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EXPERIMENTS

The Insect Predation Game: Evolving Prey Defenses and Predator Responses

W. Wyatt Hoback
Department of Biology
University of Nebraska at Kearney
Kearney, NE 68849
hobackww@unk.edu

Tamara L. Smith
Department of Biology
University of Nebraska at Kearney
Kearney, NE 68849


A dragonfly consumes a plant-feeding stinkbug. The image illustrates prey capture ability and prey defenses, which are effective against some predators but not others. The photograph was taken by W. Wyatt Hoback in 2003 while in Manaus, Brazil.

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ABSTRACT

Insect communities are structured by the biotic interactions between generalist insect predators and their prey. Among insect predators, three general feeding methods are used (mandibles, raptorial forelegs, and unmodified legs) to capture prey, which usually consists of herbivorous insects. In this game, students play the role of three types of insect predators as they forage upon three potential prey species (represented by three different types of candy). Students conduct 5-10 simulations each of which lasts about 45 seconds. After each simulation, prey reproduce based on the number remaining, and predator numbers are adjusted to reflect mortality and reproduction. In insect communities, prey species may evolve defenses, including poisons, in response to strong predation pressure. However, costs of these defenses might include slowed growth and reduced reproduction rates. In this game, one prey type becomes poisonous, but suffers a lowered rate of reproduction, while the other types remain palatable and have higher rates of reproduction. If the predator type that suffers the greatest mortality evolves to feed on poison-protected prey species, all three predator types are maintained in the community. Otherwise, one or more of the predator species may go extinct. Discussion of the results, presented graphically, allows students to understand how evolutionary tradeoffs influence community structure and function.

Class Time
The exercise takes between 2 and 3 hours, which includes time for data analysis. Extra time will be needed for extension activities.

Outside of Class Time
Students will need 1-2 hours to answer questions and write reports, with extension activities requiring more time.

Student Products
Students answer questions from the completed worksheet and graphs. Students may complete a report on how a community will evolve when driven by predator-prey relationships. As part of the extension activities, students can develop their own predator-prey system, choosing initial numbers of predators and prey, as well as prey and habitat type.

Setting
This is an indoor laboratory; it can easily be adapted to the outdoors.

Course Context
This laboratory exercise is used for non-majors biology courses. It has also been used with high school biology and middle school science students. With extensions and student-determined rules for the game, the exercise could be used for majors courses in ecology and evolution.

Institution
Mid-sized four-year public university with undergraduate and master's degree options.

Transferability
This activity can be used with both majors and non-majors in biology and entomology. Extension activities add to the difficulty level and are appropriate for students studying ecology.

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reviewers and Christopher Beck for suggestions that greatly improved this exercise. We would also like to thank Rick Simonson for his work on the illustrations.

SYNOPSIS

Principal Ecological Question Addressed

What is the interplay between competition, predator-prey interactions, and sequential evolution of prey defenses and predator responses?

What Happens

In this game, students play the roles of different insect predators (represented by foraging appendages constructed from plastic utensils (see Figure 1, drawing of appendages) as they capture suitable prey (i.e., candy). After each round, remaining prey reproduce and predators suffer differential mortality. In some rounds, a particular prey species is designated as poisonous. Student predators learn to recognize dangerous prey by getting ill after feeding. In future rounds, predators may evolve to circumvent certain prey defenses. For each generation, students follow population dynamics of the predators and prey. Students answer questions based on the outcomes and they discuss concepts, including predator-prey interactions, evolution of specialist predators, and extinction. This lab is a fun way to demonstrate natural selection and ecological tradeoffs.

Experiment Objectives

Through participating in the exercise, students will learn that:

- Insect predators use three general forms of appendages for attacking prey,
- Prey respond to predation pressure in a variety of ways, including evolving physiological defenses,
- As prey become poisonous, their numbers increase, leading to an advantage for predators to that overcome the defenses,
- Through time, a stable community supporting a diversity of predators and prey can develop.

Specifically, at the end of the lesson, students will be able to:

1. Discuss insect predation methods and tradeoffs associated with prey defenses,
2. Predict how a community will change when driven by predator-prey relationships,
3. Recognize the importance of generalist predators in responding to potential prey populations.

Equipment/Logistics Required

For a class of 24 students working independently:

- Paper cups for stomachs
- Feeding appendages consisting of pairs of plastic forks, knives, or spoons held together as forceps using rubber bands and a paper spacer (see Figure 1). Fifteen of each is typically more than enough.
- Prey items — three types of beans, candy (Skittles, M&Ms, and candy corn), plastic insects, buttons, etc., can be used. Also, Goldfish Crackers of three varieties can be substituted.
- Three balances and containers for weighing prey items
- A computer with Microsoft Excel
- 24 copies of handouts, including worksheet, blank graphs, figure of different insect predators
- Optional habitat structures that can easily be made from carpet samples taped together. If conducted outside, a grassy area can be used.
- Optional — pinned specimens of different insect predators that are simulated in this exercise (i.e., raptorial forelegs predators such as praying mantises, mandibles such as used by ground beetles, all legs such as used by dragonflies and damselflies)

Summary of What is Due

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).

At a minimum, students complete worksheets and answer questions at the end of the exercise. Students also can be instructed to write a report about their findings.

Keyword Descriptors

Ecological Topic Keywords: community ecology, predator-prey relations, predation, adaptation

Science Methodological Skills Developed: theoretical thinking (reflection on practice), identify biotic interactions, use of graphing programs, use of spreadsheets

Pedagogical Methods Keywords: active learning, guided inquiry, game to teach ecology, role-playing

DESCRIPTION

Introduction

Insects

With more than 750,000 described species, insects are the dominant terrestrial animal life on earth in diversity, numbers, and biomass. Most insects have short generation times, giving the majority of species a tremendous reproductive potential. For example, fruit fly pairs produce 30 generations per year with an average of 40 eggs per pair. With a 1:1 sex ratio, unlimited reproduction and 100% survival for a single year would produce a layer of fruit flies over the earth about 991 million miles deep! However, unlimited reproduction does not occur, nor does every organism born live to reproduce. When the size of a population approaches an environment's **carrying capacity**, competition for resources will limit reproduction. In addition, predators regulate some prey populations.

Predation

Predation involves four steps: **search**, **recognition**, **capture**, and **handling**. The possibility of co-evolution of predator and prey operates at each of these steps. Predators search the environment for acceptable prey. Predator adaptations to improve foraging success include better visual acuity, development of a search image, and limiting searches to prey-rich habitats. Predators quickly learn prey types and adapt to recognize prey and to avoid inedible species. Predators must be able to capture prey. Adaptations to improve capture efficiency include improved motor skills and appendage modification. Finally, predators must handle prey by efficiently subduing them and detoxifying any defensive compounds. Adaptations promoting handling efficiency include improved foraging appendages to reduce the probability of injury and physiological specialization on otherwise poisonous prey (Krebs and Davies 1993). Predators also improve foraging efficiency by **learned avoidance**, a behavior in which predators quickly learn to recognize poisonous or distasteful species by remembering adverse reactions from attempted predation events (Brower 1988).

Prey defenses

Because life depends on taking life, almost all organisms on earth are potential prey for at least one other species. To escape this predation pressure, natural selection has favored individuals that are more difficult to find, capture, subdue, and consume. Adaptations against predation include coloration, behavior, morphology, phenology, and physiology. Among the most spectacular examples of these different anti-predator defenses are found among the insects that range from species that are nearly invisible against the background (such as the toad bug in figure a), to species that are so heavily armored that most predators cannot subdue them (such as the ironclad beetle in figure b). Other species have spines and many have some form of chemical defense, such as ladybird beetles (figure c), which leave a yellowish, strongly smelling fluid on your hand when you handle them. Often species having chemical defenses are also aposematic, meaning they are brightly colored in order to warn a potential predator.

At top left (a) is an ambush bug that survives by being cryptic and attacks prey by jumping on their backs. At top right (b) is a darkling beetle called “an iron clad beetle” that most predators cannot consume because of its armor. To the left (c) is a ladybird beetle that is brightly colored (aposematic) and protects itself with chemicals secreted from special joints in its legs.

Predator-prey interactions

Unfortunately for both the species possessing warning coloration and for the potential predator, the recognition of potentially dangerous prey is not innate. Predators must learn to associate bad taste or illness with eating a species that possesses memorable characteristics. Ecologically, the interactions between predators and prey are complex and change through evolutionary time as predators and prey adapt to the environment and each other. Prey species may vary in their ability to create and express chemical defenses and in the costs associated with this ability, which often lead to a reduction in growth and reproductive rate but an advantage in protection when predators are abundant. In contrast, predators vary in their ability to find, capture, subdue, and consume prey. Sometimes when a prey species becomes more toxic, only one predatory species can overcome its defenses. If that predator species specializes on the toxic prey species, the predator selects for the prey to become more toxic, which in turn selects for the predator to be better able to overcome the more toxic prey. This back and forth selection can result in a tight linkage between a predator species and a prey species. When there is a tight association of mutual selection pressures acting on two or more species, the phenomenon is termed "**co-evolution**."

Insect Predator-Prey Interactions

Among the insects, three predator forms are common. Many predatory insects, including ground beetles, tiger beetles, and ant lion larvae, grasp and kill their prey with their mandibles. A second group of insects, including praying mantids, giant water bugs, and ambush bugs, use enlarged front legs (**raptorial legs**) to grab and subdue prey. A third form of prey capture most commonly used by aerial predators consists of grasping prey with all the legs while in flight. Insects that use this method include dragonflies, robber flies, and scorpionflies. All these types of insects are **generalists**, feeding on any appropriately-sized arthropod they happen upon.

Prey species have mechanisms to counter predator efficiency at each step of the predation process. Prey can be difficult to locate by way of **cryptic** or **polymorphic** forms and often disperse in the environment. Some species have developed potent defense mechanisms, including poisons, armor, and spines. To reduce recognition, some prey species **mimic** dangerous species.

Usually, warning coloration and associated poisonous characteristics are thought to protect insects from mammalian and avian predators. Berenbaum and Miliczky (1984) demonstrated that warning coloration and poisons protect some insects from predatory praying mantises. They fed one group of milkweed bugs milkweed seeds, which contain high concentrations of cardiac glycosides. They fed a second group of milkweed bugs sunflower seeds. The two groups of bugs appear identical, but those that fed on milkweed are poisonous while the others are not. Berenbaum and Miliczky then fed naïve mantises bugs from either group. When the mantises ate the poisonous bugs, the mantises threw up and quickly learned to avoid the poisonous prey. The mantises also avoided the bugs that had been fed sunflower seeds unless they had not previously encountered a poisonous prey. More recently, an experiment conducted with jumping spiders showed that terrestrial invertebrates also can exhibit associative learning, not only remembering distasteful prey, but also remembering the environment in which they encountered that prey (Skow and Jakob 2006).

So clearly, insect predators can become ill from eating poisonous prey and can learn to avoid prey that look the same. Yet, what keeps insects such as milkweed bugs and monarch caterpillars that feed on milkweed from being able to have exponential population growth? How can milkweed plants survive once insects have specialized on them and are no longer affected by the milkweed defense compounds? Part of the answer is that some insect predators have adapted to feed on prey that are poisonous. Several studies have demonstrated the effects of predators feeding on poisonous prey. For example, Strohmeyer et al. (1998) found that predatory stink bugs grew faster when eating caterpillars that had less plant-derived iridoid glycosides.

Other studies of plant-feeding herbivores have shown that the ability to overcome plant defenses and then use them for self-protection also comes at a cost in terms of growth rate. For example, Kopf et al. (1998) found linkages between the evolutionary history of the plant feeding leaf beetles and their host plants. Ballabeni and Rahier (2000) and Ballabeni et al. (2001) showed trade-offs in performance of beetles feeding on alternative plants. Beetles that acquired more defensive chemicals had slower growth. In addition, predators often force these leaf beetles into choosing nutritionally poorer plants (Ballabeni and Rahier 2000, Ballabeni et al. 2001). Dobler (1996) also showed trade-offs in reproduction associated with food plant use with beetles that either laid eggs or gave birth to live young. In these leaf-feeding beetles, the concentration and distribution of the synthesized chemicals used for the beetle's defense also depends on genetics of the beetles and the predation pressures they face (Pasteels et al. 1995). Similar trade-offs probably exist for many types of insects besides leaf-feeding beetles. For example, Smith et al. (2001) showed that a fly species (*Tipula montana*) selected among plants to maximize growth of larvae.

Slowed growth from eating chemical laden prey (in this case caterpillars that fed on plants containing iridoid glycosides that are stored in the haemolymph) also affects predators that eat these prey. In some predators, feeding on prey that have a lot of chemical defenses slows down reproductive rate and growth (Strohmeyer et al. 1998). Experimentally, this has been demonstrated in ladybird beetles that synthesize their own defensive compounds. Holloway et al. (1993) found trade-offs for the production of defensive compounds, which ladybeetles produce themselves. Ladybird beetles that produced more defense compounds grew more slowly and remained smaller. The difference between growth rates and chemical defense was genetically based (Holloway et al. 1993). When individuals of a species vary genetically in the way they use energy for either reproduction or chemical defense, populations that face few predators will adapt to have little chemical defense but high rates of growth and reproduction. Populations that are frequently exposed to predators will have much higher levels of chemical defense.

Predation and community structure

In this exercise, you will learn about predator-prey relationships and their impact on ecological communities. Competition and predation have been tested repeatedly to determine their influences on a community. The roles of competition and predation in structuring communities are often variable (see reviews by Sih et al. 1985, Chase et al. 2002). Predators can play multiple roles in a community. First, they can restrict prey distribution or reduce prey abundance, which may lead to greater species diversity (Levin 1970). Second, predation can alter the structure of a community by influencing the abundance of species at many different trophic levels. For example, in the absence of predators, herbivores are able to feed and increase in numbers, which results in a decrease of available plant material. However, when predators are in the environment, the number of herbivores decreases and in turn the amount of plant material increases. These phenomena are expressed as the cascading trophic interaction model (Carpenter et al. 1985). Third, predation is a significant selective force leading in some cases to predator-prey co-evolution (Krebs and Davies 1993).

During the exercise, you will learn about some of the many factors that constrain predator ability. Intrinsic factors include limited time available for prey searching, limited stomach size, and time needed for digestion. Extrinsic factors include competition with other predators and environmental disturbances. Predator-prey relationships often change when an environment is disturbed, such as by flooding, fire, pesticide use, or farming. If few predators are in the environment, herbivores can reproduce rapidly reaching high local densities. This effect may be countered by a numerical increase of predators moving to the area. When there are many predators and abundant prey available, the predators capture as many prey as quickly as possible. Predation under these conditions is termed "**resource competition**" or "**scramble competition**" (Birch 1957). As predation causes prey to become more limited, competing predators may interact directly, leading to injuries or limited predatory success. Such competition is termed "**interference competition**" or "**contest competition**" (Birch 1957). When the environment becomes more stable, competition may return the community to an equilibrium of predator-prey species.

Materials and Methods

Study Site(s)

The exercise can be performed in a laboratory or outside. The space chosen for the exercise should allow all students access to the "environment." For a lab of 24 students, we use a 4 x 8 foot (1.2 x 2.4 meter) table with access on all sides. We use carpet samples to create a heterogeneous environment. In advanced courses, if students are investigating different scenarios in smaller groups, smaller tables can be used.

Overview of Data Collection and Analysis Methods

In this exercise, students use a variety of feeding appendages (see Figure 1, below) as they search the environment grabbing prey items and placing them into their stomachs. For our simulations, we place equal numbers (n = 200) of three kinds of candy (M&Ms, candy corn, and Skittles) onto shag carpet samples in a 2 x 3 m area. Candy simulates foraging for edible prey and provides a handy snack at the end of lab; however, three or four small items such as beans, buttons, plastic insects, etc., could also be used. Likewise, instead of using shag carpet to simulate a heterogeneous environment, the environment could consist of a grassy lawn (here, wrapped candy would be a must), a tabletop, or a cardboard box filled with packing material.

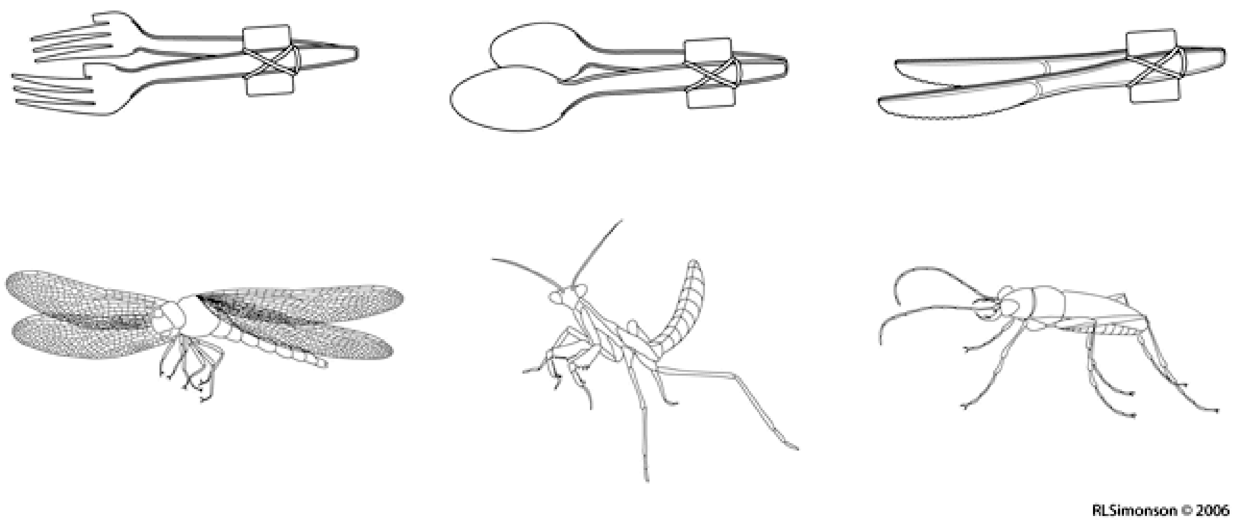

Figure 1. The pairs of forks represent grasping legs such as with dragonflies, pairs of teaspoons represent raptorial legs such as with mantises, and pairs of knives represent mandibles such as for beetles.

When the students arrive, they are shown pictures of various insect predators, and the roles of these predators in shaping a community are discussed. Assign feeding appendages based on these predator types and provide small paper cups that represent stomachs. Feeding appendages consist of pairs of plastic forks, knives, and teaspoons that are rubber-banded together to form a chopstick-like apparatus (Figure 1). The pairs of knives represent mandibles, pairs of teaspoons represent raptorial legs, and pairs of forks represent grasping legs. An equal number of each predator type is randomly assigned among the students.

To simulate learned avoidance, at the start of foraging, the student predators do not know which prey species is inedible. Foraging takes place for 30 seconds prior to the announcement of the kind of inedible prey. Then, students having inedible species in their stomachs must dump all items back in to the environment to simulate sickness prior to resuming foraging. With limited edible prey available, the students experience increasing competition and the foraging exercise is stopped after 45 seconds.

The rules of foraging are simple. The predator must only use its feeding appendage to capture prey. The predator must stop foraging when the stomach (cup) is full or when time expires. If any inedible prey are in the stomach at the end of the 45 seconds, all of that predator's prey are returned to the environment. The stomachs must be held upright at all times (no shoveling). After the end of feeding, the predators must digest their prey, represented by the time it takes to determine the number and kind of prey species in their stomachs. To speed this process, students sort their prey by kind and use balances to weigh each type. Prior to the exercise, the average weight per prey individual is determined. After foraging, the number of prey of each type eaten is determined by weighing and then calculating the number of individuals. A running tally for each predator type can be displayed on a board for later discussion.

Based on the number captured, the number of prey remaining in the environment per species is calculated (200 - # eaten = # surviving) and prey are allowed to reproduce according to the following formula. The poisonous species produces one copy of itself for each member that remains in the environment (doubles the number in the environment). The species that will remain palatable reproduces at a rate of three individuals for each that remains in the environment. The third species reproduces at an intermediate rate of two individuals for each that remains in the population.

In the second generation of the exercise, a second prey type becomes poisonous and cannot be eaten by any predator. Often, predation rates cannot keep pace with reproductive rates of some prey species. To avoid saturating the environment with prey (and to simultaneously maintain reasonable costs), we imposed a limit to reproduction by prey. Typically, we add no more than 300 prey per generation. This cap is explained ecologically as the role of intraspecific competition for resources (or environmental carrying capacity for a species). In the absence of predation, herbivorous species will increase in number until their food becomes limiting; then, only those members of the species that are able to acquire sufficient nutrients will be able to reproduce. In our exercise, each prey species is assumed to feed on different resources and thus is unaffected by interspecific competition.

The predator numbers also change. Foraging success for each predator type is calculated and the reproductive success and thus reproduction is determined as the ratio of each predator type's success divided by the total prey consumed by all predators (e.g., amount eaten by P1/ amount eaten by (P1 + P2 + P3). The ratio of predators is adjusted by changing foraging morphologies of unsuccessful predators into those of successful predators at the appropriate frequencies.

A predator type is randomly chosen to adaptively detoxify the poisonous prey species. That predator type is able to eat all prey types except the prey type that becomes poisonous in the next round. The other predator types must selectively avoid both the poisonous prey type from the previous round and the new poisonous prey type as they struggle to overcome competition and reproduce.

The exercise is continued until stability is reached or all but one predator type or prey type has become extinct. A short discussion is conducted as the prey are replaced in the environment. Predictions about the community's behavior are made and the exercise is repeated as above again randomly assigning poisonous prey and predator adaptations.

After the exercise is complete, the instructor can generate figures using the supplied Excel® predpreyblank.xls spreadsheet, and these can be printed and distributed to the class, or students can plot the changes in predator and prey species on the supplied Worksheet. The students can generate a formal laboratory report, answer questions for further thought, and speculate on the community dynamics between the insect predators and their prey.

Questions may include interpretation of the outcomes between generations. Almost certainly, the outcomes will differ even if the same prey types become poisonous and the same predator types adapt. The differences may result from the fact that the predators will be experienced and are more efficient in the second trial, and thus the outcome is affected. Additionally, predators may gamble by guessing prey types to initially avoid. Occasionally, predator or prey types are forced to extinction in one or both trials. Students should explain the results and speculate on predator-prey interactions. For introductory ecology classes, students could be assigned primary literature or instructed to find an article that reports on predator-prey interactions.

How to Conduct the Exercise

1. You will be assigned a feeding appendage that represents a specific type of insect predator (forks= dragonflies, spoons= mantises, and knives= beetles).
2. You will be given a stomach (small cup).
3. When foraging, use only the appendage to pick up prey and only the cup to store prey. You may steal prey from the appendage of other predators, but not their stomachs. In advanced classes, a few students could be assigned to steal food from other predators instead of capturing prey from the environment. An insect example of stealing prey is found in certain hangflies (Family *Bittacidae*) that rob spider webs of prey.
4. You will forage for as much prey as possible within a time limit of 45 seconds.
5. After feeding for 30 seconds, you will have an adverse reaction if you have eaten poisonous prey—you will vomit, losing all stomach contents back into the environment. In advanced classes, students could be asked how learned avoidance can be simulated. Students can be guided to the idea that predators will not initially be able to recognize poisonous prey, but after getting sick are able to distinguish among prey types. The game also could be run without poisonous prey and the results compared to those from a game with poisonous prey. In this way, students could be asked to think about the effects of poisonous prey on predator-prey dynamics.

6. After vomiting, resume feeding while avoiding all poisonous prey.
7. After feeding, sort the prey types into provided containers and weigh the prey.
8. Inform the instructor of the weight of prey eaten and the total weight eaten by each predator type.
9. The predator type that ate the most prey (by weight) will increase in frequency and inefficient predators decrease in frequency. All students play the game each generation. Students who were inefficient in capturing prey trade for new mouth parts to simulate death of some predators and birth of other types. In advanced classes, students could be asked to determine the rules for predator reproduction. Students can be guided to the idea that predators that eat more will have higher rates of reproduction. Alternatively, smaller groups of students could play the game with different rules for predator reproduction and then report back to the class on the results, either in a poster session or oral presentations. In most classes, students could be asked to calculate the new predator ratios for the next year, given a set of rules for predator reproduction.
10. You will repeat foraging for several more generations after additional prey are added to the population, based on how many escaped predation in the previous generation. The amount of prey (based on weight) to be added will be automatically calculated by the included spreadsheet (Excel® predpreyblank.xls). Again, in advanced classes, students could be asked to determine the rules for prey reproduction. In discussing the rules for prey reproduction, the instructor can introduce the ideas of intraspecific competition and environmental carrying capacity. Smaller groups of students could play the game with different rules for prey reproduction and then the results of the different groups could be compared. In advanced classes, students could calculate the number of prey to be added for the next generation, given a set of rules for prey reproduction.
11. After each generation, fill in the Worksheet (Table 1 and 2). In each generation, there is a chance that another prey type will become poisonous or that a predator type will adapt to be able to feed on a previously poisonous prey. These are determined by the instructor and called out during predator foraging. In advanced classes, students could be asked to distinguish among prey morphs (using things such as different colored M&M's or Skittles).
12. At the end of the exercise, use the Worksheet (Table 1 and 2) to generate prey and predator population sizes among generations, and complete the graphs in the spreadsheet (Excel® predpreyblank.xls) (Figures 2 and 3). Then, use both (worksheet and graphs) to answer discussion questions and those questions posed by the instructor.
13. If time permits, design your own predator-prey scenario, experimenting with initial numbers of predators and prey, carrying capacity, etc. Introduce different prey items or habitat-types (different height of carpet fibers). Develop your own set of rules for foraging.

Questions for Further Thought and Discussion

1. What are the steps for successful predation to occur?
2. When a predator consumes a chemically defended prey item and becomes ill afterwards, the predator will tend to avoid this type of prey in future encounters. What term describes this predator behavior? What features of prey items might allow the predator to more easily avoid such prey?
3. When a potential prey first becomes toxic, what happens initially to the number of individuals of this population?
4. When no predators can consume a particular prey species, will the numbers of this species increase indefinitely?
5. When a species becomes established outside of its range, often no predators exist that consume it. Other than the application of pesticides, what strategies relating to this exercise might scientists use to control these pests?
6. What happens when insect herbivores reproduce more quickly than can be controlled by predators? What other factors control populations?
7. What would happen if the environment were affected by a chance event, such as a tornado, hurricane, or severe drought? Which of the "species" in your exercise would be most likely to survive and why?

8. Was there evidence of predator specialization when a predator type adapted to feed on the poisonous prey type?
9. Are predators successful based on only the quantity of prey consumed? Are there other factors that need to be considered?
10. Did all predator types remain in the environment or was your community eventually reduced to two species? In your experience with the game, which species remained and which were eliminated? Why?
11. What would happen if the food quality varied and the prey were not able to assimilate large quantities of defensive compounds? If potential prey species varied in the amount of toxins they possessed and if the prey reproduced faster if they were less toxic, what would happen to the predator-prey relationships?
12. Consider a different predator-prey system than the one designed in this laboratory exercise. Examples can be found in the literature of predator-prey interactions of fish, mammals, birds, reptiles, etc. Pick one example and examine the outcomes of the experiments. Provide a description of the example in detail. Design a game to test possible predation patterns in your example.

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- Van Thiel, L. R. 1993. Predator-prey coevolution. 1993 *ABLE Workshop/Conference Proceedings: Tested Studies for Laboratory Teaching* 15:293-318.

Useful Web Sites

- Bartlett, T. (editor). 2006. The Bug Guide.
  Contains many pictures and information about various kinds of insects.
  http://www.bugguide.net/
- Hoback, W. W., A. Bishop, and L. G. Higley. 2003. Virtual Insect Collection.
  Contains pictures of pinned specimens of insects with five views from many different orders and families.
  http://entomology.unl.edu/lgh/insectid/Virtual_insect/home.html
- Obrycki, J. J., M. J. Tauber, C. A. Tauber, and J. R. Ruberson. 1997.
  Prey specialization in insect predators.
  http://ipmworld.umn.edu/chapters/obrycki.htm

Tools for Assessment of Student Learning Outcomes

A. Evaluation of Discussion Questions
The outcomes of this laboratory activity are assessed by grading answers to discussion questions that are submitted at the end of the laboratory period. In addition, the concepts and terms covered in this exercise are tested on class exams. In particular, students are responsible for all bold terms in their introduction. These terms should be defined by the students during their preparation for exams. The discussion questions are answered by students during the laboratory period. We have provided sample answers in the Notes to Instructors section.

1. **What are the steps for successful predation to occur?**

   4 pts. 1 point for each stage (search, recognition, capture, and handling).

2. **When a predator consumes a chemically defended prey item and becomes ill afterwards, the predator will tend to avoid this type of prey in future encounters. What term describes this predator behavior? What features of prey items might allow the predator to more easily avoid such prey?**

   4 pts. Learned avoidance. Prey that are aposematic trigger easier predator recognition and aid in this process.

   2 pts. Provide term learned avoidance but do not describe features of prey items OR vice versa.

3. **When a potential prey first becomes toxic, what happens initially to the number of individuals of this population?**

   4 pts. The prey numbers increase because no predators can consume them. Competition for resources is not a factor initially.

   2 pts. For saying that prey numbers increase because of protection from predators but students argue that competition is important.

4. **When no predators can consume a particular prey species, will the numbers of this species increase indefinitely?**

   4 pts. No. Carrying capacity related to resources will constrain population and predators will evolve to utilize the new resource.

   2 pts. No but the students do not describe factors associated with carrying capacity.

5. **When a species becomes established outside of its native range, often no predators exist that consume it. Other than the application of pesticides, what strategies relating to this exercise might scientists use to control these pests?**

   4 pts. Introduce predators from the native range of these pests as classical biological control.

   2 pts. Introduce a predator but don't discuss that the predator is from the pest's native range.

   Questions 6-11 allow advanced students to be assessed for greater subject knowledge. It also allows for instructor-led discussions of these topics. Here we provide sample answers and evaluation criteria. In the Comments section we provide discussion of ways to improve student understanding.

6. **What happens when insect herbivores reproduce more quickly than can be controlled by predators? What other factors control populations?**

   4 pts. Limitations for food control prey numbers limiting survival and affecting reproduction. Alternatively if the herbivores greatly over shoot the carrying capacity, they are extirpated because of lack of food.

   2 pts. Students discuss competition but do not mention food limitations affects on reproduction.

7. **What would happen if the environment were affected by a chance event, such as a tornado, hurricane, or severe drought? Which of the "species" in your exercise would be most likely to survive and why?**

   4 pts. Environmental change often disrupts food webs in ecosystems. Generalist species are better equipped to survive such change because they have a broader pool of resources that can be utilized.

   2 pts. Students recognize effects of environmental disruption but incorrectly answer that specialists will survive better.

8. **Was there evidence of predator specialization when a predator type adapted to feed on the poisonous prey type?**

   4 pts. Answers will vary based on the outcome of student trials. Examine student answer for correct interpretation based on the experiment. Alternatively, present a graph of data and have students interpret the likelihood of specialization. Assign partial credit based on student's demonstrated understanding.

9. **Are predators successful based on only the quantity of prey consumed? Are there other factors that need to be considered?**

   4 pts. Students should recognize that prey vary by mass, and in real systems by quality of nutrients. Prey also have the ability to fight back and predator handling efficiency may result in changes to net energy acquired.

2 pts. Students recognize differences in prey quality but fail to specifically discuss energetic considerations of predator prey interactions.

10. **Did all predator types remain in the environment or was your community eventually reduced to two species? In your experience with the game, which species remained and which were eliminated? Why?**

    4 pts. Answers will vary based on the outcome of student trials. Students should recognize that prey defenses provide a temporary advantage and that predators shift to consume common prey. Often when a single predator can detoxify a given prey, that predator will "specialize" focusing just on that prey item.

    2 pts. Students cannot explain why certain predators or prey will be extirpated.

11. **What would happen if the food quality varied and the prey were not able to assimilate large quantities of defensive compounds? If potential prey species varied in the amount of toxins they possessed and if the prey reproduced faster if they were less toxic, what would happen to the predator-prey relationships?**

    4 pts. This question is very open-ended. Predators might be unable to learn to recognize protected prey if they were variable in chemical defenses. In the absence of strong predator pressures, the prey would remain non-toxic because of their increased reproductive capacity.

    2 pts. Students recognize either that predators will have a more difficult time learning or that non-toxic prey have a reproductive advantage in the absence of a large number of predators but do not include both parts in their answer.

B. Compose and Evaluate a Laboratory Report
Have the students report their findings in a report. You could have students, working in groups of four, create their own grading rubric. This should be facilitated by suggesting that they include a minimum set of three evaluation criteria (i.e. Did the Student Identify the Problem, What are the Conclusions and Implications). These criteria should be based on a scale of 1-6 (1: Emerging knowledge of the subject, 6: Mastery of the subject). The students can use their grading rubric to evaluate their own and a peer's report.

Further discussion of assessment and evaluation is contained in the *TIEE* site:
Charlene D'Avanzo. July 2000. Evaluation of Course Reforms: A Primer On What It Is and Why You Should Do It. (http://tiee.ecoed.net/teach/essays/evaluation.html)

Extension Activities for Advanced Students

1. Have the student establish the initial population sizes of predators and prey, as well as prey defenses and habitat type. This would allow assessment of how well the student can transfer their newly-acquired knowledge to a slightly different scenario and provides for a more open-ended activity.

2. Consider a different predator-prey system than the one designed in this laboratory exercise. Examples can be found in the literature of predator prey interactions of fish, mammals, birds, reptiles, etc. Pick one example and examine the outcomes of the experiments. Provide a description of the example in detail. Design a game to test possible predation patterns in your example.

3. A term paper can be assigned that requires students to investigate biological control success and failure. Assign the students the following problem:

"Based on the laboratory activity, you have seen the effects of predation in limiting population growth of insect herbivores. This principle has become the backbone of efforts to introduce predaceous species to limit population growth of pest species. Visit the ESCAPE website (www.unk.edu/escape/) and read about the impacts of exotic species and explore the issues surrounding these species.

Based on your in class exercise and your experience with the ESCAPE website, write a 3-4 page typed double-spaced paper to address the following questions. What are the reasons that exotic species sometimes become a problem in the area where they have been introduced? Based on the results of the laboratory exercise, what should be considered when introducing a predator to control a problem exotic species?"

Paper is worth 25 points and should include at least five references.

4. Have students research current pest management strategies in their area. Have species of insects been introduced to control weed species? Are these insects immune to predation from other insects? This activity lends itself to direct student investigation either in field plots or in the laboratory using feeding trials.

5. At the end of the experiment, make all predators able to overcome all prey defenses. Have predators forage until all prey are collected from the environment and time how long it takes. Then calculate the proportion of each prey eaten by each predator type. Is there any evidence of specialization by predators on prey species?

6. A logical extension of this exercise is to have students develop rules for a simulation of one predator/one prey that mimics the arctic situation and includes predator mortality without replacement.

NOTES TO FACULTY

Challenges to Anticipate and Solve

1. **Organization.** This laboratory requires large numbers of individual "prey" to be counted and reproduced. By using mass as a substitute for counting, the times between generations are greatly reduced. Having three large bins, one for each prey type, will help you add new prey to the environment.
2. **Student analysis of feeding rates.** At the end of each exercise (round), students must sort the contents of their stomachs by predator type. It is helpful to assign a predator leader for each predator type. Provide three containers into which eaten prey can be segregated for each predator type (9 containers total). Watch for any predators that have an inedible prey item in their stomachs, as they lose all prey back to the environment. In their groups, the student predators will sort prey items and then one student can report the weights of each prey item.
3. **Depleted prey availability.** Occasionally, and especially with larger groups, the initial 200 prey items of each kind are insufficient. In the first generation, there are approximately 600 edible prey available to 24 students. This can sometimes lower numbers to point where prey cannot recover despite high rates of reproduction. In this situation, prey are allowed to migrate into the area from the outside (lots of resources are now available). Alternatively, you can start with greater prey numbers in the environment.

Introducing the Experiment to Your Students

The experiment is conducted in our General Biology for non-majors class. This laboratory activity follows evolution and is conducted during the week of ecology. In class, students have received general instruction about ecological concepts, including niche, predation, aposematic coloration, crypsis, predator-prey interactions, and population growth. In the laboratory, students are introduced to the topic by being shown pinned insect predator and prey types (from a large collection maintained at the University). As the specimens of insects are discussed, a simulation of feeding appendage also is introduced. Note, we show a number of insects, including mandibulate predators (ground beetle, ladybird beetle, tiger beetle, predaceous diving beetle), predators that use raptorial forelegs (preying mantis, ambush bug, assassin bug, mantisfly), and predators that use all six legs (flying predators including dragonflies, damselflies, and robberflies). Additional photographs of many insect families are located at the Virtual Insect Collection (http://entomology.unl.edu/lgh/insectid/Virtual_insect/home.html). Insect predators are found in Diptera: Asilidae, Neuroptera: Mantispidae, Odonata (all), Hemiptera: Phymatidae). In addition to the specimens, the students are shown the illustration of feeding appendages that they will use (see Description: Figure 1).

Next, we discuss prey types and predation. Students are asked to think about prey defense strategies. These include camouflage (we show stick insects, plain grasshoppers, and thorn insects), aposematic coloration (we show wasps [Hymenoptera: Vespidae and Apidae], bright grasshoppers [Orthoptera: Acrididae], bright tiger moths [Lepidoptera: Arctiidae]), flash coloration (we show grasshoppers [Orthoptera: Acrididae] and underwing moth specimens [Lepidoptera: Noctuiidae]). As an alternative to pinned specimens, students can be shown images. In particular, an excellent source of images of many types of insects can be found at BugGuide.net (http://bugguide.net/node/view/15740). We discuss the steps of predation from search, identification, capture, and handling. We then point out insects that have defenses against all of these steps in the predation process.

During the introduction and ensuing discussion of prey defenses, we discuss poisons. Students are asked where insects obtain poisons and why not all insects are poisonous. During the fall term, live insects, including ladybird beetles and blister beetles are shown (both possess reflex bleeding and can be shown defending themselves). During spring semester, we show PowerPoint slides of bombardier beetles and monarch butterflies. The discussion is facilitated to ensure that the topics of evolution (acquisition of defense) and response to predation pressure are covered. We also discuss how a predator recognizes or "knows" if a prey item is poisonous. We show slides of the blue jays regurgitating after eating a monarch. We then talk about praying mantises doing the same thing when eating chemically defended prey.

In this exercise, students use a variety of feeding appendages constructed from plastic utensils (see Description: Figure 1) as they search the environment grabbing prey items (i.e., candy) and placing them into their stomachs (i.e., paper cups). For our simulations, we place equal numbers (n = 200) of three kinds of candy (M&M's, candy corns, and Skittles) onto shag carpet samples in a 2 x 3 m area. Candy represents edible prey and provides a handy snack at the end of lab; however, three or four types of small items, such as beans, buttons, plastic insects, etc., could also be used. Likewise, instead of using shag carpet to simulate a heterogeneous environment, the environment could consist of a grassy lawn (here, wrapped candy would be a must), a tabletop, or a cardboard box filled with packing material.

The instructors then assign feeding appendages based on these predator types and provide small paper cups that represent stomachs. Feeding appendages consist of pairs of plastic forks, knives, and teaspoons that are rubber-banded together to form a chopstick-like apparatus. The pairs of knives represent mandibles, pairs of teaspoons represent raptorial legs, and pairs of forks represent grasping legs. An equal number of each predator type is randomly assigned among the students (see Description: Figure 1).

Below are the rules that we use in the game. In our experience, non-majors have difficulty determining the rules based on ecological concepts. As a result, we have found it more useful to provide students with the rules and then discuss the ecological concepts related to those rules. However, in more advanced courses, students might be asked to determine the rules for foraging, learned avoidance, predator reproduction, prey reproduction, and the evolution of poisonous prey and predators that can eat them. With this approach, a guided inquiry could be used such that students are guided to the rules outlined below. It also may be possible to divide the class into smaller groups and have each group play the game with their own set of rules. Then, the groups could report back to the class in the form of a poster session or oral presentations to discuss how the rules they chose led to the results they found. Students at all levels could be asked to calculate the predator ratios and prey densities in the next year based on the rules. Although this step might increase the amount of time that it takes to complete a given game, it reinforces quantitative skills and increases student understanding of the dynamics of the game.

Foraging:

1. The predator must use only its feeding appendage to capture prey.
2. The predator must stop foraging when the stomach is full or when time expires.
3. If any inedible prey are in the stomach at the end of the 45 seconds, all of that predator’s prey are returned to the environment.
4. The stomachs must be held upright at all times (no shoveling).
5. To simulate learned avoidance, at the start of foraging the student predators do not know which prey species is inedible. Foraging takes place for 30 seconds prior to the announcement of the kind of inedible prey. Then, students with inedible prey in their stomachs must dump all items back in to the environment to simulate sickness prior to resuming foraging. With limited edible prey available, the students experience increasing competition and the foraging exercise is stopped after 45 seconds.

Potential Concerns and Questions: Make sure that predators are represented in approximately equal numbers. Students may wonder how they will know that a given prey item is poisonous. Mention that after 30 seconds if they eat something poisonous they will be informed of feeling ill.

Students foraging on prey items on a table-top shag carpet environment.

After Foraging/Digestion:

1. After the end of feeding, the predators must digest their prey, represented by the time it takes to determine the number and kind of prey species in their stomachs.
2. Prior to the exercise, the average weight per prey individual is determined. After foraging, the number eaten are determined by weighing and then calculating number of individuals.
3. A running tally for each predator type can be displayed on a board for later discussion. The students should use these numbers to fill in their Worksheet.

Potential Concerns and Questions: It takes a long time to count individual prey items that were consumed. To speed this process, students sort their prey by kind into different cups and use balances to weigh each type. This way the number of prey of each type that has been consumed can be calculated quickly.

Calculations for the Next Round:

Based on the number captured, the number of prey remaining in the environment per species is calculated (200 - # eaten = # surviving) and prey are allowed to reproduce according to the following formulae. The poisonous species of the first round produces one copy of itself for each member that remains in the environment (doubles the number in the environment). The species that will remain palatable to all predators throughout the exercise reproduces at a rate of three individuals for each that remains in the environment. The other species will become unpalatable in the second round. It reproduces at an intermediate rate of two individuals for each that remains in the population.

In the second generation of the exercise, a second prey type becomes poisonous and cannot be eaten by any predator. Often, predation rates cannot keep pace with reproductive rates of some prey species. To avoid saturating the environment with prey (and to simultaneously maintain reasonable costs), a limit to reproduction by prey is imposed. Typically, no more than 300 prey per generation are added to the environment.

Potential Concerns and Questions. Students may question why there is a population cap on each species. This cap is explained ecologically as the role of intraspecific competition for resources (or environmental carrying capacity for a species). In the absence of predation, herbivorous species will increase in number until their food becomes limiting; then, only those members of the species that are able to acquire sufficient nutrients will be able to reproduce. In this exercise, each prey species is assumed to feed on different resources and thus is unaffected by interspecific competition.

Potential Concerns and Questions. Students also wonder how the number of predators are established for the next round. The predator numbers change in response to foraging success. Foraging success for each predator type is calculated and the reproductive success and thus reproduction is determined as the ratio of each predator type's success divided by the total prey consumed by all predators (e.g. amount eaten by P1/ amount eaten by (P1 + P2 + P3). The ratio of predators is adjusted by changing foraging morphologies of unsuccessful predators into those of successful predators at the appropriate frequencies.

Potential Concerns and Questions. Students wonder how a given predator type is chosen to adaptively detoxify the poisonous prey species. The predator type is chosen either at random or to favor the predators with the least members by the laboratory instructor. That predator type is able to eat all prey types except the prey species that becomes poisonous in the next round. The other predator types must selectively avoid both the poisonous prey type from the previous round and the new poisonous prey type as they struggle to overcome competition and reproduce.

Potential Concerns and Questions. Students will ask when the exercise is completed. The exercise is continued until stability is reached or all but one predator type or prey type has become extinct. A short discussion is conducted as the prey are replaced in the environment. Predictions about the community's behavior are made and the exercise is repeated as above again randomly assigning poisonous prey and predator adaptations.

Potential Concerns and Questions. Students at first are confused that they input mass into the spreadsheet (Excel® predpreyblank.xls) whereas the graph output is in numbers of individuals. Note that Table 1 and 2 are generated from the supplied Excel spreadsheet based on internal conversions. Students can create their own graphs using the blank table forms. For a more formal assessment of the laboratory, students can generate a formal laboratory report, answer questions, and search the literature to determine the community dynamics between insect predators and their prey. Informally, the principles can be discussed in terms of other predator-prey systems.

Potential Concerns and Questions. Non-majors and majors in their first year struggle with interpreting the outcomes between generations. Almost certainly, the outcomes will differ even if the same prey types become poisonous and the same predator types adapt. The differences may result from the fact that the predators will be experienced and are more efficient in the second trial. Additionally, predators may gamble by guessing prey types to avoid initially. Occasionally, predator or prey types are forced to extinction in one or both trials. Students should explain the results and speculate on the evolutionary process. For introductory ecology classes, students could be assigned primary literature or instructed to find an article that reports on predator-prey interactions.

Experiment Description

The Excel spreadsheet makes the calculations for this experiment automatic and produces graphical output of the results. The instructor should try out the spreadsheet (Excel® predpreyblank.xls) prior to conducting the exercise. It is important that the spreadsheet only have data input in the blue areas. No other part of the spreadsheet should be edited.

The spreadsheet consists of two tables and two graphs of the results. The first spreadsheet table consists of prey reproduction rate (intrinsic rate of increase) and weight per prey. When preparing for the lab exercise, the instructor should decide which prey type is initially poisonous and which prey type will become poisonous in the second generation. Based on the organisms becoming poisonous, a reproductive rate is established.

After each generation, measure and record the total weight of each type of prey consumed (Mass of Prey Consumed [Designated in Blue]) and the total weight consumed (Prey Mass Consumed by Predator Type [Designated in Blue]). Have each predator type sort their prey into three labeled pre-tared containers (one for each prey type). The instructor then weighs the amount of prey eaten by the predators and determines the total mass of prey eaten. This is also a good time to identify poisonous prey that should not have been eaten and eliminate that predator's contribution from the tally.

The second table shows the experimental results. Prey reproduction is generated by subtracting the total weight of prey eaten by the predators from the starting biomass and then multiplying this result by the species-specific reproductive rate. The spreadsheet generates the mass of new prey to add and shows this as number on the graph. Note that the spreadsheet shows zeros for generations that have not yet been simulated.

The spreadsheet also displays the number of each predator type for the next generation. The change in predator numbers results from differential feeding efficiency. Initially, there are approximately equal numbers of predators. Numbers in subsequent generations are the result of the proportion of total prey consumed by predator type. Explain changes to predator types as differential reproductive success when a predator acquires more energy than its competitors.

The first figure shows the changes in prey numbers versus generation time. The second figure shows changes in predator proportions with generation time. During the laboratory exercise, the students complete their own graphs on the blank figures provided (Excel® predpreyblank.xls), Figures 2 and 3). They can use these graphs to make predictions about the change in population numbers in response to predation pressures and or evolving chemical defenses. At the end of the exercise, the two figures generated by the Excel spreadsheets can be printed and then photocopied and given to students or can be uploaded to a website for later access.

Questions for Further Thought

Answering the Discussion Questions:

6. What happens when insect herbivores reproduce more quickly than can be controlled by predators? What other factors control populations?

> *Answer*: The prey population may become a pest and is not regulated by predation. The population will eventually be controlled by other factors, including competition for resources, weather, and disease.
>
> *Conceptual Problem*: Students believe that the population will increase indefinitely.
>
> *Solution*: Direct the students to the concepts resource limitation (competition for prey) and carrying capacity.

7. What would happen if the environment were affected by a chance event, such as a tornado, hurricane, or severe drought? Which of the "species" in your exercise would be most likely to survive and why?

> *Answer*: Environmental change can open niches and eliminate species. The population of prey that has the highest reproductive rate will be most likely to survive a changing environment, since in this exercise it is assumed to be least specialized. In this exercise, the development of toxicity assumes that the prey are feeding on plants containing chemicals. As the environment changes, plant species are expected to be lost, as are the prey that feed on them. Generalist species with high reproductive rates are expected to be less dependent on particular prey species and thus, be more likely to survive changing environments.
>
> *Conceptual Problem*: Students, especially non-majors who are presented K- and r-strategies in their textbook, will sometimes be confused by the difference in K- versus r-strategists with populations including insects, although current ecological literature does not recognize this continuum.

Solution: For mammals, low reproductive rates are offset by high maternal care and better buffering against change. For insects, high genetic diversity and large numbers of offspring allow survival despite environmental change.

8. Was there evidence of predator specialization when a predator type adapted to feed on the poisonous prey type?

Answer: Usually the predator that can detoxify a prey increases in number by specializing on a prey resource that others cannot eat. This is especially true when the poisonous prey is larger than other prey items when students are playing the game. In natural systems, insect predators are often generalists. However, a number of well-studied cases show specialization including the vedalia beetle, Rodolia cardinalis, and the green lacewing Chrysopa slossonae, that feed on only one species of prey. For a review, see Obrycki et al. 1997 (http://ipmworld.umn.edu/chapters/obrycki.htm).

Conceptual Problem: Trouble with predator specialization.

Solution: This is a good moment to facilitate a discussion on specialized versus generalists predators. This may lead to a general discussion of co-evolution between a specialist predator and a prey with strong chemical defenses.

9. Are predators successful based on only the quantity of prey consumed? Are there other factors that need to be considered?

Answer: In this exercise, quality of prey items is not considered directly as long as the predator is able to detoxify a given item if it is poisonous. So, for the exercise, prey quantity is measured and those predator types that consume a greater mass of prey reproduce at higher rates.

Conceptual Problem: Students should consider the nutritional value of each food item versus the quantity of food to be eaten.

Solution: This is an excellent opportunity to facilitate a discussion about food quality. In terms of predators, most predatory species, including insects, are generalists rather than specialists. This not only buffers them against a changing prey base, but also allows them to acquire necessary micronutrients.

10. Did all predator types remain in the environment or was your community eventually reduced to two species? In your experience with the game, which species remained and which were eliminated? Why?

Answer: Depends on the trends observed. Usually the community is fairly stable with all species co-existing. Sometimes only the toxic prey and the predator that can eat them remain and then because of low reproductive rates, the prey are eliminated and the predators starve to death.

Conceptual Problem: Ecological equilibrium and predator-prey dynamics.

Solution: Students should be made aware of the arctic system in which lynx numbers track hare numbers. Then, other ecosystems that do not show these trends should be discussed. When multiple prey and predator types are available, changes to numbers of one species often result in shifts in other species numbers. A logical extension is to have students develop rules for a simulation of one predator/ one prey that mimics the arctic situation and includes predator mortality without replacement.

11. What would happen if the food quality varied and the prey were not able to assimilate large quantities of defensive compounds? If potential prey species varied in the amount of toxins they possessed and if the prey reproduced faster if they were less toxic, what would happen to the predator-prey relationships?

Answer: In the presence of predators, the toxic, but slower reproducing, prey would survive. However, in the absence of predators, the non-toxic members of the group would out-compete the toxic if resources were limited and the non-toxic reproduced faster or in greater number (a similar phenomenon with drug resistant bacteria). This situation could lead to mimicry complexes and better predator recognition of non-toxic prey.

Conceptual Problem: Students need to understand that individuals experience trade-offs.

Solution: Have students brainstorm about why all species are not toxic, after all it seems to be a big benefit. There must be some cost to being poisonous or being able to survive exposure to poisons from resources that others cannot consume. Whether it is from enzymes for detoxification or from the energetics of digestion and incorporation into their own arsenal, members of the population that are the most efficient will leave more offspring. However, what happens if selection pressures shift? In the absence of predators, a mutation that results in a non-toxic form may gain an advantage if the cost to carrying a chemical defense is high enough. Faculty may want to consult the references or make them available for more advanced students.

Assessment of Student Learning Outcomes

Students fill in answers to the discussion questions and then later are tested on the materials. Make sure to define all bold terms in case of questions. In addition to later quizzing, students also could be asked to write a paper or make a class presentation.

Evaluation of the Lab Activity

This laboratory exercise has been conducted with college students in non-majors biology and as an ecology laboratory exercise. In addition, the exercise has been conducted with middle school students as part of learning about insects. During development, student feedback was solicited using interviews and "muddiest point" style questions. Students expressed concerns about not "seeing" the calculations in Excel. This concern is addressed by having the students fill out their own worksheets after each round. For laboratory rooms that contain computers, students can work in groups of 3-4 to enter their own data.

In a summative assessment, we can observe if the students learn what we had hoped they would learn. Additionally, the pre-test provides formative assessment of the students' knowledge going into the laboratory exercise.

Pre- and post-tests are designed and included to evaluate the amount of student learning through this laboratory exercise. The results of pre- and post-testing from Fall 2005 are included below.

Pre- and post-tests consisting of five short discussion questions worth 4 points each (listed in Description: Tools for Assessment of Student Learning Outcomes) were given to assess student progress. A total of 132 non-majors in biology were tested. The pre-test was given at the beginning of the laboratory period that presented the predation exercise. The post-test was provided at the beginning of the next week's laboratory period. After giving these tests, the laboratory instructors completed a form that presented how many students answered each item correctly on each test. These data were collected, pooled by student and analyzed using a paired t-test.

The average test score on the pre-test was 5.2 out of 20. The average score on the post-test improved to 14.5 out of 20. This change was highly significant ($t = 30.1$, d.f. = 131, $P < 0.001$).

Translating the Activity to Other Institutional Scales or Locations

This activity is suitable for multiple classes without modification. Very small classes should reduce the number of initial prey and large classes should increase the prey amount. Extension activities add depth and increase difficulty, while allowing a focus on current problems associated with exotic species. For middle school students, the emphasis is on students learning about insect predators and their role in the environment. Ecological concepts are appropriate for high school and college students. The exercise has been conducted successfully with both non-majors and majors. Students with physical or other disabilities can still participate in the laboratory through observation and measurement of prey eaten.

STUDENT COLLECTED DATA

A representative data set is included in: predpreysample.xls