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EXPERIMENTS

Observing and Quantifying Predator-avoidance Behavior: Habitat Shifts by Snails in Response to Predator Cues

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Students looking for snails at the end of the experiment.
Photograph by T.W. Stewart.

Table of Contents:

CITATION
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ABSTRACT

Natural selection promotes evolution of predator-detection mechanisms and escape behaviors in species lacking physical or chemical defenses. This 3-5 hour exercise uses aquatic snails to illustrate predator-avoidance strategies used by many species of small animals. A laboratory experiment is conducted to test student-generated hypotheses about how snails might detect predators through chemical cues, and how they may respond to those cues (e.g., by increasing refuge use through crawling into structurally-complex habitat or out of water) to avoid being eaten. The actual experimental design should be determined from discussions among students and the course instructor. However, one experimental plan that I have used successfully is described here. Students record the numbers of snails that are visible in underwater aquarium habitats, and therefore vulnerable to fish predation, before and after adding water with (predator-cue treatment) or without (predator-free treatment) chemical cues originating from crushed snails or fish. Statistical tests are then used to determine if cues induced increased refuge use that should enhance snail survivorship.

Class Time

The experiment described here can be introduced and completed in 1-3 hours. Approximately two additional hours are needed to complete statistical analysis and discuss results. Time required for the experiment is affected by chemical cue concentration in water added to aquaria. Expose snails to high chemical cue concentrations to elicit a rapid response and reduce time needed to complete the experiment. Mechanisms for accomplishing this are described in the Notes to Faculty (see Comments on Challenges to Anticipate and Solve: 3. Generating snail responses to predator cues).

Outside of Class Time

The instructor will need 1-2 hours to set up the experiment. Additional time is required to obtain and care for animals. Biology majors need 6-10 hours outside of class to read background literature and complete a paper based on experimental results. Non-science majors need 1-2 hours at the conclusion of the experiment to complete calculations and answer questions related to the experiment.

Student Products

Biology majors write a short paper using the format of a peer-reviewed scientific journal article. Non-science majors are evaluated on the quality of answers to specific questions and the accuracy of calculations and interpretations of results from statistical analyses. Methodological details of assessing student performance in this activity are described in the Description and Notes to Faculty sections below.

Setting

The study is conducted in the classroom/laboratory setting. Snails needed for this experiment can usually be collected from a local pond or lake. Fish can also be obtained from ponds or lakes, or from a hatchery. Animals used in this experiment survive well in laboratory aquaria, and breeding snail colonies are easily established on a diet of goldfish flake food.

Course Context

I use this experiment in a general ecology course for biology majors, and a general biology course for non-science majors. Class sizes range from 10-25 students.

Institution

I have used this exercise while teaching at a large university (Bowling Green State University) and a small four-year undergraduate institution (Longwood University).

Transferability

This activity is very adaptable to a variety of educational scales. I have conducted the experiment in freshman-level non-science majors courses in biology and environmental science, and used the experiment to illustrate components of experimental design and statistical analysis in a graduate-level course in scientific methods. Because it relies on live animals and collection and analysis of real data, this experiment should also stimulate interest in ecology among junior high and high school students, as well as students at lower educational levels. Snails used in this experiment occur almost worldwide in a variety of freshwater ecosystems, so this experiment can be conducted in a variety of geographic regions at any time of year. It is ideal for students with physical disabilities.

Acknowledgements
Andy Turner's (Clarion University) work on predator-avoidance behavior in freshwater snails was a primary inspiration for scholarship that culminated in this experiment. I thank Jeff Miner, Rex Lowe (Bowling Green State University), James Haynes (SUNY Brockport), and Rob Dillon (College of Charleston) for supporting my interest in freshwater snail ecology. I also thank Charlene Waggoner (Bowling Green State University) who encouraged me to develop this teaching activity. Comments by Kathy Winnett-Murray and two anonymous reviewers greatly improved the presentation of this laboratory activity.

A modified version of this experiment was presented at the 21st workshop/conference of the Association for Biology Laboratory Education (ABLE) at the University of Nebraska-Lincoln, June 1-5, 1999 and published in ABLE's *Tested Studies for Laboratory Teaching*, Volume 21 (Stewart and Waggoner 2000, http://www.zoo.utoronto.ca/able/volumes/volume21.htm).

SYNOPSIS

Principal Ecological Question Addressed

What physiological, physical, or behavioral characteristics enable individual prey to avoid being eaten by a predator? What evolutionary forces might have caused these predator-avoidance traits to emerge and become common in prey populations? Can predator-avoidance adaptations actually contribute to long-term survival of a predator population, as well as persistence of prey and other species in the ecosystem? How might habitat features of an ecosystem (e.g., availability of structurally-complex habitat) influence predation rates and predator-avoidance adaptations of prey? Can human-generated habitat destruction influence predator-prey interactions, and if so, what are the likely effects on prey and predator populations and other living and nonliving ecosystem components?

What Happens

Through a lecture and class discussion, students are provided basic biological and ecological background information pertaining to characteristics of common predators (fish) and prey (snails) of aquatic ecosystems. Additionally, I introduce students to basic elements of experimental design (e.g., hypotheses, replication, standardization, use of statistics to make objective conclusions). Students are then challenged to design an experiment that answers the following questions:

1. Can snails use chemical cues to detect threats to their survival in the form of shell-crushing predators?
2. Do snails then move to habitats that provide refuges from these large predators?

Students are made aware of available resources and time-limitations, and then divide into small groups to design an experiment. Each group describes their proposal to the entire class. Using a guided-inquiry approach, I attempt to incorporate at least one component of each group’s design into a common experimental plan that the entire class will follow. A typical scenario (and one that I describe here in detail) would include students observing and quantifying changes in habitat use of snails exposed to chemical cues that signal the immediate presence of predatory fishes. Using aquaria containing equal quantities of dechlorinated water, structurally-complex habitat (e.g., stones, ceramic tiles), and snails, students first record numbers of snails that are visible in underwater habitats, including on aquarium walls and upper surfaces of stones and tiles where they would be vulnerable to fish predation. Aquaria are then randomly assigned to predator-free or predator-cue treatments (n = 5 replicates or aquaria per treatment). Water in aquaria of the predator-cue treatment is replaced with water containing chemical cues produced by crushed snails or fish. Water in predator-free treatment aquaria is replaced by dechlorinated water lacking these cues. Snails that detect and respond to cues will increase movement rates until finding a possible refuge from predation. Once snail activity in the predator-cue treatment slows or ceases, students again record numbers of "vulnerable" snails (i.e., snails visible on aquarium walls and upper surfaces of stones and tiles). Simple statistical tests are used to determine if chemical cues stimulated increased use of habitats that provide refuges from predators, including undersides of tiles, interstitial spaces between stones, or aquarium walls above the water line.

Experiment Objectives

1. Use live animals to illustrate important ecological/evolutionary topics, including natural selection, predator-prey interactions, animal behavior, and habitat heterogeneity,
2. Demonstrate the complex nature of species interactions in ecosystems, including rarely observed mechanisms that enable populations of small organisms to coexist with predators,
3. Provide an example of a study that includes essential experimental design components (independent and dependent variables, experimental and control treatments, replication, standardization),
4. Enhance skills and confidence in using statistical analysis techniques to answer research questions objectively,

5. Generate increased student interest in ecology, as well as appreciation of snails and other small organisms that are ecologically important yet poorly understood.

Equipment/Logistics Required

Equipment needed to collect animals and maintain them in captivity

- Dipnets
- Sorting pans (e.g., plastic dishpans)
- Plastic buckets
- Aquaria
- Dechlorinated water
- Aeration system (air pumps, air tubing, airstones)
- Siphon (to clean aquaria)
- Fish food (e.g., goldfish flake food)
- Fishing pole and earthworms, or seine (required only if fish are desired or needed to produce chemical cue)

Equipment needed for the experiment (for a class of 10-25 students)

- Ten 19-L (5-gallon) aquaria
- Two larger aquaria, at least 38-L (10-gallon) capacity
- 300 L of dechlorinated water
- 10 L of patio stones (approximately 4-5 cm in diameter) and 20 ceramic tiles (15 X 15 X 1 cm), or similar forms and quantities of structurally-complex habitat
- At least 300 physid snails (3-6 mm shell length)
- Molluscivorous fish (e.g., redear or pumpkinseed sunfish; required only if fish are desired or needed to produce chemical cue)
- Ten 2-L containers
- Data tables and worksheets:
  ‘Predator-free Treatment Data Table and Worksheet’
  ‘Predator-cue Treatment Data Table and Worksheet’
- Calculators
- Appropriate table of critical test-statistic values (e.g., t distribution; see Description: Overview of Data Collection and Analysis Methods)

Logistic Requirements

- Lake or pond with physid snails
- Pond, lake, or fish hatchery with redear or pumpkinseed sunfish (required only if fish are desired or needed to generate chemical cue)
- Dechlorinated water or chlorine-neutralizing agent (e.g., Aquasafe water conditioner®)
- Laboratory or classroom space for holding animals and storing aquaria

Summary of What is Due

Biology Majors

Each student writes a short (approximately five double-spaced pages) paper based on the experiment. The paper is written in standard scientific journal style. Students are also graded on completeness of data tables and worksheets and accuracy of calculations.

Non-Science Majors

Each student must complete data tables and worksheets. Additionally, students must submit answers to questions that are intended to evaluate understanding of objectives, results, and applications of the experiment.

Keyword Descriptors

Ecological Topic Keywords: abiotic factors, biotic factors, chemical ecology, community ecology, ecosystems, environmental adaptation, experimental design, feeding strategies, life history, multispecies interactions, population ecology, predation, predator-prey relations, species diversity, species interactions, trophic dynamics

Science Methodological Skills Developed: collecting and presenting data, data analysis, designing experiments, evaluating alternative hypotheses, experimental design, hypothesis generation and testing, identify biotic and abiotic interactions, natural history, quantitative data analysis, scientific writing, statistics, use of primary literature, writing primary research paper

Pedagogical Methods Keywords: background knowledge, cognitive skill levels, guided inquiry, problem-based learning, project-based teaching

DESCRIPTION

Introduction

From an evolutionary perspective, an individual's success, or fitness, is measured by its relative contribution to the gene pool of the next generation (Begon et al. 1996, Krebs 2001). Because reproduction is the only way that an individual contributes its genotype to future generations, natural selection should favor organisms with genetically-determined traits that increase their likelihood of surviving to sexual maturity (Krohne 2001). These adaptive traits should therefore become and remain common in a population or species.

Predation is among the most common causes of pre-reproductive mortality in animals (Begon et al. 1996, Krebs 2001). Consequently, evolutionary forces have produced an impressive variety of predator-avoidance adaptations. Specific adaptations include speed that enables prey to outrun predators, or chemical or physical defenses that make an organism unpalatable or difficult to handle (Riessen 1992, Holzinger and Wink 1996, Lingle 2002). Organisms lacking these defenses must rely on different strategies to avoid being eaten, many of which are unusual and not immediately obvious. For example, snails in the family Physidae are slow-moving, edible, and have thin shells that make them quite vulnerable to predation by fishes and other shell-crushing predators (McCollum et al. 1998, Turner and Montgomery 2003). However, many physids possess a chemosensory system that is used in combination with behavioral strategies to reduce encounters with predators (Covich et al. 1994, Turner and Montgomery 2003). Specifically, many physids recognize the nearby occurrence of fish and other shell-crushing predators through chemical cues produced by crushed snails or the predators themselves, then move to habitats that provide refuges from predators (Stewart et al. 1999, Turner and Montgomery 2003).

Physa acuta (family Physidae), an ideal snail for this experiment.
Photograph by T.W. Stewart.

In this activity, you will gain an improved understanding of the complex ways that predators and prey interact in ecosystems, and how predator-avoidance behaviors help ensure coexistence of prey and predator populations and persistence of entire biological communities. You will also increase your familiarity with essential components of experimental design, and will use statistical analysis techniques to answer research questions objectively.

Through assigned readings (Covich et al. 1994, DeWitt et al. 1999, Stewart et al. 1999, McCarthy and Dickey 2002, Turner and Montgomery 2003), lectures, and class discussions, you will be provided basic biological and ecological background information pertaining to characteristics of common predators (fish) and prey (snails) of aquatic ecosystems. Additionally, your instructor will introduce basic elements of experimental design (hypotheses, replication, standardization, use of statistics to make objective conclusions), and show you available resources (prey species, predator species, stones, aquaria) that can be used in the experiment.

After this laboratory activity and relevant background information are introduced, you and some classmates will form a small group to design an experiment that can answer the questions:

1. Can snails use chemical cues to detect threats to their survival in the form of shell-crushing predators?
2. Do snails then move to habitats that provide refuges from these large predators?

After a pre-determined period of time, your instructor will ask each group to describe its proposed experiment to the entire class. Based on group responses, your instructor will devise a common experimental plan that the entire class will follow. All members of the class will be responsible for collecting, analyzing, and interpreting data that are required to answer research questions listed above.

Materials and Methods

Study Site

This experiment will be conducted in the laboratory or classroom. Snails used in the experiment were collected from the wild, or are captive-reared offspring of wild snails. Fish, if used, were captured from the wild or obtained from a fish hatchery.

Overview of Data Collection and Analysis Methods

Form a small group with other students. Together design an experiment to answer the questions:

1. Can snails use chemical cues to detect threats to their survival in the form of shell-crushing predators?
2. Do snails then move to habitats that provide refuges from these large predators?

Be prepared to describe components of your experiment's design to the entire class. Together, we will then design a single experiment that incorporates experimental design components of various student groups.

For example, one possible experimental design consists of two treatment levels, hereafter referred to as predator-cue and predator-free treatments. In the predator-cue treatment, you would record numbers of snails occupying aquarium habitats where they are vulnerable to fish before and after adding water containing chemical cues produced by fish or crushed snails. In the predator-free treatment, numbers of vulnerable snails would also be recorded before and after adding water. However, water added to aquaria of the predator-free treatment would not contain chemical cues produced by crushed snails or fish.

Below I describe data collection and analysis methods for the example experimental design described in the previous paragraph. You and your instructor might need to modify these methods to fit the experimental design used by your class.

Setting Up the Experiment

The following steps should be taken at least 24 hours before beginning the experiment. Therefore, your instructor might have completed these procedures for you.

1. Place ten 19-L aquaria at evenly-spaced locations throughout the classroom. Aquaria should be distributed so that 2-3 students can observe activity in each aquarium. Fill each aquarium with dechlorinated water, but leave a 5-cm space between the water line and the top of the aquarium. If dechlorinated water is unavailable and tap water must be used, you will need to add chlorine-neutralizing solution (e.g., Aquasafe water conditioner®) to each aquarium because chlorine kills snails and other aquatic animals.
2. Construct underwater refuges for snails by arranging patio stones, or similar objects, in a pile on each aquarium floor. The instructor might also provide ceramic tiles to be placed on top of the pile of stones. Each aquarium must contain the same volume of stones (e.g., 1 L), tiles (e.g., 2 tiles; 15 X 15 X 1 cm dimensions), or other objects.

3. Carefully place 20 snails in each aquarium. Snails should have shell lengths between 3 and 6 mm. Shell length is measured from the spire tip (apex of coil) to the extreme tip of the aperture (shell opening). Snails in the 3-6 mm size range are large enough for you to see and small enough for many fish to eat.

A snail (Physa acuta) from the family Physidae.
Distinctive features of physids include a thin, coiled shell with a high spire, and an aperture (shell opening) that occurs on the left side of the shell.
Photograph by R.T. Dillon, Jr.

4. Fill two additional large aquaria (e.g., 38-L capacity) with dechlorinated water. One of these aquaria will be the source of chemical cues for aquaria constituting the "predator-cue" treatment of the experiment. Water in the second 38-L aquarium will lack these chemical signals, and this water will later be added to aquaria in the "predator-free" treatment of the experiment. Aerate water using a pump, airline tubing, and airstones.
5. If fish will be used to generate chemical cues in the predator-cue treatment, release healthy fish into one of the 38-L aquaria. Fish placed in this aquarium should be individuals that have been previously observed to feed on snails. Your instructor will have already determined sizes and numbers of fish needed in this aquarium from preliminary trials that generated strong chemical cues. Add nothing to the second 38-L aquarium, or to either aquarium, if fish will not be used in this experiment.

A pumpkinseed sunfish (Lepomis gibbosus). Pumpkinseed and redear sunfish (Lepomis microlophus) prey on physid snails and generate chemical cues that induce habitat shifts in these snails.
Photograph by J.M. Haynes.

The following steps should be taken 10-30 minutes before the experiment begins. Students should be present and participating in these procedures.

6. If fish are not used in this experiment, simulate fish predation by crushing a large number of snails between your fingers, and placing them in one of the 38-L aquaria present in the classroom. If fish occur in one of the 38-L aquaria, feed them a large number of snails. Your instructor will predetermine the quantity of snails that must be crushed or fed to fish to generate a strong chemical signal. Again, add nothing to the second 38-L aquarium.
7. Divide into 10 groups of approximately equal numbers of students. Each group will be assigned a number from 1-10, and will be responsible for managing one 19-L aquarium containing living snails and reporting data from it. The five odd-numbered student groups will manage aquaria of the predator-free treatment, and the five even-numbered groups are assigned to aquaria of the predator-cue treatment.
8. Examine snails in your aquarium. Note snail behaviors, including crawling speed. If any dead snails are observed, remove and replace them with living snails of similar sizes.

The Experiment

9. At the instructor's signal, count initial numbers of snails in your aquarium that occupy habitats where they would be vulnerable to fish. Snails are considered "vulnerable" if you can see them on aquarium walls or floors, or upper surfaces of stones or tiles where visually-oriented fish could easily find and eat them. In contrast, snails inhabiting undersides of tiles, interstitial spaces between stones, or occurring above the water line on aquarium walls are considered "invulnerable" or inaccessible to fish. In other words, all non-visible snails, and those that have left the water, should be considered invulnerable. Report the initial number of vulnerable snails (X1) in your aquarium to the instructor, who will use data from all student groups to help you complete the second column of the predator-free and predator-cue treatment data tables located below.

Students looking for snails at the end of the experiment.
Photograph by T.W. Stewart.

Complete Data Tables and Worksheets

Follow steps 10-25 below and use these handouts:

Predator-free Treatment Data Table and Worksheet
Predator-cue Treatment Data Table and Worksheet

10. After initial numbers of vulnerable snails are recorded, remove and discard 2 L of water from your aquarium. Remove water carefully to avoid damaging or disturbing snails. Students managing 19-L aquaria of the predator-cue treatment will now transfer 2 L of water from the 38-L aquarium

containing fish or crushed snails to their aquarium. Students overseeing aquaria of the predator-free treatment will transfer 2 L of water from the 38-L aquarium without fish or crushed snails to their 19-L aquarium. Depending on results from preliminary trials conducted by your instructor, it might be necessary to repeat this procedure one or more times to produce a sufficient chemical cue concentration in the predator-cue treatment.

11. After completing water transfers, observe behavioral responses of snails in your own aquarium, as well as aquaria under the care of other student groups. Do you recognize any behavioral differences among snails in predator-free and predator-cue treatments?
12. Using scratch paper, record the number of vulnerable snails in your own aquarium at five-minute intervals. Report these numbers to your instructor. As snails in the predator-cue treatment begin to detect and respond to elevated predation risk, numbers of vulnerable snails in these aquaria should decline. When there are no further changes in numbers of vulnerable snails in aquaria of the predator-cue treatment, your instructor will give the signal to end the experiment. Report the final number of vulnerable snails (X2) to the instructor, and record class results in the third column of the data tables provided on the handouts.

Data Analysis

Now complete data tables and worksheets, and use paired-sample t tests (your class might use a different statistical test that is preferred by your instructor) to determine if initial and final numbers of vulnerable snails differed in predator-free and predator-cue treatments. Your instructor will assist with calculations and interpreting statistical analysis results. Additionally, if paired-sample t tests are used, you should also work through completed examples available in the Student Data section:

Student Dat Set #1: Previous class data and paired-sample t test results

Procedures described below are adapted from Zar (1999). The box below provides additional infomation on paired t-tests.

From: Zar, J.H. 1999. Biostatistical analysis. 4th edition. Prentice-Hall, Upper Saddle River, NJ.

A paired-sample t test is used to determine the significance of the difference between two sets of paired data. In the experimental design described here, initial and final counts of vulnerable snails in each aquarium within one treatment are paired for the analysis. These pairings are based on our expectation that final counts of vulnerable snails in each aquarium should be affected by initial counts of vulnerable snails in addition to whether or not predator cues were introduced.

Two paired-sample t tests are needed to test our experimental hypothesis that snails detect predator cues, then increase use of refuges from these predators. In the first t test we investigate for differences in initial and final numbers of vulnerable snails in the predator-free treatment. This first test is necessary to rule out physical disturbance associated with water transfer procedures as a cause for shifts in snail habitat use, and to separate this disturbance from chemical-cue effects in the predator-cue treatment. We should not find statistically significant changes in numbers of vulnerable snails in the predator-free treatment. However, in the second paired-sample t test (predator-cue treatment), we should find statistically significant declines in numbers of vulnerable snails following addition of water with chemical cues to aquaria.

As the box above explains, we will need to perform two paired-sample t tests, one for the predator-free treatment and one for the predator-cue treatment. First, use the following procedures to complete the predator-free treatment data table and worksheet, and obtain t test results. We will then use the same procedures to obtain t test results for the predator-cue treatment.

13. In the appropriate space on the predator-free treatment worksheet, enter the number of replicates (i.e., number of student groups or aquaria; n) constituting this treatment.

    Your answer should be "n = 5" if five student groups each managed a separate predator-free aquarium.

14. Calculate difference values (d) for each pair of observations $(d = X1 - X2)$ in the treatment. For each aquarium or student group, subtract the final number of vulnerable snails (third column of data table; X2) from the initial number of vulnerable snails (same row in second column of data table; X1). Enter results in the fourth column of the data table.

    Sum the difference values $(\sum d)$, and enter the result in the final row of the fourth column of the data table.

15. Calculate the mean, or average, difference value $(\bar{d})$ from the difference values (d) present in the fourth column of the data table. Show your work and enter the result in the worksheet.

    $$\bar{d} = \sum d \div n$$

    Where $\sum = sum$

16. Now subtract the mean difference value from each individual difference value.

    $$(d - \bar{d})$$

    Enter these values in the fifth column of the data table.

    The sum of these values, $\sum (d - \bar{d})$, will be 0 if all calculations were done correctly.

17. Square each value in the fifth column of the data table $(d - \bar{d})^2$, and enter results in the sixth column.

    Sum values located in column six, $\sum (d - \bar{d})^2$, and enter the result in the last row of the sixth column.

18. Determine the number of degrees of freedom (DF) in this treatment. This value is equal to the number of replicates (i.e., student groups or aquaria) of this treatment, minus a value of 1. Enter results in the appropriate space on the worksheet.

    $$DF = n - 1$$

19. Now use results from previous calculations to determine the variance of difference values $(s^2 d)$.

    $$s^2 d = \sum (d - \bar{d})^2 \div DF$$

20. Now calculate sd, the standard deviation of difference values.

    $$sd = \sqrt{s^2 d}$$

21. Calculate $s\bar{d}$, the standard error of the mean difference value.

$$s\bar{d} = sd \div \sqrt{n}$$

22. Finally, calculate the t statistic (t) for this treatment.

$$t = \bar{d} \div s\bar{d}$$

23. To determine if initial and final numbers of vulnerable snails differed, we must compare the t statistic calculated above to a critical t value. The appropriate critical t value for any test is based on 1) the significance level chosen (α), or accepted probability of erroneously concluding that paired samples differ when they actually do not (in biological investigations, this is usually α = 0.05), 2) the number of degrees of freedom in the data set, and 3) whether a one- or two-tailed test is to be used. Critical t values for one- and two-tailed tests and a 0.05 significance level are available in the table below. To identify the appropriate critical value for a paired-sample t test, first identify the row in the table below that corresponds to the number of degrees of freedom you previously calculated (DF = n - 1). Then read across the table to find the appropriate critical t value, dependent on whether you conducted a one- or two-tailed test. The decision to use a one- or two-tailed test should be made before conducting the experiment, and is based on student hypotheses of snail responses to predator cues. For example, a one-tailed test should be used if students predicted fewer vulnerable snails to occur in the predator-cue treatment at the conclusion of the experiment than at the beginning of the experiment (or vice versa). Alternatively, a two-tailed test should be used if students hypothesized that initial and final numbers of vulnerable snails would differ, but that snails could either increase or reduce their refuge use after exposure to predator cues (e.g., students might reason that refuge use could decline after exposure to chemical cues due to snail flight responses). If you have 4 degrees of freedom, critical t values are 2.13 and 2.78 for a one- and two-tailed test, respectively. Record your critical t value on the worksheet.

Some critical values of the t distribution (from Zar 1999)

Degrees of freedom (DF)	**Critical t value (α = 0.05; one-tailed)**	**Critical t value (α = 0.05; two-tailed)**
1	6.31	12.71
2	2.92	4.30
3	2.35	3.18
4	2.13	2.78
5	2.02	2.57
6	1.94	2.45
7	1.90	2.37
8	1.86	2.31
9	1.83	2.26
10	1.81	2.23

24. The absolute value of the calculated t statistic must equal or exceed the critical t value for you to conclude that there is a difference in initial and final numbers of vulnerable snails. What do you conclude based on comparison of the t statistic and critical t value, and an examination of the raw data you recorded? Write your response on the worksheet.

25. Repeat steps 13-24 to complete the data table and worksheet for the predator-cue treatment.

Questions for Further Thought and Discussion

1. Describe snail behaviors in each treatment used in this experiment. Did you observe any changes in behavior after completing water transfers from the large aquarium with or without fish or crushed snails? Explain.
2. What do you conclude from results of this experiment? For example, was the experimental hypothesis that snails use chemical cues to detect predators and subsequently increase use of refuges supported? How did you arrive at your answer?
3. What questions emerged from this study? In other words, what additional questions would you address in a future experiment focusing on predator-prey interactions between snails, fish, or other organisms?
4. How do predator-avoidance adaptations affect prey and predator population dynamics in natural ecosystems? Use information from lectures and reading materials to create and support your argument.
5. Many species, including the snail you studied in this exercise, avoid predators by inhabiting structurally-complex habitat. Loss of structurally-complex habitat is a common consequence of human-mediated habitat destruction. Use results from this experiment and information from readings and lectures to predict effects of habitat destruction on 1) populations of prey that used the lost habitat as a refuge from predation, 2) populations of predators that rely on the prey for food, and 3) other species that depend on the prey or predator for food or some other resource.

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Useful Web Sites

- Alabama Wildlife and Freshwater Fisheries Hatcheries Section: Producers of redear sunfish
  http://www.sdafs.org/aqua/aquadir.pdf
- Fender's Fish Hatchery: Ohio-based producer and distributor of redear sunfish
  http://fendersfishhatchery.com/Shellcracker.htm
- Freshwater Gastropods of North America Project: An informative site focusing on freshwater snail conservation and ecology
  http://www.cofc.edu/~dillonr/fwgnahome.htm
- Indiana Division of Natural Resources Commercial Fish Suppliers Directory: Contact information for suppliers of redear sunfish are available here
  http://www.state.in.us/dnr/fishwild/fish/fishing/commfish.htm
- Iowa DNR Fish and Fishing: Identification and natural history notes for redear and pumpkinseed sunfish
  http://www.iowadnr.com/fish/iafish/iafish.html
- Iowa DNR Scientific Collector's Permit Application
  http://www.iowadnr.com/cs/files/542-1367.pdf

- Missouri Department of Conservation Fish Hatcheries and Trout Parks: Warmwater hatcheries, including the Hunnewell hatchery, have supplied redear sunfish to me in the past http://mdc.mo.gov/areas/hatchery/
- Pennsylvania Fishes (Chapter 22: Sunfishes): Identification notes for redear and pumpkinseed sunfish
  http://sites.state.pa.us/PA_Exec/Fish_Boat/pafish/fishhtms/chap22.htm
- Producers of Fish For Stocking Purposes: Contact information for many southeastern U.S. distributors of redear sunfish are available here
  http://floridafisheries.com/docum/fish-sup.html

Tools for Assessment of Student Learning Outcomes

1. **Biology majors (general ecology course)**
   A student's grade on this exercise will be based on three components: 1) the instructor's assessment of student effort and level of participation in the experiment (10 points), 2) completeness of data tables and worksheets, and accuracy of calculations (20 points), and 3) a short (approximately five double-spaced pages) paper written in the format of a professional scientific journal (70 points). Modified versions of in-class discussion questions from this activity will also appear on an upcoming lecture or laboratory examination. See ‘Questions for Further Thought and Discussion’ for examples of possible exam questions.

   Using data collected by a previous class, the instructor will demonstrate how to record data needed for statistical analysis. Your class will also work through two examples of paired-sample t tests so that you will become familiar and comfortable with calculations needed to generate t statistics. Your instructor will also help you interpret results of statistical analyses. Refer to the example:

   ‘Student Data Set#1: Previous class data and paired-sample t test results’

   and re-read the help box above for additional assistance.

   Class time will also be directed to scientific writing methods. The class will discuss each major section of a scientific paper, and what should be included in each section. A handout and checklist describing scientific manuscript components is provided in an appendix linked below to supplement lectures and discussions on this topic. In particular, you should periodically review the "Checklist for a Scientific Manuscript" as you write the paper. Your instructor will use this checklist to assist in grading your paper.

   ‘Appendix 1: Handout on scientific writing and checklist of scientific manuscript components’ (adapted from Morgan and Carter 1999 and McMillan 2001)

2. **Non-science majors (general biology course)**

   Non-science majors are evaluated on 1) an assessment of level of participation in the experiment (10 points), 2) completeness of data tables and worksheets, and accuracy of calculations and interpretations of results (20 points), and 3) the quality of written answers to questions based on this experiment (20 points). Your instructor will prepare you for answering these questions through in-class discussions of experiment objectives, results, and ecological applications of these results.

NOTES TO FACULTY

Challenges to Anticipate and Solve

These comments are based on the example experimental design that is described above. Relevance of some comments will vary depending on the experimental design used by your class.

1. **Obtaining snails and maintaining them in captivity:** I recommend using snails from the family Physidae because they are well known to detect predators through chemical cues and alter habitat use to avoid predation (Turner 1996, Stewart et al. 1999, Brown 2001, Bernot and Whittinghill 2003, Turner and Montgomery 2003). Physids are generally easy to find; they might be the most abundant and cosmopolitan of all freshwater gastropods, occurring throughout North America, Eurasia and much of Africa (Dillon et al. 2002). Physids are particularly abundant in slow-flowing waters with aquatic vegetation, but occur in almost any freshwater environment (Brown 1997, Brönmark and Vermaat 1998). Diagnostic features of physids include a thin (easily crushed between your fingers), coiled shell with a raised spire, and an aperture (shell opening) that opens to the left when the aperture faces the observer and the spire points toward the sky (see images below; Brown 2001). Physids can be collected from shallow waters by hand, or by examining vegetation collected with a dip net (Brown 2001). Use water-filled buckets to transport snails to the classroom or laboratory. Hold snails in aquaria containing aerated, dechlorinated water. Physids will survive, grow, and reproduce on a diet of goldfish flake food. Juveniles hatch from jellylike, crescent-shaped egg masses that are attached to aquarium walls and other hard surfaces.

2. **Obtaining fish and maintaining them in captivity:** See "Generating snail responses to predator cues" (item #3 below) to determine if actual predators are needed for this experiment. If you and your students require or desire predators to produce chemical cues, use molluscivorous fish that consume many snails in a short time period, and therefore produce a strong chemical signal. I use redear or pumpkinseed sunfish (*Lepomis microlophus* and *Lepomis gibbosus*, respectively) to generate chemical cues for this experiment (see image below, Page and Burr 1991, and Useful Web Sites to identify these sunfish). Redear and pumpkinseed sunfish readily eat snails and have stimulated habitat shifts among physids in my experiment and other investigations (Turner 1996, McCollum et al. 1998, Stewart et al. 1999, Turner and Montgomery 2003). These fish can be obtained from fish hatcheries (see Useful Web Sites), or from ponds or lakes using a seine or hook and line baited with earthworms. Both species generally survive well in captivity on a diet of snails or commercial fish food. Aquaria containing fish should be aerated continuously, and feces should be removed from aquarium floors every few days using a siphon. Visibly sick fish should be isolated from healthy individuals to reduce disease transmission and mortality rates. Because captured fish generally require several days to resume feeding, fish should be obtained at least one week before running this experiment.

   Before obtaining fish, be sure to apply for and obtain legal permission for collecting and possessing vertebrate animals. Generally, use of fish in teaching requires approval from an institutional animal care and use committee. If fish are obtained from the wild, a collector's permit may also be required by your state's natural resource agency (e.g., Iowa DNR Scientific Collector's Permit, http://www.iowadnr.com/cs/files/542-1367.pdf).

3. **Generating snail responses to predator cues:** Snails in any predator-cue treatment of your experiment must detect and respond to chemical cues for this activity to be successful (see Materials and Methods for descriptions of treatments that can be used in this experiment). Physids exhibit interpopulation variability in behavioral responses to predator cues, and some wild populations might not respond to predation at all (Turner 1996, McCollum et al. 1998, Stewart et al. 1999, McCarthy and Fisher 2000, Bernot and Whittinghill 2003, Turner and Montgomery 2003). However, chemical cues and statistically significant habitat use shifts can

almost always be generated from at least one of three sources:

a. crushed or injured snails,
b. predators themselves, or
c. excretory products of predators that have eaten snails.

Conduct preliminary trials to identify the signal(s) that elicit a behavioral response in your snails. Often, snails respond to cues produced by crushed conspecifics, and fish will not be required for this experiment (Turner 1996, McCarthy and Fisher 2000). To determine if fish predation can be simulated by manually crushing snails, crush several large snails between your fingers, place them in a large aquarium (at least 38-L capacity) equipped with an air pump, air tubing, and an airstone. A carbon filter should not be present in this or any aquarium used in this experiment because filters eliminate odors and other chemical cues.

Between 10-30 minutes after crushing snails, transfer 2 L of water from the aquarium with crushed snails to a 19-L aquarium containing living snails, dechlorinated water, and structurally-complex habitat (e.g., pile of stones and ceramic tiles; see item #4 – Structurally-complex habitat) that provides hiding places for snails. To avoid overfilling the 19-L aquarium, 2 L of water will have to be removed from this aquarium before the water transfer is made. Just before making the water transfer, and every five minutes thereafter, record numbers of snails visible in underwater habitats (i.e., aquarium walls or upper stone and tile surfaces). These snails are considered vulnerable to fish because they would be easily seen by and accessible to these predators. If snails detect and respond to crushed snails, they will begin to crawl about with increased speed until encountering a habitat they perceive as providing shelter from shell-crushing predators (i.e., undersides of tiles, spaces within piles of stones, aquarium walls above the water line). Consequently, numbers of vulnerable snails will decline dramatically. Increase chemical cue concentration through additional water transfers if snails do not respond within 10 minutes of adding water containing cues from crushed snails. Continue periodic recordings of numbers of vulnerable snails. Don't conclude that crushed snails fail to elicit a behavioral response until after you have added more crushed snails to the 38-L aquarium, and repeated water transfer procedures several times.

Snails from some populations might not respond to cues produced by dead or injured snails alone. Additionally, even if your snails do respond to crushed snails alone, you may wish to use fish to generate stronger cues, or to enable students to view fish in the lab. To generate a strong fish cue, place several large, healthy fish in a large, aerated aquarium (again, 38 L or larger capacity). Feed fish large quantities of snails 10-30 minutes before conducting preliminary experiments to determine if snails respond to fish-generated cues. Conduct water transfers and record numbers of vulnerable snails as previously described until snail habitat shifts are evident. As a guideline, I observe strong habitat shifts in snails inhabiting 19-L aquaria after adding 2 L of water from a 100-L aquarium that contains 4 redear sunfish (85-105 mm total length) fed 10 physids 10-30 minutes before the water transfer was made.

Finally, verify that the chemical cue concentration you plan to use is sufficient by conducting a preliminary experiment with replication and data analysis (see Materials and Methods for descriptions of example experimental procedures). If snails in a predator-cue treatment do not increase refuge use after exposure to the cue, increase chemical cue concentration in subsequent preliminary experiments until strong, consistent responses by snails occur.

Chemical cues degrade rather quickly, and snails will likely leave refuges a few hours after the last addition of water containing chemical cue is made to their aquarium. Therefore, an actual in-class experiment can be run within a day of completing preliminary trials.

4. **Structurally-complex habitat:** Behavioral response to predation in this experiment can be measured through increased refuge use by snails after exposure to chemical cues produced by

predators or by other snails that have been injured or killed by a predator. Structurally-complex habitat is the primary refuge used by snails in this experiment, and sufficient quantities of structure must be available for behavioral responses to be quantified. At least 1 L of patio stones or similar objects should be placed in each aquarium of predator-free and predator-cue treatments. This is equivalent to the amount of submerged stones required to displace the water line in a volumetric container from the 1-L to 2-L mark. Snails respond to predation risk by seeking out dark, interstitial environments to hide in. To create this habitat, stack stones in multiple layers. To further improve the refuge quality, place ceramic tiles (15 X 15 X 1 cm) or similar cover on top of this pile of stones. Snails seeking refuge from predation that encounter stones or tiles will generally come to rest deep within this pile of stones, or on undersides of tiles. In either case, these snails would no longer be visible to fish or students.

5. **Setting up the experiment:** For best results, this experiment should be set up at least 24 hours before it is scheduled to begin. This is advisable so that snails and fish can become acclimated to conditions in the aquaria and classroom, and sufficient time is available for fish in 38-L aquaria to generate strong chemical cues. Depending on how often your class meets, the instructor might have to complete this pre-experimental setup on their own. See ‘Overview of Data Collection and Analysis Methods’ for detailed descriptions of example pre-experimental procedures.

6. **Data recording and analysis:** For this experiment to be successful, students must distinguish snails that are vulnerable to predation from those that are not, and established criteria must be used consistently by all students recording data. The instructor could use input from student groups to establish criteria for designating a snail as vulnerable or invulnerable. However, since this is so critical to the experiment's success, I often establish vulnerability criteria for students and tell them how to distinguish a "vulnerable" snail in an exposed underwater habitat from an "invulnerable" snail inhabiting a refuge from predation. Briefly, any snail that is visible on aquarium walls (including the aquarium floor), or upper surfaces of stones or tiles is vulnerable to predation by fish. A snail that occurs above the water line, or that cannot be seen by fish because it inhabits the underside of a tile or a crevice within a pile of stones is unlikely to be eaten and is considered invulnerable. I prepare students for data analysis by guiding them through two examples of a paired-sample t test using instructions from Zar (1999) and past results from this experiment (see ‘Overview of Data Collection and Analysis Methods’, ‘Student Data Set #1’, and t-test help box).

7. **Writing the paper:** I use a lecture and discussion session and handouts adapted from Morgan and Carter (1999) and McMillan (2001) to help biology majors write their scientific paper (see ‘Appendix 1’). Additionally, I demonstrate how to perform an online literature search, and provide students a list of relevant background literature that will help them write the introduction and discussion sections of the paper. Selected background literature are also summarized and discussed in class.

Experiment Description

Introducing the Experiment to Your Students: This activity integrates many evolutionary and ecological concepts. I have used this experiment to supplement lecture units on natural selection and conservation biology, in addition to population, community, and ecosystem ecology. Before initiating the experiment, I establish a central theoretical framework by introducing students to the concept of natural selection, as well as related terms including fitness and adaptation. I stress that predator-avoidance characteristics result from evolutionary forces. Ecological consequences of predator-avoidance adaptations, and the importance of structurally-complex habitat, are also discussed at the conclusion of the study. See ‘Questions for Further Thought and Discussion’ for a list of some specific questions I ask. At a basic level, students will understand that predator-avoidance behavior and structurally-complex habitat benefit individual prey and the prey population by increasing the likelihood that some individuals escape predation until after they produce offspring. However, readings and class discussions designed to promote higher-level thinking also help students gain improved understanding of the importance of predator avoidance to the entire biological community. By enabling prey population persistence, predator-avoidance adaptations facilitate long-term survival of all species that rely on this prey for survival (Begon et al. 1996, Krebs 2001). Similarly, due to complex direct and indirect interactions among species, chains of species extinctions can occur if loss of structurally-complex habitat (i.e., refuges from predation) causes a single prey species to become extinct (Begon et al. 1996, Krebs 2001).

Data Collection Methods Used in the Experiment: It is critical that all students understand criteria used in this experiment to classify a snail as vulnerable to predation. I confront this issue by asking the students to think of themselves as fish that can only eat visible snails that also occur underwater. Therefore, snails located underwater that are visible to the observer at the end of the experiment are recorded as "vulnerable," whereas all remaining individuals are considered "invulnerable" to predation. See 'Overview of Data Collection and Analysis Methods' and item #6 ('Data recording and analysis' under 'Challenges to Anticipate and Solve') for criteria used to distinguish vulnerable and invulnerable snails.

Data Analysis: Several different statistical tests could be used to analyze data (see Zar 1999 for examples). Student experience in experimental design and statistics should be considered when making the decision of which test to use. A repeated-measures analysis of variance (ANOVA), with treatment type as the main factor, is very appropriate for analyzing data produced from this experiment. An advantage of this tool is that a single test could be used to analyze all experimental data. Results should yield a significant statistical interaction between time and treatment, due to change in numbers of vulnerable snails in one treatment (i.e., predator-cue treatment) but no change in the other treatment (i.e., predator-free treatment). Although repeated-measures ANOVA could be used to analyze these data in advanced undergraduate and graduate-level classes, I find that most undergraduate students have difficulty understanding the concept of statistical interaction. Additionally, repeated-measures ANOVA calculations are relatively cumbersome, and frequent calculation errors frustrate students. Students conducting this experiment in my general biology course are usually non-science majors. For these students, I use paired-sample t tests to analyze data from this experiment because statistics are easier to calculate, and students appear to have little difficulty interpreting results. To assist with data analysis, I supply detailed instructions and two completed examples of paired-sample t tests (see 'Overview of Data Collection and Analysis Methods', 'Student Data Set #1', and t-test help box). We work through both paired-sample t test examples as a class before students analyze their own data.

Questions for Further Thought

1. There should be evidence that students were carefully observing snail behavior throughout the experiment. Students should notice that snails not exposed to chemical cues (i.e., the predator-free treatment) behave similarly before and after the experiment begins. In the absence of chemical cues, snails tend to crawl about lazily or remain motionless. Alternatively, if chemical cues are added to aquaria, students should see that snails soon perk up and crawl faster as they initiate a flight response. Snails will come to rest within structurally-complex habitat, or above the water line. Some snails in a predator-cue treatment will wander continuously, apparently never finding a habitat they perceive as safe.

2. A primary purpose here is to assess a student's ability to interpret data and use results from statistical analysis to objectively make the correct conclusion. Using my examples, students will need to understand how to use a t statistic and a critical t value to determine if results support the experimental hypothesis that predator cues induce habitat shifts in snails.

3. The objective here is to illustrate that science is a continuous process of generating and testing new hypotheses for purposes of improved understanding. New and important questions emerge from results of previous studies.

4. A main point here is that prey populations cannot survive unless sufficient numbers of individuals avoid being eaten until producing offspring. If prey cannot avoid predators, the prey will go extinct, and predator populations might also become extinct due to loss of food. There should be

evidence that a student has used lecture/discussion notes, ecology textbooks, and/or peer-reviewed literature to formulate a reasonable argument.

5. An objective here is to stimulate student thought about direct and indirect effects of habitat destruction on community stability and biological diversity. Additionally, I wish to get students to think of a biological community and ecosystem as a functioning unit, and species as individual components of that unit. Using information from lectures, class discussions, and readings, a student should demonstrate their understanding that loss of critical habitat of one species can adversely affect many species through a variety of direct and indirect mechanisms, including reduced food and habitat resources, and altered nutrient and energy flow pathways (Begon et al. 1996, Krebs 2001). Examples of classic and recent primary literature that can help guide discussions on relationships between habitat complexity and abundance changes and biological features of ecosystems include Huffaker (1958), Macarthur and Wilson (1967), Walters (1991), Bart and Forsman (1992), and Haddad (1999). Additionally, Krebs (2001) provides an excellent overview of direct and indirect effects of habitat destruction and fragmentation on populations and biological communities.

Assessment of Student Learning Outcomes

One component of each student's grade on this activity is based on his or her effort and level of participation. A student's effort and participation score is based on my overall assessment of an individual's active participation in group discussions, and data collection and analysis. Students are also graded on completeness of data tables and worksheets, and accuracy of calculations, and either a short (approximately five double-spaced pages) paper written in the format of a professional scientific journal (biology majors) or the quality of written answers to questions based on this experiment (nonscience majors).

Most students in my general ecology class are sophomore and junior biology majors. Many of them have had few prior opportunities to use statistical tools to analyze their own data. Additionally, some of these students have not yet written a scientific paper. Therefore, I direct much effort toward helping students feel comfortable with statistics and scientific writing techniques. We complete two examples of a paired-sample t test, and discuss how to interpret results from this test (see ‘Student Data Set #1’, and t-test help box). Additionally, I provide students with examples of peer-reviewed journal articles, and we discuss what should be included in each section of their own paper. A handout and checklist of scientific paper components assist with this (see ‘Appendix 1’). Students are informed that I refer to this checklist of scientific paper components when I grade their papers.

I find that use of experiments and statistics in my non-science majors general biology class stimulates learning, critical thinking, and interest in the subject. I often introduce this exercise by stressing that knowledge of the scientific process among nonscientists is important because it can help them critically evaluate information received from a variety of sources, including marketing agencies, politicians, and the news media. Similarly, for biology majors I guide students through two examples of a paired-sample t test before they analyze their own class data. After the experiment and data analysis are concluded, we address several questions in a class discussion (see ‘Questions for Further Thought and Discussion’). We begin with relatively simple questions focusing on the value of antipredator behavior to individual prey, and gradually move toward increasingly complex questions that address the combined importance of predator-avoidance strategies and structurally-complex habitat in promoting persistence of biological diversity and natural resources. Following this discussion, I give students some related questions and ask them to submit written responses to me for a grade.

Some of my ‘Questions for Further Thought and Discussion’ are specifically designed to evaluate student abilities to transfer and apply knowledge gained from this experiment. In this activity, students learn that snails possess chemosensory and behavioral traits that enable them to reduce their mortality risk. However, through a series of questions and class discussions conducted at the conclusion of this exercise, I look for evidence that students also understand the broader applications of their findings. For example, students should demonstrate an understanding that, in a natural ecosystem, predator-avoidance adaptations of prey promote long-term survival of both prey and predator populations, by ensuring that some prey survive until after they reproduce. Furthermore, persistence of predator and prey populations reduces extinction rates among additional species that directly or indirectly depend on the focal prey or predator species for survival. Finally, students should be able to visualize effects of habitat destruction on biological communities, particularly if lost habitat provided organisms with refuges from predators.

Formative Evaluation of the Lab Activity

At the conclusion of this activity, instructors can use several techniques to evaluate effectiveness of this exercise in facilitating student learning. Alternative methods are described in ‘Evaluation of Course Reforms: A Primer’. In the "minute paper," students are asked to provide a written response to a question that is related to the experiment they have just completed. I prefer to ask a simple question such as: "What did you learn from this activity?" By reviewing responses, I gain an improved understanding of how well students understand basic concepts illustrated through the experiment (e.g., small organisms possess physiological and behavioral traits that enable them to avoid being eaten) as well as their ability to relate results to broader ecological issues (e.g., loss of habitat that provides an essential refuge from predation can result in increased predation rates and eventual extinction of the prey species). The instructor can use the minute paper as an additional student-learning tool by reading and discussing student responses during a subsequent class session. If the instructor finds student responses to be incomplete or otherwise unsatisfying, appropriate modifications can be made to this activity to increase its effectiveness as a learning tool.

Translating the Activity to Other Institutional Scales or Locations

1. This experiment can be translated to larger scales by increasing replication (i.e., using more aquaria and student groups) or by increasing the size of student groups. I have little difficulty using this exercise in a large laboratory class of 28 students. Because snails move slowly, a small class consisting of 5-10 students can also easily collect all required data.

2. Snails used in this experiment occur almost worldwide in a variety of freshwater ecosystems, so this experiment is applicable to a variety of geographic regions. This is a laboratory experiment, and animals can be maintained and bred in the laboratory. Therefore, this experiment can be conducted at any time of year. Although I have only used physid snails and two species of sunfish in this experiment, it is likely that other snail families exhibit predator-avoidance responses similar to those in physids, and that additional kinds of fish elicit behavioral responses in snails.

3. This experiment is conducted indoors, and data are collected at fixed stations. Therefore, this activity is ideal for students with physical disabilities.

4. One of the most effective ways to get young people excited about biology is to allow them to work with live animals and to witness unique behaviors and interactions among different species. In fact, I originally developed this activity for use in a freshman-level non-science majors environmental science course because I wanted to stimulate interest by incorporating live animals into the laboratory curriculum. This activity could easily be adapted for lower grade levels by streamlining or eliminating statistical analysis, or focusing strictly on basic principles of animal behavior, or ecological and evolutionary concepts.

STUDENT COLLECTED DATA

Student Data Set #1: Previous class data and paired-sample t test results
Contains actual class data, and examples of paired-sample t tests calculated from these data.

Teaching Issues and Experiments in Ecology (TIEE) is a project of the Education and Human Resources Committee of the Ecological Society of America (http://tiee.ecoed.net).