Chapter 14

Insect Predation, Prey Defense, and Community Structure

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Reprinted From: Hoback, W. W. and L. G. Higley. 2000. Insect predation, prey defense, and community structure. Pages 293-304, *in* Tested studies for laboratory teaching, Volume 21 (S. J. Karcher, Editor). Proceedings of the 21st Workshop/Conference of the Association for Biology Laboratory Education (ABLE), 509 pages.

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Instructor's Introduction

Insects

Insects are the most numerous, most diverse, and most ecologically important terrestrial animals. Numbering over 1,000,000 species (mammals including humans have about 4,000 species), insects were the first organisms to successfully colonize land. They occur in virtually all terrestrial habitats, excepting the most extreme (the arctic, antarctic, and peaks of the highest mountains).

Key features of insect biology are that insects have an exoskeleton, three body regions (head, thorax, and abdomen), and six jointed legs. Insects must molt as they grow, and immature forms may resemble the adult (incomplete metamorphosis) or be completely distinct in appearance and habits (complete metamorphosis). Insects have passive respiration (air diffuses into the body through a series of tubes called tracheae, and insect "blood" has no oxygen carrying capacity).

Understanding the biological classification of insects is important, because it helps in denoting ecological and evolutionary commonalties among species. Key levels for insects are the Order and Family, as these divisions often provide useful levels for generalizing about insect morphology (structure and function), physiology, and ecology.

The levels of classification are:

- Kingdom Animalia – The animals.
- Phylum Arthropoda – The arthropods, animals with exoskeletons and jointed feet, including insects, spiders, scorpions, mites, ticks, crabs, lobsters, shrimp, and their ilk.
- Class Insecta or Hexapoda (the name depends on what source you read) – the true insects.
- Order – Insects have between 28 to 33 of these (again, depending on what source you read). We may not all be entomologists (mores the pity), but almost everyone can identify some insect orders. Among the kinds are Hemiptera and Homoptera (two orders containing the true bugs), Coleoptera (beetles), Lepidoptera (butterflies and moths), Diptera (flies), and Hymenoptera (ants, wasps, and bees).
- Family – The key level below the Order that entomologists use for generalizing about insects. For example, tiger beetles, belong to the Order Coleoptera, Family Cicindelidae.
- Genus and species – In principle at least, a reproductively (genetically) distinct group.

Because insects were the first group to be successful in a terrestrial environment, insects occupy every ecological niche from herbivore to predator to decomposer to farmer (in the case of some ants and termites). As insect species evolved, the interaction between predatory and non-predatory species resulted in co-evolution of prey defenses and the resulting requirement for predators able to overcome these defenses.

Insect Foraging Methods

At present, there are three common foraging methods used by predaceous species. The majority of insect predators subdue potential prey using their mouths. Common examples include antlion larvae, ants, and tiger beetles. A second convergently evolved method of predation is the use of enlarged and modified (raptorial) forelegs to grasp and subdue prey. Insects that have raptorial forelegs include preying mantises, giant water bugs, and ambush bugs. Lastly, many flying insect predators collect prey using their legs like a net. Common examples include dragonflies and robber flies.

This Exercise

This exercise creates an active simulation of insect predator-prey relationships in a recently disturbed environment where potential prey have become abundant. This exercise represents a modification and extension of an exercise presented by Van Thiel (1993) at a previous ABLE conference. This exercise differs from the Van Thiel version by modeling prey evolution of defenses against predators followed by predator evolutionary response. The exercise simulates all four stages of a predation event as students play the roles of insect predators employing one of the three principle feeding morphologies as they capture different species of prey. The predator-prey co-evolutionary arms race is demonstrated by causing certain prey to become unpalatable. The cost of adapting to be able to consume the poisonous form is simulated by a reduced reproductive rate of the poisonous species. To mimic co-evolution, one predator type adapts to be able to consume the poisonous species. After each foraging bout, prey species are reproduced based on formulae that account for differences in reproductive rates. Predator efficiency is calculated based on the proportion of prey consumed by each predator type. Selection reduces inefficient predators and reproduces efficient ones. The change in predator ratio is tracked simultaneously with changing prey numbers. The simulation is conducted until predator and prey reach equilibrium (usually about 10 generations) or until only one predator type remains.

Preparation and Lab Time

This exercise requires one laboratory period (2-3 hours) and is suitable for introductory biology and ecology classes. The exercise requires construction of predatory structures (created from plastic silverware, rubber bands, and spacers), acquisition of carpet samples, and candy, beans, or other suitable prey. It also requires access to a computer with Microsoft Excel.

Analysis of the exercise involves discussion concerning co-evolution and predictive hypothesis generation. Time permitting, the exercise is repeated and the outcomes of both compared. A lab report containing information about insect predatory forms, relative importance of different steps in predation for different predator types, potential prey defenses, the costs and benefits of defense against predators, and the interaction between predators and prey in shaping an environment should be prepared.

Materials

- One set of each type of predatory appendage per student are pre-constructed using plastic forks (preferably 3-tined salad forks), plastic long handled teaspoons, and plastic knives. The appendages are separated by a spacer and held together with a rubber band to form tongs.

- Three appropriate prey types are selected. In our exercise, the prey types consist of three types of candy (M and M's™, Skittles™, and candy corns). This exercise potentially requires a maximum of about 1,500 pieces of candy. There are about 500 pieces in a pound of each variety, so 3 pounds of each candy provides plenty (and a good feed for 25 students, graduate students, secretaries, etc.!) Other objects can be substituted depending on the numbers of students and available resources.
- Predator stomachs consist of 4 oz. Dixie™ bathroom cups.
- The habitat is created on tables or the floor and is made with 1.5 x 1 foot carpet samples. Carpet samples can be obtained from major carpet stores free of charge. By randomly building the environment, spatial heterogeneity can be created.
- Access to an IBM-compatible computer with a spreadsheet (ideally) or a calculator and graph paper.
  Contact Hoback at **hobackww@unk.edu** or check the ABLE webpage for a copy of the spreadsheet.
- A balance with pre-tared containers speeds the process of determining the amount of prey consumed.

Costs

This exercise is fairly inexpensive, except for the cost of candy. For three pounds each of M and M's™, Skittles™, and candy corns, the cost is about $30.00. The cost of cups is about $3.00, and the cost of plastic silverware is about $5.00. For large numbers of laboratories, prey types that can be recycled such as dried beans (Thiel 1993) or buttons may be used to reduce costs. An alternative form of edible prey is Goldfish crackers which can be purchased in two pound boxes of assorted flavors from wholesale outlets such as Sam's Clubs.

Notes for the Instructor

In this exercise, students use a variety of feeding appendages 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 and M's, candy corns, 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, but, three or four small items such as beans, buttons, plastic insects, etc. could be used. Likewise, instead of using shag carpet to simulate a heterogenous 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.

When the students arrive, they are shown pictures of various insect predators and their roles 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 held together with a rubber band 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.

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 use only its feeding appendage to capture prey. The predator must stop foraging when the stomach 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 eaten are determined by weighing and then calculating 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 species remaining in the environment are calculated (200 - # eaten = # surviving) and allowed to reproduce according to the following formulae. 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 (approximately an exponential growth rate). 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 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 be 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 detoxify the poisonous prey species adaptively. That predator type is able to eat all prey types except the morph that becomes poisonous in the next round. The other predator types must selectively avoid both the poisonous prey and the poisonous morph 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.

Generate figures using the supplied Excel spreadsheet. Print these and distribute them to the class. Have the students generate a formal laboratory report, answer questions, and speculate on the community dynamics between the insect predators and their prey.

Questions may include the interpretation of outcomes between generations. Almost certainly, the outcomes of different trials 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 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 co-evolutionary process. For introductory ecology classes, students could be assigned primary literature or instructed to find an article that reports on predator-prey interactions.

Features of the Spreadsheet

The spreadsheet consists of four tables that require data entry, two tables that show results from the data entry, 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 carrying capacity is established.

The second and third tables are generated during the exercise and consist of measuring and recording the total weight of each type of prey consumed and total weight consumed by each predator type. Each predator type should sort their prey into three labeled pre-tared containers (one for each prey type). The instructor then weighs the amount of prey eaten by mandibulate, raptorial, and grasping predators and the total amount 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 to the tally.

The fourth table represents prey reproduction and 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 number of new prey to add.

The fifth table generates the proportion of each predator type for the next generation. The change in predator numbers results from differential feeding efficiency. Initially, there are equal numbers of predators. Numbers in subsequent generations are the result of proportion of total prey consumed by predator type and are presented in table five.

Figure 14.1 plots table four and shows changes in prey numbers versus generation time. Figure 14.2 plots table five and shows changes in predator proportions with generation time. At the end of the exercise, the two figures can be printed, photocopied, and given to students or can be uploaded to a website for later access.

Student Introduction and Background

This exercise is designed to teach the principles of insect predator-prey relationships and their impact on ecological communities. It is an important teaching exercise because predator-prey relationships have remained a contemporary focus of ecological research for over a century. Predation plays at least three critical roles in shaping communities. First, predation may 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. The presence or absence of predators creates ecosystem effects at multiple 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. But when predators are in the environment, often there are fewer herbivores and in turn more plant material. These phenomena are expressed as the cascading trophic interaction model (Carpenter et al. 1985). Third, predation is the major selective force leading to predator-prey co-evolution (Krebs 1994).

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 are adapted to recognize potential 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 species have mechanisms to counter predator efficiency at each step of the predation process. Prey can be difficult to locate because they have **cryptic** or **polymorphic** forms. They may be difficult to locate because they are dispersed in the environment. To reduce recognition, prey species are often mimics of dangerous species. Prey also have developed quick escape or defensive mechanisms. Finally, if captured, prey species have adaptations to reduce handling efficiency including spines, tough cuticles, and toxins (Krebs and Davies 1993).

Insects provide dramatic examples of predator-prey co-evolution and are ideal subjects for illustrating the principles of predator-prey interactions and their role in shaping ecological communities. Among the insects, three predator forms are common. First, many 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 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.

Insects use a variety of defenses against predators. Defenses include being cryptic or polymorphic, being able to escape rapidly, being armored, and being poisonous. Additionally, many edible species gain protection from predators by mimicking the appearance of poisonous species. A different protection from predation occurs when there are **refugia** where prey can reproduce without being eaten by predators.

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 preying 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.

So clearly, insect predators can become ill from eating poisonous prey and can learn to avoid prey that look the same. But, what keeps insects like 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 to feed 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 which are poisonous.

Beyond the obvious co-evolutionary arms race between predators and prey, many factors 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. Often, when an environment is disturbed, such as by flooding, fire, pesticide use, or farming, predator-prey relationships change. If few predators are in the environment, herbivores can reproduce rapidly to reach 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 returns the community to an equilibrium of predator-prey species.

Insects, Pests, and Integrated Pest Management

Insects are the dominant terrestrial animal life on earth. With over 1,000,000 described species, insects comprise 80% of all described species. Insects occupy all feeding niches, feeding on plants (**phytophagous**), animals (**predaceous**), and on decaying material (**saprophagous**). Most insect species have 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 for a single year would produce a layer of fruit flies over the earth about 991 million miles deep!

With such a high potential for reproduction, herbivorous insects have the ability to become **pests** (defined as a species whose activities usually enhanced by numbers, causes economic losses to human possessions). Some examples of pest species for agricultural crops include corn rootworms, European corn borers, and cotton boll weevils. Despite these and many more well-known pests, the number of insects that are classified as pests are less than 1% of the total described species! In fact most populations are kept in check by natural predators.

One of the best methods of controlling insect pests is through biological control. Though usually focussed on insect parasitoids which are specific to certain pests, insects predators including ladybird beetles, preying mantises, and green lacewings have been widely introduced for the purpose of reducing pest numbers naturally. Insect predators are usually large compared to their prey, are generalists, feeding on a wide range of species, and often showing a time lag between prey population increase and predator population increase.

When successful, biological control is an environmentally safe tactic, which can achieve long-term control and is ultimately inexpensive compared to conventional pesticide applications. An example of successful biological control through the use of a predator is the control of cottony cushion scale in California's citrus region by the Vedalia beetle achieved in 1889 by C.V. Riley. Unfortunately, biological control requires a long time to become established, and may be incompatible with other tactics. Biological control through predators may also fail if the predation rate is insufficient to counterbalance the pest's reproductive rate.

In the absence of predation, many herbiverous insects still do not become pests. This is because when they reach high numbers, members of the species are forced to compete more and more for limited resources. When faced with increasing competition, not all members of the species can acquire enough resources to reproduce successfully. Thus, resource limitation due to increased competition can regulate population size. This principle is called the **carrying capacity** of the environment.

Exercise Instructions

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 (a 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 <u>not</u> from their stomachs.
4. You will forage for as much prey as possible within a time limit of one minute.
5. After feeding for 30 seconds, you will have an adverse reaction if you have eaten poisonous prey. You will vomit, losing all your stomach contents back into the environment.
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 which ate the most prey (by weight) will reproduce, replacing ineffecient predators.
10. You will repeat foraging for several more generations after the instructor reproduces prey.
11. 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.
12. At the end of the exercise, get data sheets and answer questions posed by the instructor.

Acknowledgements

We thank Tina Svatos, Doug Golick, and Steve Spomer for their assistance during the developmental phase of this project. Funding for the project development was provided by the Agricultural Research Division, UNL, University of Nebraska Agricultural Experiment Station Project 17-068.

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Appendix A

Sample Questions for Discussion

1. What happens when insect herbivores reproduce so quickly that their numbers can not be controlled by predators? What other factors control populations?

2. Was there evidence of predator specialization and co-evolution when a predator type adapted to feed on the poisonous prey type?

3. What factors make a predator most successful: the quantity or the mass of prey?

4. Which predator type would eventually become dominant?

5. What would happen if the food quality varied and the prey were not able to assimilate large quantities of defensive compounds?

Appendix B

Data Entry

Prey Name	Reproductive Rate	Weight/Prey	Starting Prey #'s	Carrying Capacity

Predator Numbers	
Mouth (knives):	
Raporial (spoons):	
Legs (forks):	

	Mass of Prey Consumed							
	1	2	3	4	5	6	7	8
Prey 1:								
Prey 2:								
Prey 3:								

	Prey Mass Consumed by Predator Type							
	1	2	3	4	5	6	7	8
Mouth (knives)								
Raporial (spoons)								
Legs (forks)								

Figure 14.1. Shaded cells in the spreadsheet require data entry. The instructor decides prey types, weights, which prey will become poisonous, and the carrying capacity before the experiment. Predator numbers are generated by dividing students into three groups.

Data Entry

Prey Name	Reproductive Rate	Weight/Prey	Starting Prey #'s	Carrying Capacity
Milk Duds	1.5	1.03	200	500
Candycorns	2	0.21	200	750
M and Ms	2.5	0.19	200	1000

Predator Numbers	
Mouth (knives):	6
Raporial (spoons):	7
Legs (forks):	6

	Mass of Prey Consumed							
	1	2	3	4	5	6	7	8
Prey 1: Milk Duds	0	104.5	270.5					
Prey 2: Candycorns	37.7	52.4	52					
Prey 3: M and Ms	27.2	0	11.6					

	Prey Mass Consumed by Predator Type							
	1	2	3	4	5	6	7	8
Mouth (knives)	31	30.1	40.8					
Raporial (spoons)	24	110.6	254.8					
Legs (forks)	28.8	28.6	44.3					

Experimental Results

	Prey to Add at Start of Generation							
	1	2	3	4	5	6	7	8
Prey 1: Milk Duds		100	99	18				
Prey 2: Candycorns		21	209	248				
Prey 3: M and Ms		85	213	441				

	Population by Generation (Constant Predation Rate)							
	1	2	3	4	5	6	7	8
Prey 1: Milk Duds	200	300	298	53				
Prey 2: Candycorns	200	41	0	0				
Prey 3: M and Ms	200	142	355	735				

	Predator Numbers by Generation							
	1	2	3	4	5	6	7	8
Mouth (knives)	6	7	3	2				
Raporial (spoons)	7	5	12	14				
Legs (forks)	6	7	3	3				

Figure 14.2. Sample data sheet showing predatio rates and change in prey numbers. In this exercise, candycorns went extinct after two generations, and milk duds after four generations.

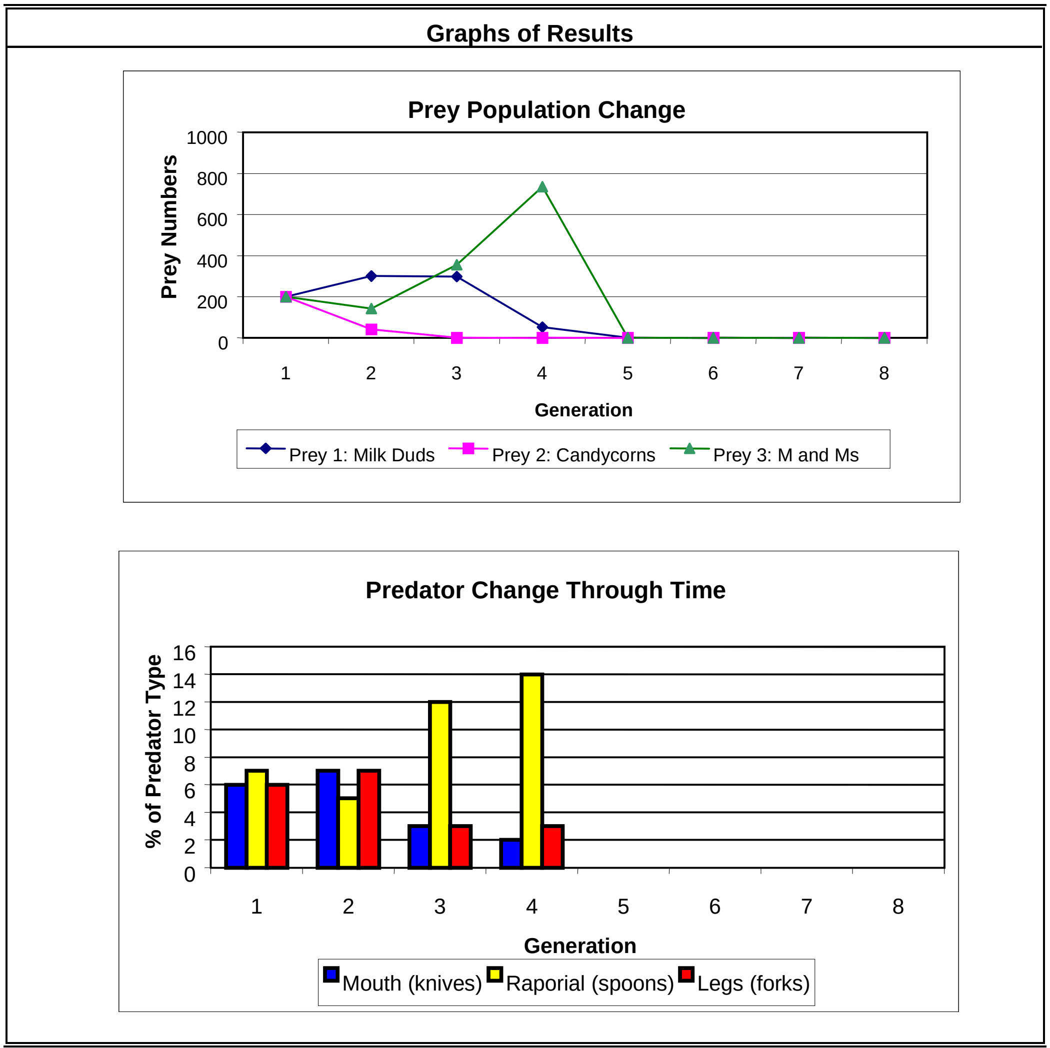

Figure 14.3. Graphs of results. The first graph shows prey population changes versus generation. The second graph shows change in predator numbers by generation. In this exercise, raptorial predators adapted to poisonous prey and subsequently increased in number.