptotic population growth rate of *A. pisum* predicted from a matrix model would match the observed population growth rate in the laboratory. We did not have similar assurances for the predator-prey model, and the match of prediction to observation was not very good. It was instructive for the students to see that the success of mathematical modeling depends heavily on how adequately the model assumptions describe the biological system. Predator behavior is more complicated than what we could incorporate into our model.

To understand the challenges of biological control fully, students need an understanding of the natural history of pest and biological control organisms, the large spatial and temporal variation of life history traits between populations, and population dynamics. Delivering this much material was challenging. First, teaching the quantitative course material was time consuming, leaving little time for presenting the ecological background knowledge. Second, we had to use primary literature since there was no textbook available. Reading and digesting primary literature is hard for lower-division students; in particular, most of the papers include specialized vocabulary and statistical methods that are inaccessible to students with no prior statistics course. Older papers are generally easier to understand, but they tend to use outdated experimental methods, such as extremely small sample sizes. We selected recent papers and encouraged the students to focus on the main results and general conclusions, skipping over any complicated details. With the help of the biology instructor, the students acquired the most important content of the papers but were generally dissatisfied with only partially understanding the papers.

10.7.2 Teaching Mathematics and Mathematical Modeling

Our philosophical principle that theoretical work should be motivated by an ecological question has the benefit of showing the value of mathematics, but it poses a pedagogical problem. Theory begins with observation, but full observation of the aphid life cycle requires most of four weeks and we needed to start the theoretical work much earlier. We solved this problem by providing means for collecting simulated experimental data to motivate the theory when needed. The BUGBOX-predator computer applet (Ledder, 2007b) simulates interaction between a moving predator and stationary prey. Experiments performed with this applet yield a data set with which to examine the influence of handling time on predation rates and derive the Holling type II functional response model (Ledder, 2008). The BUGBOX-population computer applet (Ledder, 2007a) simulates stage-structured population growth for a virtual insect species with a simplified life history. The students derived a stage-structured model and obtained numerical values for the parameters by collecting data corresponding to the real aphid data from the *vital rates experiment*. We investigated the model with a simple simulation that the students wrote in R (R Development Core Team 2012). This was the first computer programming experience for nearly all of the students and nearly all found it difficult. We wrote the program together in class, line by line with each line explained, over the course of an hour. The crucial feature of our simulation is the chosen output format: a graph of N_t/N_{t-1}, where N is the total population. This graph led the students to discover that the growth rate converges to a fixed value independent of initial conditions, which in turn leads to the eigenvalue problem of matrix algebra (Ledder, 2008).

Thus far, all mathematical work was done from first principles, rather than using out of the box methods. For the statistical work and mathematical analysis of the real data, we used a combination of basic statistics instruction and instructor-supplied R scripts. We used R rather than Excel because of the easy portability of computer program statements from one program to the next.

Our final three days of work in mathematics class consisted of a very fast introduction to first-order differential equation models. Since we did not require any calculus background for the course, we restricted ourselves to graphical and numerical methods for autonomous scalar differential equations. We constructed the models (2) and (4) in stages:

1. We introduced the derivative as the slope of a tangent line and as the value approached by the secant slope $\Delta x/\Delta t$ as Δt becomes arbitrarily small.
2. We examined the linear model for unrestricted population growth without predators, asserting the exponential solution formula without proof. We used this solution to calculate the rate constant r from the dominant eigenvalue λ_1.
3. We obtained the models (2) and (4) by adding a predation model to the linear growth model.

We then studied the models (2) and (4) using phase line arguments and computer simulations written by Dr. Ledder.

10.7.3 Teaching Scientific Writing

The two major challenges in teaching scientific writing in a mathematics or science course are limits of time and instructor expertise. Students entered the course with widely disparate writing ability; even the best had little, if any, prior experience in scientific writing. Lab reports written in high school are more often a source of misconceptions than a valuable writing experience. Time for writing had to come at the expense of time that could instead be spent on mathematics or science content and is likely to be undervalued by instructors who are content experts but who are not trained teachers of writing (teaching of writing being a distinct skill from writing itself). We approached this problem in 2007 by hiring Mr. Adams as a writing specialist; after observing the 2007 writing classes, Dr. Ledder taught the writing classes in 2008 and 2009. The graduate students who taught the biology and mathematics components in 2010 also taught the writing.

Because most of our students were generally good writers already, we did not need to spend time on remedial or basic writing instruction, but we did need to teach students the expectations for scientific writing. Once the students had learned the appropriate stylistic conventions of scientific writing, the quality of their scientific writing improved considerably. We have learned that lecturing about writing styles does not improve student writing; it is much better to have students read well-written scientific papers and identify the conventions themselves. After a classroom discussion, most of the students were able to articulate the elements of scientific writing style.

Improvement in writing comes largely from directed revision, which means that someone has to read and comment on drafts of student work. The use of author's notes to direct review saves time by focusing the reviewer's attention on the points the writer has targeted for improvement. Peer review significantly lessens the time commitment for each instructor and can be done during writing class. In our experience, the willingness of students to accept suggestions from peers makes up for their decreased editing ability compared to instructors. The instructors were available for review of any work voluntarily submitted by email. The combination of peer response, optional submission to an instructor, and author's notes stresses student ownership of their writing, which we believe leads to better results.

Many of the students were surprised that they were not given class time for their writing, a concern we attributed to their being used to the high school setting and which helps explain the limited effort many freshmen put into their writing for mathematics and science courses.

10.8 Assessment

10.8.1 Outcomes

The principal outcomes of the course were the scholarly products, which originally consisted of a group poster and a group research paper, but became an individual research paper. A typical student paper was written in a style approximating professional academic style. The introduction indicated a good understanding of the purpose and context of the research. The experimental methods descriptions were good, although not as careful as in a professional paper. The results section included good descriptions and graphical displays of data and also indicated some understanding of the statistical work, the mathematical models, and the interplay between the models and the experimental data. The short conclusion section (rather than the complete discussion section of a professional paper) stated appropriate conclusions restricted to what could justifiably be claimed from the experimental work. We judged this typical paper worthy of an A- grade; there were always weaker papers, as well as A+ papers from students who we judged to be potential PhD students. Several such students are in PhD programs now or have already finished. Several research posters, all of which we evaluated as A work or better, can be found on the RUTE web page (University of Nebraska-Lincoln, 2012); we welcome feedback on the quality of the student work in the posters. One of the posters was presented at a conference at the National Academy of Sciences in 2010, alongside posters of research projects done by advanced undergraduates.

Our one traditional assessment was a quiz on stage-structured models, including modeling, simulation, and eigenvalue analysis. The median quiz score in 2007 was 76%, which we judged to be a B given the difficulty of the questions. Those students who did poorly were given a second chance with a make-up quiz, which was substantially different from the first quiz but comparable in difficulty. All the students who took the second quiz showed significant improvement, increasing the median to 90%. With improvements in teaching, we achieved a median of 88% on the quiz in subsequent years without a make-up.

10.8.2 Feedback

Student feedback was illicited by two questionnaires, one for attitudes and beliefs and the other for content. We used categorical responses (Strongly Disagree, Disagree, Neutral, Agree, Strongly Agree) for all items, supplemented by written responses on questions about the value of the writing class. We computed a numerical score in the usual way, with scores of -2, -1, 0, 1, and 2 for the responses from Strongly Disagree to Strongly Agree. The key results appear in Table 1.

Statement	Score
1. Math is a worthwhile and necessary subject for biologists.	1.57
2. I don't need to know the math when I can do a problem using a computer.	0.86
3. Mathematical models help me to think about biology.	0.43
4. I learned a lot of mathematical modeling from the course.	1.29
5. I learned a lot from writing the research paper.	1.29
6. I learned a lot from writing the mathematics paper.	1.29
7. Before this program, I was considering a research career.	0.07
8. I am now considering a research career.	0.57

Table 1. Average student agreement on some subjective statements, on a scale from -2 for complete disagreement to 2 for complete agreement.

The first item indicates our success in helping the students experience the synergy between biology and mathematics. An anecdote shows the extent to which this lesson took hold. Towards the end of our 2007 class, two of the students went through advising and registration procedures at the small college they were enrolled in for Fall 2007. Their academic advisor told them that biology students should take only the minimum number of mathematics courses. We asked them what they did with that information; they replied that "of course we went to talk to a different advisor!" Both students marveled at how they could get such ignorant advice from someone who should know better.

The broad agreement that getting an answer by computer means not having to understand the mathematics seems inconsistent with the recognition of the importance of mathematics in biology, but the weak response to item 3 suggests that many of the students saw mathematics as a tool rather than a way of thinking. The agreement is less than what we would have liked, but more than it would have been without our course.

Item 4 was one of a number of similar items; responses for learning of biology, mathematics, statistics, and computing obtained average scores of 0.86 to 1.14.

Based on items 5 and 6 and the written comments, our students judged the writing assignments to have significant value beyond the value of the work on which they were reporting. That is, having to write about their work contributed to improving their writing and also to their learning of science and mathematics.

10.9 Recommendations

We believe that courses such as ours can be successful at other institutions. Some features of the course are universal and some are local. Our design principles are essential, with the possible exception of item 6. Any course intended to introduce research skills must be based on a coherent experiment plan, must integrate the components of that plan with the course material and structure, and must require serious scientific writing. The mathematics part of an interdisciplinary course should be taught from a modeling perspective (Ledder, 2008), and scientific writing should be taught explicitly.

Some aspects of our program are not easily duplicated because of the level of resources that was available. During the period of NSF funding, *RUTE* students received a $1500 stipend for the five-week program. We also paid for room and board in a university dorm and some travel expenses for students coming from more than 100 miles away, so we could create a summer program for students from a variety of institutions. With the funding gone, we considered running the course as a Freshman Honors course during the academic year. Because data needs to be collected every day, it would have been tricky to manage the laboratory work with an academic year schedule, but we do not believe this difficulty to be insurmountable. Every student does not need to work in the laboratory every day. The most serious resource problems are the need for a dedicated laboratory space and the necessity for having two instructors, each of whom needs to have the course count as part of their teaching load. Teaching as one half of an interdisciplinary team requires more time and energy than teaching one half of a standard course. We did not give serious consideration to solving the staffing problem because of the impossibility of finding laboratory space.

The choice of research topic for a freshman-level research course needs to be based on local facilities and expertise. There are many topics that could be used for laboratory research conducted by beginning undergraduates, given sufficient instruction in biological principles and laboratory methods. Other population dynamics projects would have similar mathematical requirements, and other areas of biology may have mathematical models that could be presented at the introductory level.

We hope that other institutions will try interdisciplinary research courses, and we are interested to hear about faculty experiences with them.

One other issue merits mention, although it is beyond the scope of what the creators of a single college course can do. We believe that students who are interested in mathematics primarily because of its value in theoretical science learn more mathematics when it is presented in a modeling context than when it is presented as mathematical theory. Many topics, such as the matrix eigenvalue problem, can be taught in a scientific context rather than from a strictly mathematical point of view (Ledder, 2008). It remains difficult to teach mathematics in a modeling context to students who have not done any modeling before; this problem could be addressed in part by incorporating parameters into mathematics problems beginning with secondary school mathematics. Early experience with parameters would also help prepare mathematics majors for the mathematical abstraction they need in advanced mathematics courses.

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