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13



Great White Shark

Predation

Understanding the ecology of biological populations usually comes from a consideration of the physical and biological environment. The biological environment includes other organisms with which members of a population interact. Some of these other organisms may be competitors for important resources. Others may be an important food source for some species. **Predation** occurs when one animal species feeds on another and, in that process, kills it or consumes most of the organism. An animal that is killed is called the **prey**. Animals that feed on plants are called **herbivores**. There are many important similarities between predation and herbivory, but here we will treat each separately.

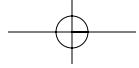
One obvious effect of predator-prey relationships is that the numbers of predators will be affected by the numbers of prey, and vice versa. Prey numbers decline as a result of predation, but predators must

consume prey to survive and reproduce. One important goal of this chapter is to develop an understanding of the numerical effects of predation on population sizes of predators as well as their prey.

It is clear that animals will try to avoid being eaten. In fact, we would expect natural selection to favor genotypes that possess adaptations to reduce or avoid risks of predation. In this chapter we examine the ways in which many species have attempted to avoid the clutches of hungry predators.

Predators must also be able to overcome the adaptations of prey. In some cases this might occur through the evolution of morphological characters that aid in being an effective predator, like the massive jaws of the shark. However, more subtle aspects of predator adaptation may affect how predators search or hunt for prey. This chapter also reviews the different strategies that are used by effective predators for capturing food.





PREDATOR-PREY DYNAMICS

13.1 The dynamics of predator-prey populations are intimately connected

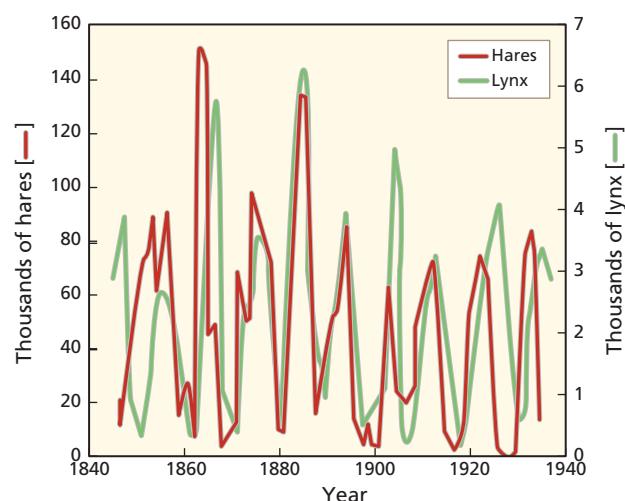


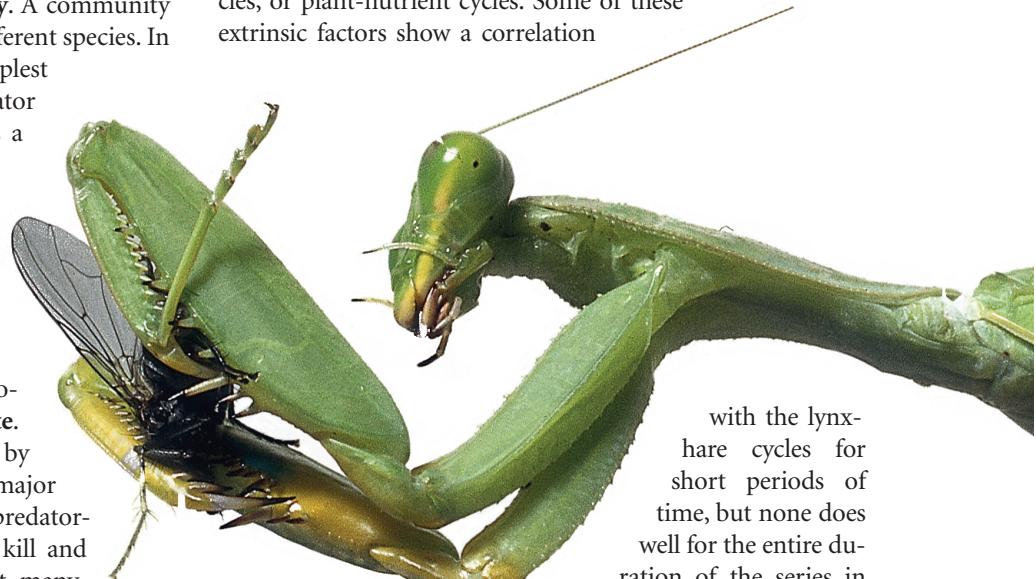
FIGURE 13.1A Predator-Prey Cycles The cycles of lynx (green lines) and hare (red lines) across Canada (from Hudson Bay Company's records). Notice the regularity of the cycle and that rises and declines in lynx numbers come after rises or declines in hare numbers.

In nature, populations do not exist in isolation from other populations. In any physical area, we find many different species that interact in a variety of ways. This collection of species is usually referred to as a **community**. A community would require the existence of at least two different species. In this chapter we will consider one of the simplest types of community, one consisting of a predator and prey. This type of community also has a very special relationship between its two members. The major source of food for the predator population is the prey species. Thus, the prey have a positive effect on the survival and population growth of the predators, while the predators have a negative effect on the prey species.

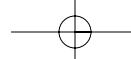
In Chapter 14 we consider a related two-species interaction called **host and parasite**. The host-parasite interaction is also marked by the host serving as food for the parasite. The major difference between the host-parasite and predator-prey relationships is that predators usually kill and consume a whole prey individual. In contrast, many hosts may live indefinitely, supporting large numbers of parasites. Of course these parasites drain energy from their host and make them more susceptible to death from other causes.

Much of the great interest in predator-prey dynamics is a consequence of extraordinary observations made in natural populations. One of the best-documented examples is of the Canadian lynx and its prey, the snowshoe hare (Figure 13.1A). The estimates of numbers come from the records of the Hudson Bay Company's fur trade. Trappers were paid a fixed amount for lynx and hare hides during much of this period, and thus the fluctuations in number of hides are thought to reflect variation in numbers of lynx and hare. This assumption is certainly not precisely correct. For instance, it is known that when hares are common, it is more difficult to trap lynx than when the hares are rare. This trapping bias would tend to make the troughs in the cycles higher than they should be, and the peaks smaller. A more important source of bias is trapper effort. Because the Hudson Bay Company paid the same amount every year, one would expect trappers to intensify their efforts during the peaks of the cycles and perhaps to be discouraged during the troughs.

In any case, more recent information on lynx-hare biology and careful population size monitoring suggests that the basic impression of cycles is certainly correct. In fact the data are remarkable for the consistency of their fluctuations, which take about 10 years per cycle. In addition, the cycles appear in many areas of Canada. This fact led early investigators to suggest that the cycles were a consequence of extrinsic factors like sunspot cycles, ozone cycles, weather cycles, forest-fire cycles, or plant-nutrient cycles. Some of these extrinsic factors show a correlation



with the lynx-hare cycles for short periods of time, but none does well for the entire duration of the series in Figure 13.1A. More important, there are no reasonable connections between the lynx-hare cycles and these extrinsic factors. As we review models of predator-prey dynamics, we will see that the observed cycles may be a natural



by-product of predator-prey interactions and density-dependent population regulation.

Observations like those made for the lynx and hare are not always possible. For instance, there are very good records of the numbers of voles, a small mammal, in many parts of Europe. It is known that many animals prey on voles, but there are no good records of the predator numbers. There is a consistent north-south transition in vole population dynamics (Figure 13.1B). In more northerly locations, vole dynamics may be chaotic; but toward the south, more stable dynamics appear. One hypothesis for these observations revolves around the predator community that feeds on voles. In the north, predators are more likely to be specialists on voles; in the south, generalists are more common. A generalist predator is one that will feed on a wide variety of prey. The generalists are believed to stabilize the dynamics of vole populations in the south. ♦♦

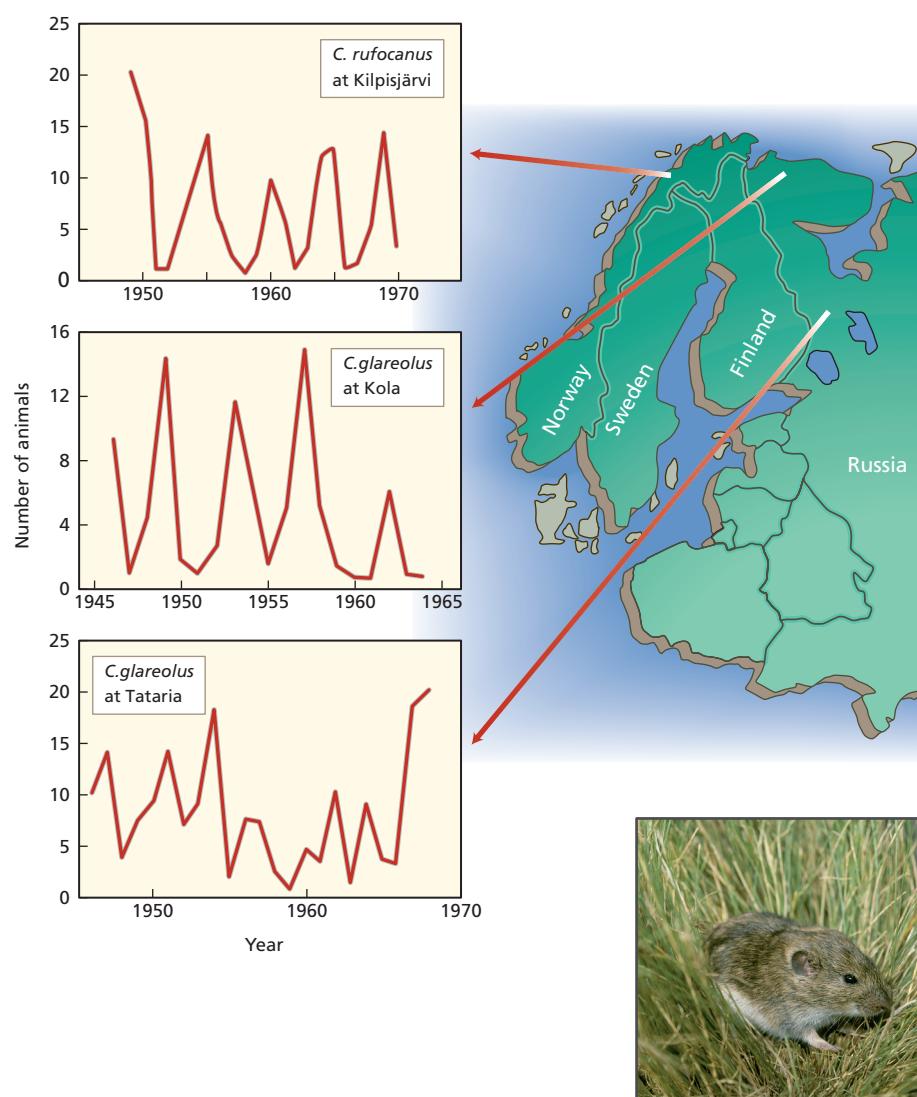


FIGURE 13.1B Population Size Variation in Three Vole Populations Voles of the genus *Clethrionomys* display highly variable population sizes in Northern Europe. However, detailed examinations of the numbers from the most northern populations, Kilpisjärvi and Kola, reveal that they are less stable than the population in Tataria.



13.2 The Lotka-Volterra model of predator-prey dynamics predicts cycles, although for reasons that probably do not apply to natural populations

Observations of natural populations of predators and prey have revealed some dramatic cycles. The case of the lynx and snowshoe hare is certainly one of the best known and most dramatic. Ecologists attacked this problem theoretically in the 1920s. Alfred Lotka was the first to develop a theory of predator-prey dynamics in 1920. Vito Volterra independently derived these results in 1926, so today this ecological theory is referred to as the **Lotka-Volterra predator-prey equations**.

The predator-prey theory makes some very simple assumptions (Figure 13.2A). From our earlier discussion of population growth, we will recognize that some of these assumptions are overly simplistic (Module 10.1). However, it will be easier to understand the more complicated models if we start first with this very simple formulation. Since the words *predator* and *prey* both start with the letter *P*, we will refer to the prey as *victims* and use the letter *V* to represent the number of prey in the population. Likewise, the number of predators in the population is represented by *P*. Unlike some of our previous models, the life cycles of predator and prey are not broken into discrete generations. Instead, the Lotka-Volterra model follows the changes in the size of the predator

and prey population over very short time periods.

In this model, change in the size of the prey population over short periods is symbolized by ΔV (Figure 13.2A). A positive value for ΔV means the prey are increasing over time; a negative value means the prey are decreasing in size over time. When ΔV is 0, that means there is no change in the population size. In a similar fashion, the change in the predator population size is symbolized by ΔP .

The model is developed by considering what happens to each population in the absence of the other. The prey population is assumed to grow exponentially, at a rate r , in the absence of predators. You may wonder how the prey grow exponentially since the equation for ΔV in Figure 13.2A suggests a simple

linear increase

in ΔV . Recall that ΔV is

the size change occurring in a short time period. The principle that gives rise to exponential growth is the same as that regard-

ing the growth of money in your bank account. Your bank adds a small, constant fraction of your money to your account every day as interest. Over a long period of time, because you are adding interest onto interest, the total amount of money in the account grows at an exponential rate. Since the only source of food for the predators is assumed to be the one prey species in our model, in the absence of prey, the predators will die out (Figure 13.2B). For simplicity, the Lotka-Volterra model assumes that the predators also die out at an exponential rate, given by $-d$, where d is a positive number.

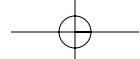
When both predator and prey are together, prey will be caught and eaten by the predators (Figure 13.2C). The Lotka-Volterra model assumes that the number of prey caught by each predator increases in direct proportion to the number of prey in the population. Thus, if the number of prey is doubled, the number of prey caught per unit of time by a predator will also double. The relative efficiency of the predator at catching prey is given by the parameter c . The higher c is, the more efficient the predator. The loss of prey per unit of time due to predation is equal to $-cPV$. This term, sometimes called the **functional response**, reflects important aspects of the

predator's hunting capabilities. The

conversion of captured prey into new predators is determined by the parameter k .

The Lotka-Volterra model inevitably predicts that the predator

and prey population will continuously cycle (Figure 13.2D). The problem with these cycles is that they are not stable (see Module 10.7). So, if some outside force slightly perturbs the predator and prey away from their current cycle, they simply move to a completely new cycle (Figure 13.2D). This is odd behavior that is not exhibited by real populations; it suggests that certain assumptions of the Lotka-Volterra model need to be changed. We address this issue next. 



Instantaneous change in prey population size = ΔV
 In the absence of predators, prey $\rightarrow \Delta V = -rV$

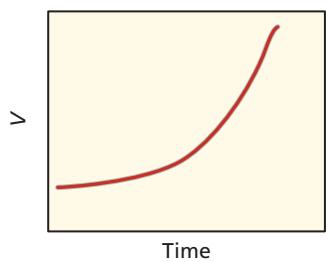


FIGURE 13.2A Prey (V = Victims) Alone

Instantaneous change in predator population size = ΔP
 In the absence of prey, predators $\rightarrow \Delta P = -dP$

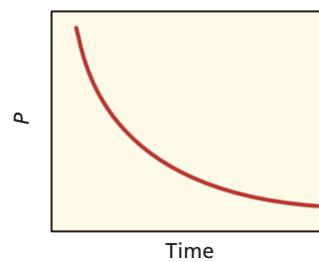


FIGURE 13.2B Predators (P) Alone



The functional response = number of prey captured per predator
 $= cV$

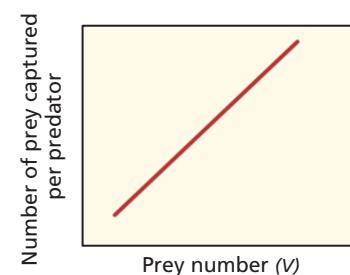


FIGURE 13.2C Prey and Predators Together

Total number of prey lost per unit time = cVP .
 The captured prey are converted to new predators at a rate = kVP .
 So,
 $\Delta V = rV - cVP$
 and
 $\Delta P = kVP - dP$

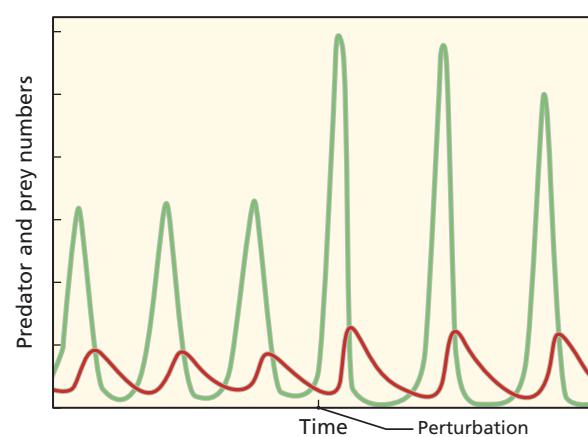
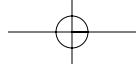


FIGURE 13.2D Cycles in the Lotka-Volterra Model Are Not Stable.

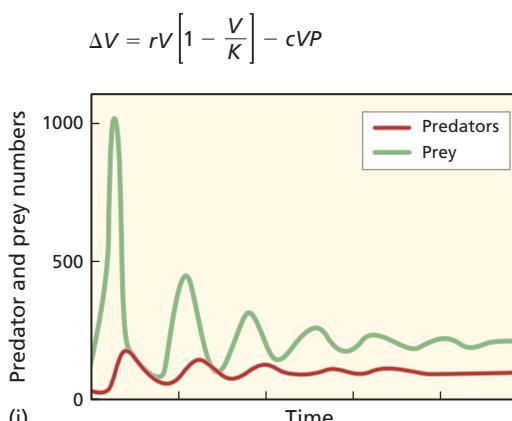


13.3 More realistic models incorporate density-dependent prey dynamics and predator satiation

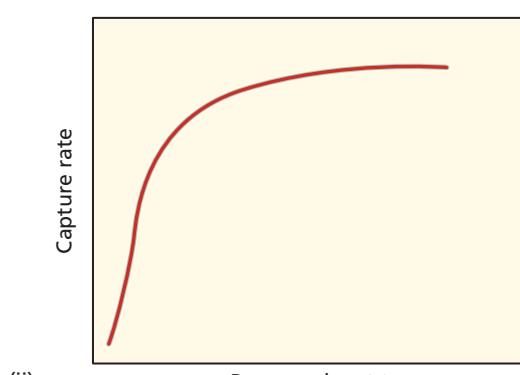
The Lotka-Volterra model was based on several overly simplistic assumptions. These assumptions lead to some predictions by the Lotka-Volterra model that seem hard to defend. For instance, cycles in predator-prey numbers can be generated by the Lotka-Volterra model; but if the numbers of predator and prey are slightly displaced from their cycle, they start a new cycle with different peaks and valleys.

The first assumption that we might consider relaxing is the assumption that the prey grow exponentially. It would seem that in the absence of predators, the prey will eventually feel the effects of density dependence—for all the reasons considered in Module 10.1. In Figure 13.3A, part (i), we have modified the equation reflecting the growth of the prey population to include logistic population growth of the prey. The

We can assume that the prey will eventually be density regulated in the absence of predators. If the carrying capacity of the prey is K , then logistic growth of the prey results in:



Predator and prey population sizes oscillate initially, then both approach an equilibrium. Although the carrying capacity of the prey is 2000, in this example the predators keep prey numbers well below that amount.



A more realistic functional response would look like the curve on the left. The predator-prey model with prey density-dependence and a functional response with a plateau can give rise to stable cycles.

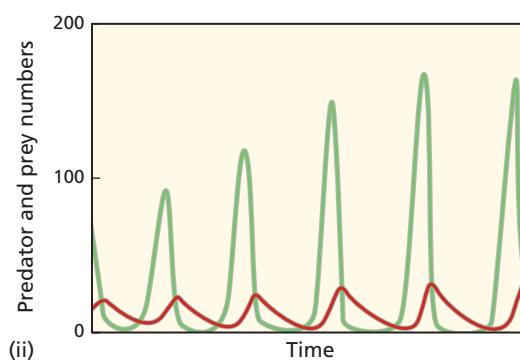
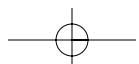


FIGURE 13.3A Refinements to the Lotka-Volterra Predation Model



logistic part of the red equation in Figure 13.3A is written as $rV[1 - V/K]$. This form of the logistic was encountered earlier in the box at Module 10.6. The addition of this density dependence to the Lotka-Volterra model in Figure 13.3A results in the predator and prey populations approaching a stable population size. It is worth noting that even though the carrying capacity of the prey is 2000, in this example the predators keep the equilibrium number of prey well below this value, at about 200 (Figure 13.3A).

Some assumptions about the behavior of the predators in the Lotka-Volterra model are also overly simplistic. The Lotka-Volterra model assumed that the predators would continue to catch more prey in direct proportion to the number of prey in the population. We know that this cannot always be true, for at least two different reasons: (1) There will be a point at which the number of prey that a predator has captured and eaten is so great that the predator simply cannot eat any more prey. At that point we say the predator is **satiated**. Satiation should produce a leveling off of the functional response, as shown in part (ii) of Figure 13.3A. When we say “level off,” we mean that adding more prey to the population will not result in more prey being caught, since the predators are already eating as much as they can. (2) The predator must consume the prey it catches. The consumption of prey will take some time because it involves biting, chewing, and swallowing the prey. The time to complete these activities is called **handling time**. Again, we expect that eventually the handling time for a large number of prey will be so great that the predator is unable to catch more prey. At that point the functional response should again level off.

In part (iii) of Figure 13.3A we see the changes in predator and prey numbers that are predicted from the model with logistic population growth of the prey and a functional response that shows the effects of handling time and satiation. In this case we see there are

cycles (although that is not always the case), and these cycles are stable, unlike those for the Lotka-Volterra model. So if the predators or prey populations are perturbed away from the cycle they will, over time, return to the same original cycle. Most cycles observed in nature are believed to be stable because they regularly experience perturbations due to random environmental fluctuations.

Do real populations show these types of cycles? In fact they do. Luckinbill (1973) has studied a predator-prey system consisting of unicellular flagellates. The prey species in this system is *Paramecium aurelia*, and the predator is *Didinium nasutum*. *Paramecium* grows in an approximate logistic manner in the absence of *Didinium*. In Luckinbill's laboratory cultures the equilibrium number of *Paramecium* is about 850 per milliliter. When both species are present, they show cyclic fluctuations (Figure 13.3B). The predator always reaches its peak numbers slightly later than the prey species. Likewise, the valley—or lowest number—of predators is also always slightly later than the valley of the prey. This is the same behavior we see in the theoretical model shown in Figure 13.3A. ♦♦

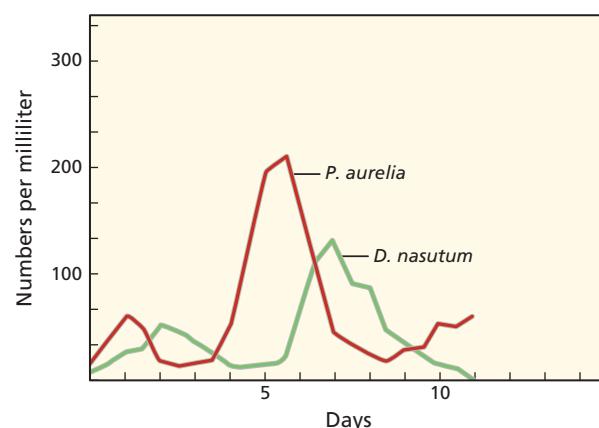
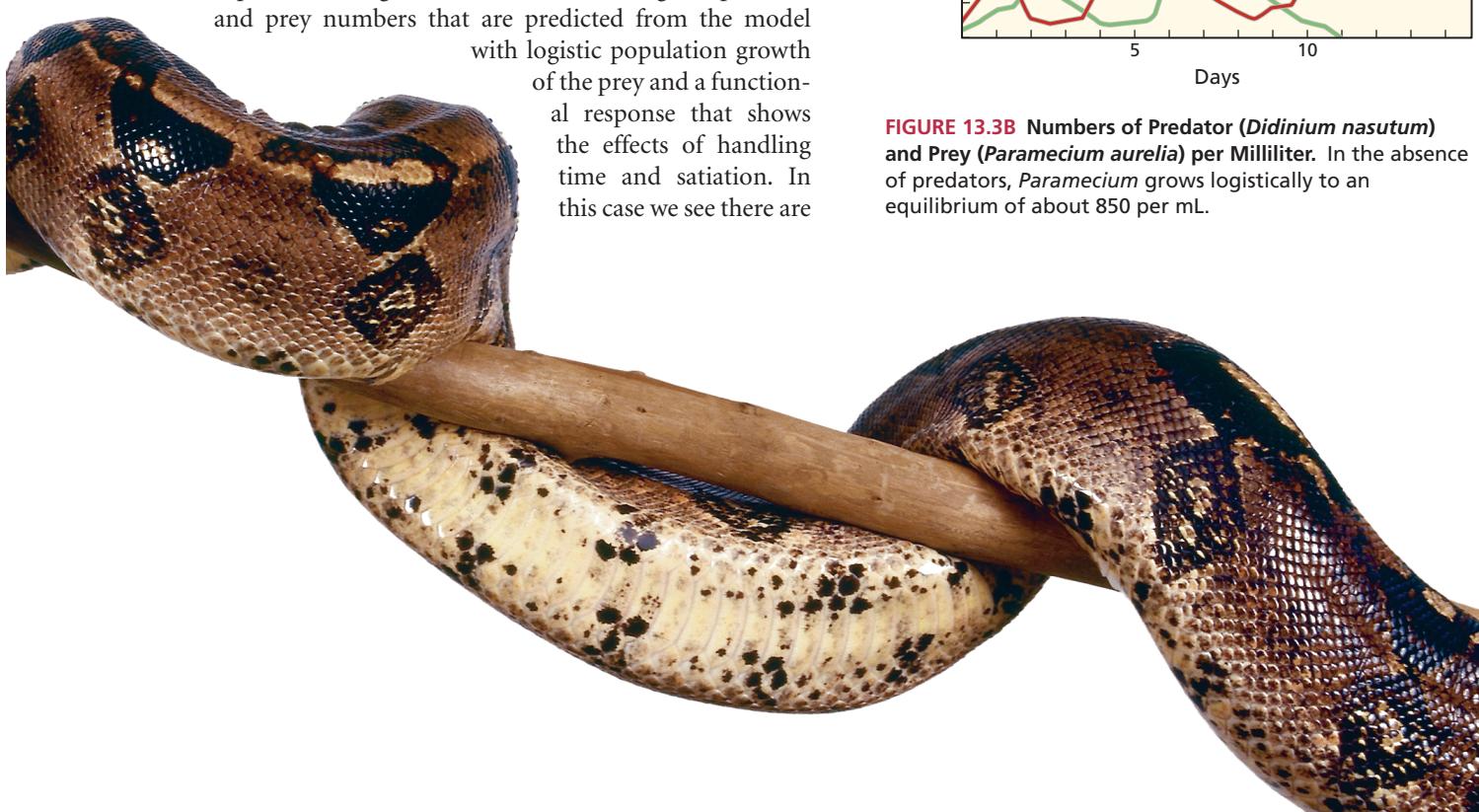
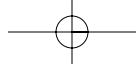


FIGURE 13.3B Numbers of Predator (*Didinium nasutum*) and Prey (*Paramecium aurelia*) per Milliliter. In the absence of predators, *Paramecium* grows logically to an equilibrium of about 850 per mL.





HOW TO BE A PREDATOR

13.4 A variety of factors determine how predators forage

Predators are faced with many decisions that do not always have simple answers. However, the way predators deal with these decisions may have a substantial impact on their long-term survival and the survival of their offspring (Figures 13.4A through 13.4C). For instance, it is worth recalling that even predators have enemies. Many birds will feed on insects, but themselves may be prey for other birds or small mammals. Consequently, predators may have to evaluate the relative danger of foraging in particular places or for extended periods of time. All other things being equal, many predators may seek to minimize the time they spend foraging in order to reduce their exposure to predators or other hazards. If this is the case, then it may turn out that some species are better to include in the diet than others. For instance, insects that need to be dug out of the bark of a tree may take much longer to find and eat than insects that live on the surface of leaves.

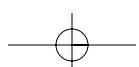
Suppose a predator can expect to encounter more prey in a short period of time than can possibly be eaten. Which prey should that predator ignore, and which should it pursue and eat? We will see in the next few modules that sever-

al factors are important in determining the answer to this question. What is clear is that factors such as the nutritional value of the prey, ease of capture, and number of prey all may have an impact on the behavior of predators. Many of the decisions that predators make concerning which prey to consume are also factors for nonpredatory animals that consume resources like seeds or plants. Thus, although the following modules refer to predators, most often many of the problems we discuss are also encountered by a wide range of foraging animals.

Do Animals Forage Optimally? One approach to the study of foraging behavior has been to assume that the rule used by foragers to make decisions leads to optimal solutions. In this context, *optimal* can mean several things. If it appears that it is most important for an animal to minimize the time it spends in foraging, then the optimal solution would be the one that leads to the minimum time to gain a certain level of nutrition. Alternatively, *optimal* could refer to achieving the maximum return of energy from a fixed foraging effort.



FIGURE 13.4A Lions will cooperate to capture prey.



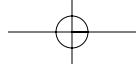


FIGURE 13.4B Birds of prey often must rely on their keen sense of vision for hunting.

Why Would We Expect These Behaviors to Be Optimal? One view on this question is that behaviors are the product of natural selection, and thus the animal with the optimal behavior ought to have the highest fitness, all other things being equal. While this idea seems reasonable, several other factors may prevent behavior from being optimal.

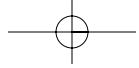
One fact about natural selection is that it is not always able to maximize fitness or produce the best phenotype. This can be due to complications in the way the genetic system works, or in aspects of the way fitness is determined. For example, when a heterozygote at a single locus is the most fit genotype, the optimal solution would be to have a population composed entirely of heterozygotes. Due to Mendelian segregation, we know that in every generation we will continue to see less-fit homozygotes in the population; there is no way to get rid of them.

Another complication is that fitness is determined by many things, not just how well an organism forages. Thus, the evolution of foraging behavior must occur along with the evolution of many other traits—like reproductive behavior and competitive ability. Optimal foraging behavior may not evolve due to the conflicts with the direction of evolution of other traits. What

use, then, are models that determine the optimal pattern of foraging? If the model has been constructed correctly, then no animal should be able to do better than the optimal. For these reasons, the optimal behavior can be used as a standard against which real behavior can be compared. The construction of these models can also suggest the importance of different factors that can affect rates of energy intake, for instance. This in turn can help the experimental ecologist in designing appropriate experiments to test which factors are most important for determining the foraging behavior of real organisms. As we will see in the next few modules, many animals forage in a manner that is consistent with predictions based on some very simple models.



FIGURE 13.4C Web-building spiders wait for prey to come to them rather than moving to find them.



13.5 Foragers may optimize energy gain per unit of time, or minimize time spent foraging

Predators employ a diverse set of strategies to capture prey. Some predators, like spiders, sit still and wait for prey to come to them and become tangled in their webs. Large predators, like lions, may move great distances to find prey and then often need to run at great speeds to capture prey. Can we detect any patterns to these foraging strategies? Ecologists have addressed this question by trying to determine what the best foraging behavior might be and then seeing if animals forage in this manner. However, determining the best foraging behavior requires that we know how to measure how well a forager is doing.

It may be that the time spent foraging exposes the individual to potential danger, perhaps to other predators, or alternatively takes away from time the individual could use for reproduction or watching and caring for offspring. In this case the best predator would be one that can get sufficient food in the shortest period of time. Another possibility is that the forager simply tries to gain the most energy possible per unit of time spent foraging. These two views of what foragers are attempting to do in many cases will yield the same prediction of the best strategy. We first review the strategies used by time minimizers.

There are two components to the time spent in finding and consuming prey. The first component, usually called the **waiting time**, refers to the average time between encounters with prey. For these calculations we will assume that a foraging predator will catch and consume each prey encountered. Once a prey is caught, the predator must consume it. The time spent catching and consuming the prey is called the handling time. Obviously, a predator cannot be pursuing or catching another prey while it is still handling the first. It may turn out that several prey are available for predator consumption. In Figure 13.5A we have examples where the predator has a choice of two prey. If each prey is equally nutritious, then the preferred prey would be the one with the smaller handling

time. The small red prey (A) takes only a half-hour to handle, while the large green prey with thorns (B) takes an hour to handle.

It would seem reasonable for the predator to take the preferred prey; but are there circumstances where the predator should take both types of prey? In Figure 13.5A we compute the average time between prey consumption under two different circumstances. To do this calculation we need to know

the encounter rate, P_i , of each prey. The encounter rate is the number of times per hour a particular prey will be encountered. If this rate is five times per hour, then the average time between encounters, or the waiting time, is the reciprocal of five, or 12 minutes. In case 1 and case 2 the preferred prey (A) is five times more likely to be encountered than the less-preferred prey (B). However, in case 1, both prey are 10 times more common than they are in case 2.

In case 1 we see that if the predator takes only prey A, the average foraging time is 0.7 hrs. If the predator takes both prey, then it will encounter six prey per hour, so the waiting time is 1/6 hr. The handling time is the average over both prey. Since prey A is five times more common, it will represent five-sixths of all prey caught, resulting in an average foraging time of 0.75 hrs. For case 1 we see that the predator will do best by taking only prey A and ignoring prey B.

In the second case of Figure 13.5A, the absolute frequencies of both types of prey have decreased. Doing calculations like those in case 1, we see that the predator would

now do best to take both prey. The reason for this conclusion is that now the predator spends most of its time in waiting for a prey as opposed to handling it. Therefore, even if a prey is the less-desirable type, the predator should take one because it will be a long time before another prey of either type comes along.

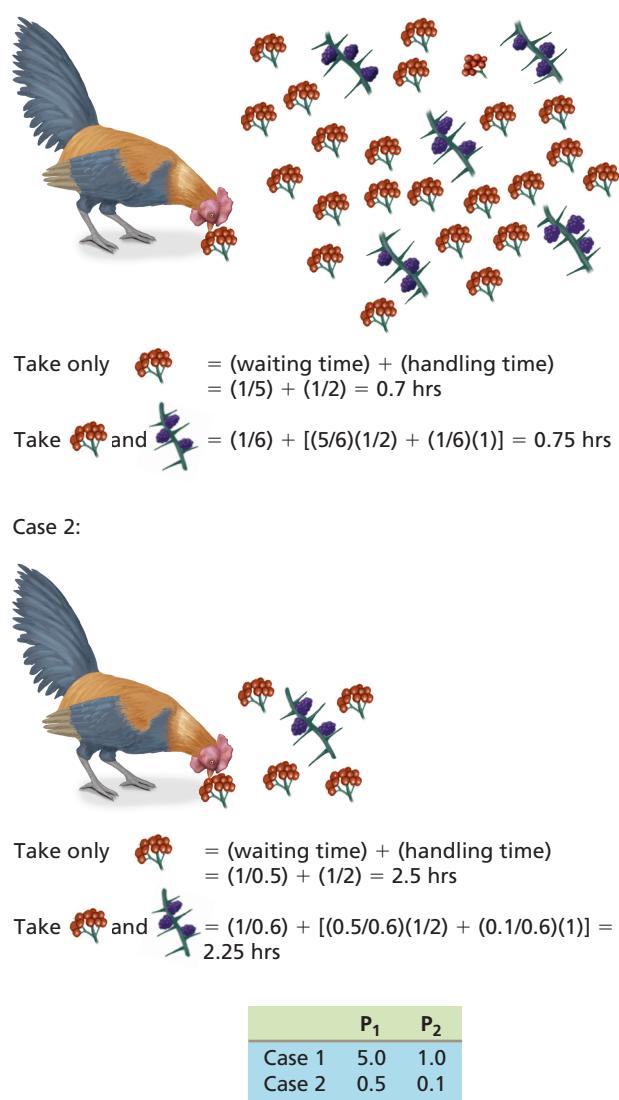
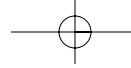


FIGURE 13.5A Foraging Strategies That Minimize Time



The behavior of foraging animals often conforms to simple predictions 13.6

Predators may search for and capture prey by methods that maximize the amount of energy that they take in per unit of time. This would certainly seem to be an efficient way to be a predator, but are animals capable of making decisions that can result in such efficient use of their time? There are no first principles in evolution that will allow us to claim that this must be the case, so we need to make direct observations of foraging behavior to test this idea. N. B. Davies (1977) has studied this issue by observing the foraging behavior of small insectivorous (insect eating) birds called wagtails (*Motacilla alba yarrellii* and *M. flava flavissima*). Davies found that the various insects eaten by these birds often differed greatly in size (Figure 13.6A). The very small prey could be eaten immediately, while larger prey were often held and bashed against a perch prior to eating. This behavior might result in a handling time of 5–10 seconds. We see that the energy ingested per second has a maximum for wagtails at about size 7 mm (Figure 13.6A). Even though larger prey will have more energy per individual, the increased handling time reduces the rate of energy return. The wagtails also show a preference for prey in the 7-mm size category. Of course, this result could simply reflect that the insects in the 7-mm size class were the most common. However, it turns out that insects in the 8-mm size class were most common. These results suggest that wagtails are modifying their selection of prey toward those that give the greatest energy return per unit of time.

We previously reviewed how predators might change their foraging behavior, going from specialization to generalization

as prey become scarce. This prediction followed from a time-minimization perspective. If predators instead try to maximize the rate of energy gain, then the most efficient behavior will be to specialize on the highest-energy prey when these are common, but accept multiple prey when they are rare. John Krebs and colleagues (1977) studied the foraging behavior of birds called great tits (Figure 13.6B). These experiments were carried out in the laboratory. Birds were exposed to two “prey” types that were made up of pieces of mealworms. Large prey had about twice as much energy per prey item as the small prey did. The small prey was constructed in a fashion that resulted in both large and small prey having about the same handling time. As a result, the energy return per unit of time was much higher for the large prey. A conveyor belt was used to run these prey past the birds, who were then free to forage. The conveyor belt permitted the scientists to control precisely the relative frequency of encounters with both prey types. When both prey types were equally abundant and encountered frequently, the birds chose the larger, higher-energy prey more

often (Figure 13.6C). However, when the frequency of both prey was reduced, the birds became less choosy and were equally likely to select small and large prey (Figure 13.6C).

Thus, from these two studies, we see support for the idea that predators can assess the relative quality and abundance of prey. With that information, predators can then make relatively rapid changes in their foraging behavior that will help them maintain a high level of energy intake. This ability to alter foraging behavior is certainly advantageous, since most predators will over their lifetime experience a range of environmental conditions that will not be best handled by a single strategy.

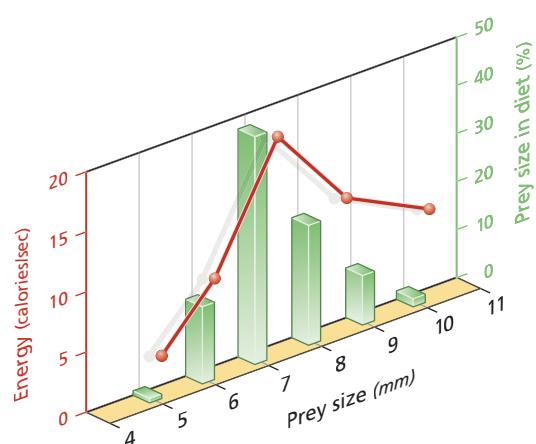


FIGURE 13.6A Maximization of Energy Intake

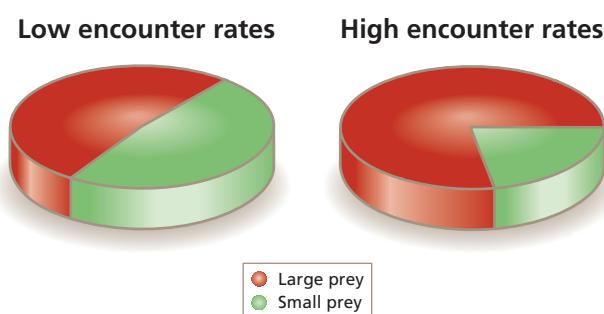
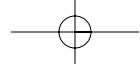


FIGURE 13.6C The Fraction of Two Prey Types in the Diet of Great Tits



13.7 Central-place foragers should recover more food the farther they travel

Some animals forage from a single location. Thus, all trips to recover food are followed by a return trip to the central place. For instance, many birds that are caring for young will hunt and catch prey, and they bring them back to the nest in order to feed their young. A crucial component of this type of foraging is the time spent traveling from the central place to the foraging site. Based on our previous examples, it is clear that if the forager attempts to minimize the time spent foraging, or to maximize the rate of energy capture, an important component of this calculation will be the travel time. The predator in Figure 13.7A may forage in two locations. The nearby location has a travel time of T_1 , whereas the distant location has a travel time of T_2 , which is greater than T_1 . Suppose that the time to capture prey were effectively zero (of course, this is not true; see Figure 13.7B). Then, if T_2 is twice as large as T_1 , the forager must bring back twice as much food from the distant location simply to equal the return that is possible from nearby foraging.

But are animals able to take these factors into account? Krebs and Avery (1985) attempted to address this question by studying the feeding habits of the European bee-eater (*Merops apiaster*). The researchers observed adult bee-eaters that were actively foraging to feed their young. A number of different insects were available to the bee-eaters, including small bees with a dry weight of about 25 mg and large dragonflies of about 315 mg. The amount of energy provided by these insects is roughly proportional to their dry weight. As we can see in Figure 13.7C, the number of small prey in the diet of bee-eaters decreases the farther they have to travel. One possible alternative explanation for these observations is that there are just fewer small prey at the distant sites. Field surveys demonstrated, however, that the different prey types did not vary in abundance as a function of proximity to the bee-eater nesting sites. It is reasonable, then, to conclude that the birds are purposefully changing their diet.

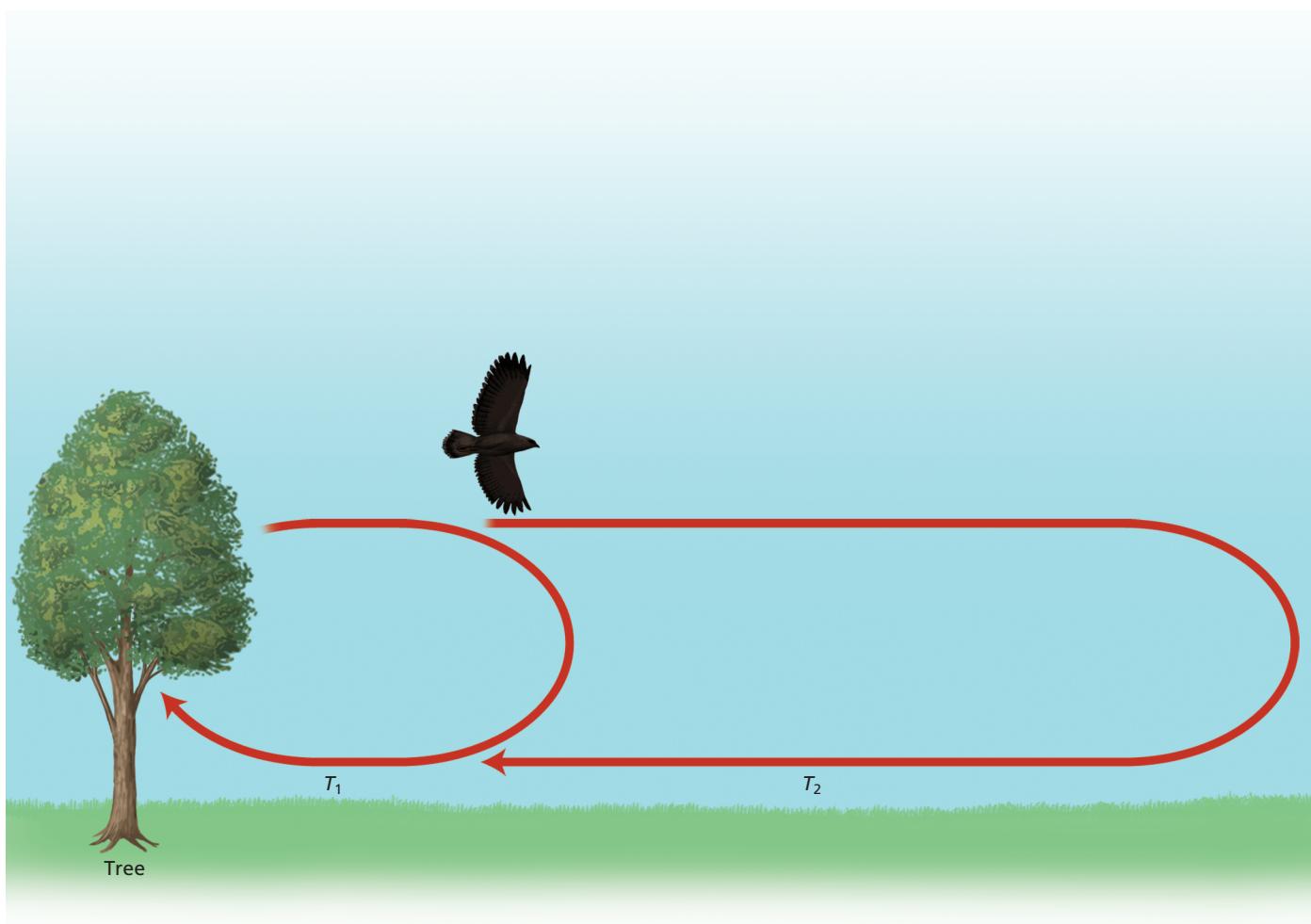
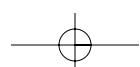


FIGURE 13.7A Central place foragers make many trips to and from one location. The time between foraging sites may vary substantially and therefore have an important impact on the foraging behavior in each site.



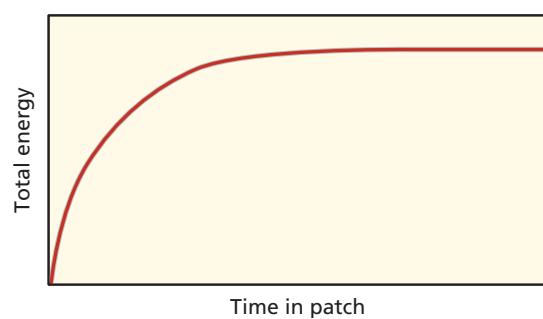
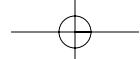


FIGURE 13.7B Total Energy Gain in a Single Patch We expect that initially food will be easy to find and the energy gain will be rapid. As time goes on, the easy food items will be gone; more effort and time will be required to get additional energy. Eventually no additional energy will be found, and the total energy gain will reach an asymptote. At this point the energy return per unit of time is zero.

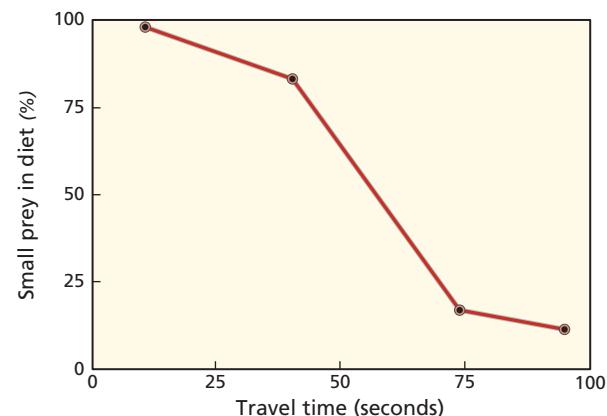
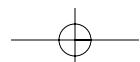
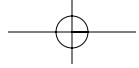


FIGURE 13.7C This figure shows the results of a study with a bird, the European bee-eater. Bee-eaters make many trips from their nest and back to feed their young. Usually they bring back only one insect-prey item at a time. It is clear that they bring fewer small insects when they travel farther from the nest.





HOW TO AVOID BECOMING PREY

13.8 | The process of prey capture can be broken down into multiple stages

Predation can be a major source of mortality for many animals. Consequently, any behavior, morphology, or physiological traits that would help prey avoid predators should be favored by natural selection. There are many stages of predation where prey may employ adaptations to avoid being eaten. In this module we review some of these stages.



FIGURE 13.8A Flounder on the Sandy Bottom of the Ocean

Encounter Predators must come into close physical proximity or encounter prey before they can be consumed. Prey may avoid encounters by being active at different times of the day or the seasons than predators. Prey may also rest in inconspicuous places to avoid encounters (Figure 13.8A). Some prey may develop more acute senses than their predators and be able to leave an area before being encountered by predators.

Detection Prey may have morphological structures or colors that make them blend into the background. We review this possibility in more detail in the next module. Prey may attempt to confuse prey by making sudden, unpredictable movements. Large schools of fish may overwhelm and confuse predators (Figure 13.8B).

Identification Predators need to be able to identify prey, once detected, as something that is worthwhile eating. Some animals may manufacture or consume toxic compounds that make them unpalatable (Figure 13.8C). In these situations the prey will take on colors or morphological patterns to advertise that condition. As we discuss in the next modules, some palatable animals may try to take advantage of this adaptation by looking like unpalatable species.

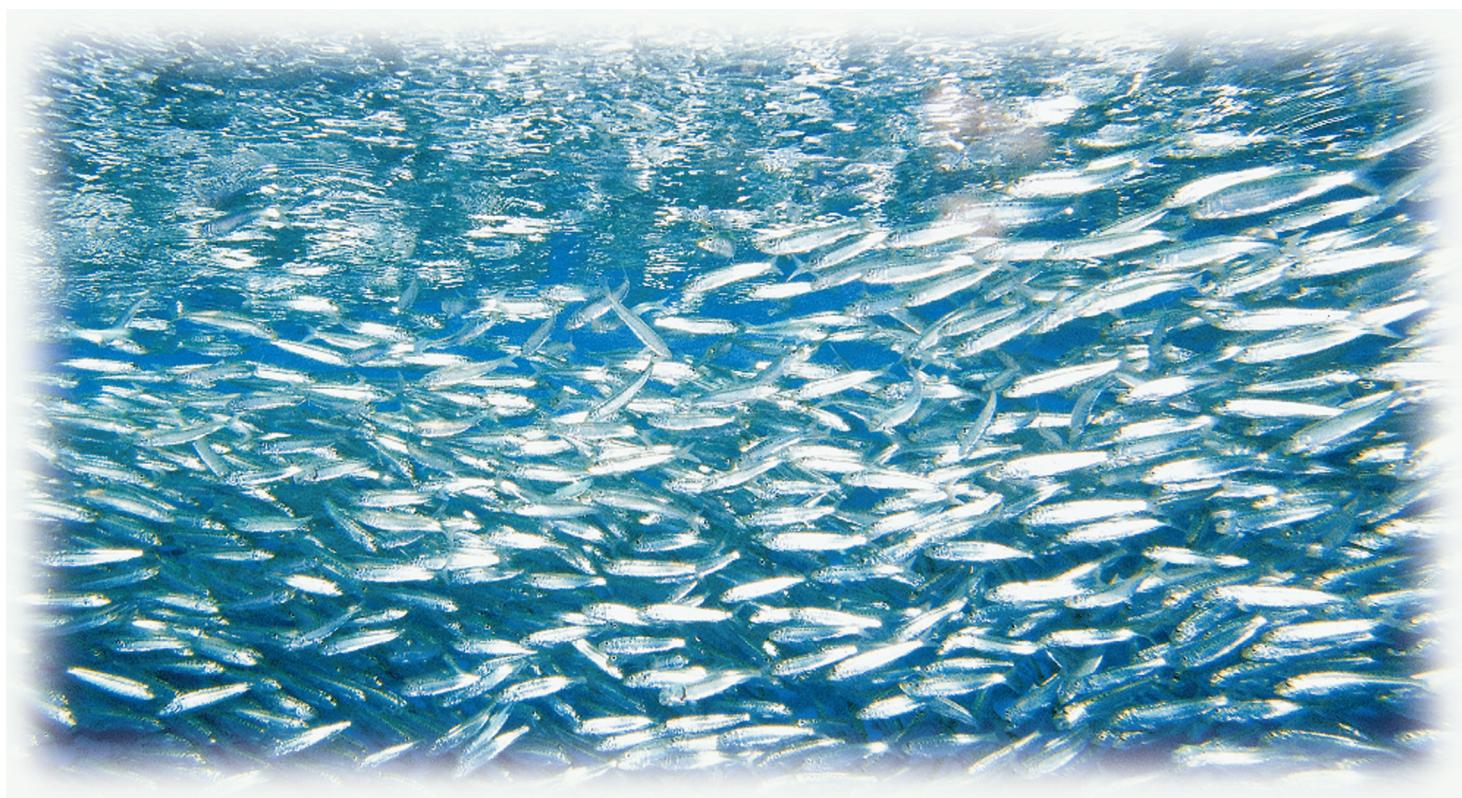
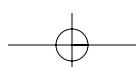


FIGURE 13.8B Large School of Fish





Approach Once a predator has encountered and identified a prey, it must attack and capture the prey. The prey may still escape capture. It may simply be faster than the predator and be able to escape, or it may be near a hiding place to which it can escape. The prey may startle the predator by assuming an aggressive stance that momentarily delays the predator and allows escape (Figure 13.8D).

Subjugation After the predator has captured the prey, it must either gain control of it or kill it before it is eaten. Some prey may be strong enough to simply escape from a predator. Other prey may have physical properties, like shells or mucus and slime, that can prevent predators from gaining control. Some prey may detach body parts to help them elude predators (Figure 13.8E). Many salamanders and lizards can detach their tails when caught by a predator. Some prey are simply noxious and cause predators to release them due to spines, stings, or bad taste.



FIGURE 13.8D Puffer Fish, Blown Up

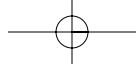


FIGURE 13.8C Monarch Butterflies These butterflies incorporate toxic and distasteful cardiac glycosides from their milkweed food plants.

Consumption By the time a prey is about to be consumed, it has few options for escape. However, if the consumption of a prey causes the predator to become sick, the predator may avoid this type of prey in the future. If this experience prevents that predator from consuming relatives of the prey, then the production of the toxins that cause these types of negative reactions in predators may nevertheless be favored by natural selection.



FIGURE 13.8E Lizard with Detached Tail



13.9 Prey may avoid predators by being difficult to find

There are many ways for an animal to avoid being eaten by a predator. One of the most obvious is simply to avoid being detected by predators. Many animals have been extremely successful at blending into the background to avoid detection. These animals often have **cryptic coloration** that resembles a random sample of the visual background they are most likely to be found in. The insects shown in Figures 13.9A through 13.9C illustrate the range of remarkable adaptations to predator avoidance.

Cryptically colored animals do not have to be drab in appearance. Many birds—like parrots, orioles, and tanagers—are brightly colored, but not conspicuous in their natural habitat. Some animals may have coloration that is conspicuous to other members of the same species but

cryptic to important predators. This effect can occur when the visual acuity of the prey and predators differs.

Some animals have bright coloration to warn predators that they are innately distasteful. Coloring that serves as a warning is sometimes called **aposematic coloration**. This is a very different strategy than that of cryptic coloration because the goal is to be seen by the predator. The colors used for these warnings are often black and either yellow or red. It appears that many predators have a general aversion to these colors. Animals may communicate their unpalatability in other ways. Some animals, like bees or rattlesnakes, make noises that serve as warnings. Others, like skunks and stinkbugs, have odor signals. Some species of arctiid moths are distasteful to bats. These moths emit ultrasonic pulses that bats can sense and use to avoid them.

Bright colors appear to help predators avoid distasteful prey. In an experiment with chickens, two types of distasteful bait were offered: cryptically colored or conspicuously colored (Figure 13.9D). Initially the conspicuous bait was found more easily and consumed at a greater rate, but over time the chicks quickly learned to avoid this bait. They had a more difficult time learning to avoid the cryptically colored bait. ♦♦

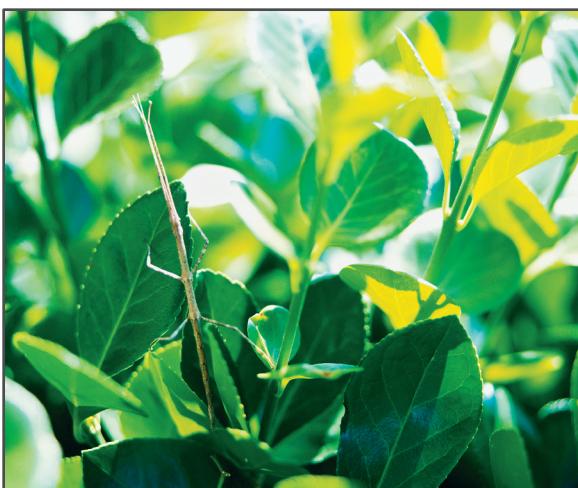


FIGURE 13.9A A Walking Stick, *Diapheromera femorata* The color of walking sticks varies from green to brown. To assist with their disguise, they walk slowly and may stay motionless for extended periods.



FIGURE 13.9C A geometrid larva appears to be an extension of the branches of this plant. If you were a predator, how well would you do finding this larva?



FIGURE 13.9B A Branch Covered with Thornbugs (*Umbonia crassicornis*) These insects cling to the stems of plants and are especially abundant in subtropical habitats including Florida.

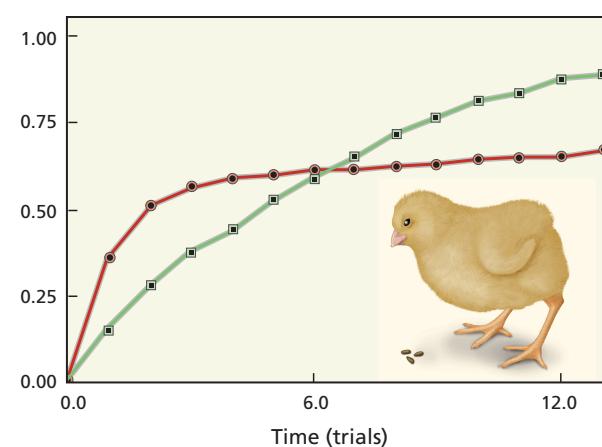
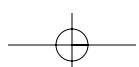
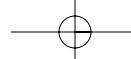


FIGURE 13.9D Chickens learn to avoid conspicuously colored, distasteful bait more quickly than they do cryptic, distasteful bait.





Prey may avoid predators by looking like other distasteful species 13.10

We have seen that predators can learn to avoid distasteful prey, but this requires several trials on the part of the predator. If several different species of prey are all distasteful, a common predator may learn to avoid those prey more quickly if they look similar. Thus, two distasteful species that have a similar appearance will both benefit from the negative reinforcement they exert on a common

predator. This type of process can lead to different species looking remarkably similar. These similar-looking species are called **Müllerian mimics**. Müllerian mimics are most likely to evolve when both species are equally unpalatable and equally common.

Mimicry can also evolve between two species—one that is palatable and one that is not. This type of mimicry is called **Batesian mimicry**. Some examples of Batesian mimics are shown in Figure 13.10A. The unpalatable species is called the model, and the palatable species is the mimic. In this case the mimic is benefiting from the model's negative effects on predators. However, the protection enjoyed by the model is negatively affected by the mimic. This is because, as the mimic becomes common, predators learn to associate its appearance with palatability. As a result, natural selection should favor the model to evolve a different appearance from that of the mimic; meanwhile, the mimic should always try to look as similar as possible to the model. In some species of Batesian mimics, there appears to be a polymorphism in coloration (Figure 13.10B); one morph appears to mimic a distasteful species, while a second is cryptic. ❖

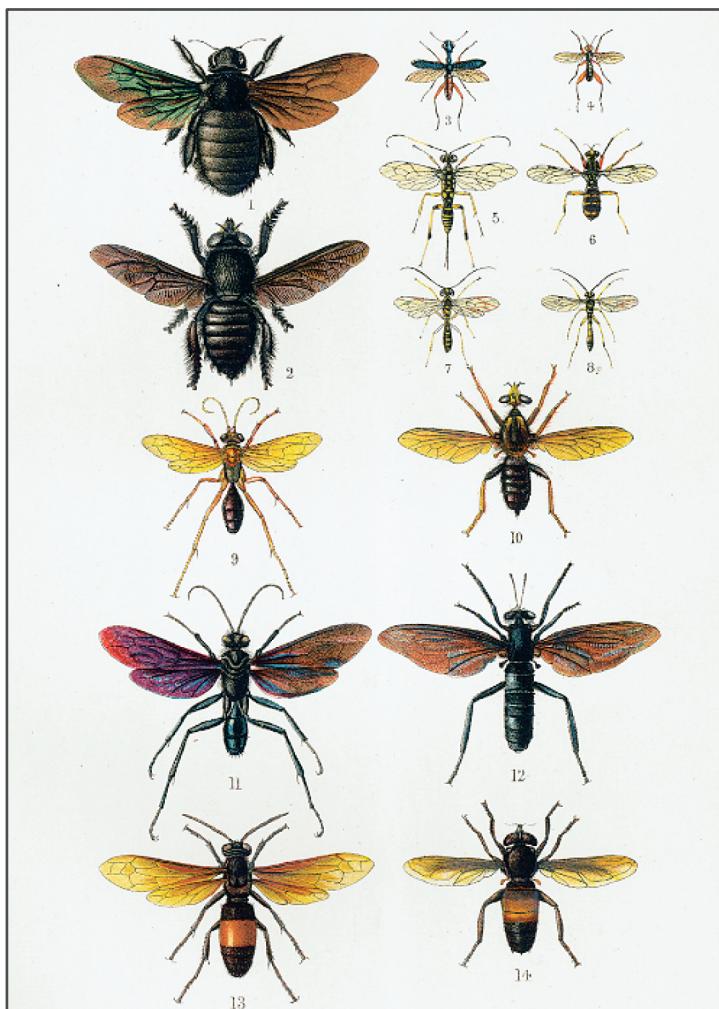


FIGURE 13.10A Wasps and Their Fly Mimics *Xylocopta latipes* (1) and the fly mimic *Hyperechia fera* (2). Note that the wasp has two pairs of wings, while the fly has only one. The model *Collyris emarginata* (3) and its mimic *Sepedon* sp. (4). The model *Mesostenus* (5) and its mimic from the family *Stratiomyidae* (6). The mimic *Xylophagus* (8) shows a great elongation of the antennae to match its model species *Mesostenus* (7). The *Solias* wasp (9) and its fly mimic *Laphria* (10). The wasp *Macromeris violacea* (11) hunts spiders. Their mimics from the genus *Midas* (12) have an enlarged wing that makes it appear as large as the pair in *M. violacea*. The fly mimic *Milesia vespoides* (13) has a striking resemblance to the wasp *Vespa cincta* (14), including yellow wing color.

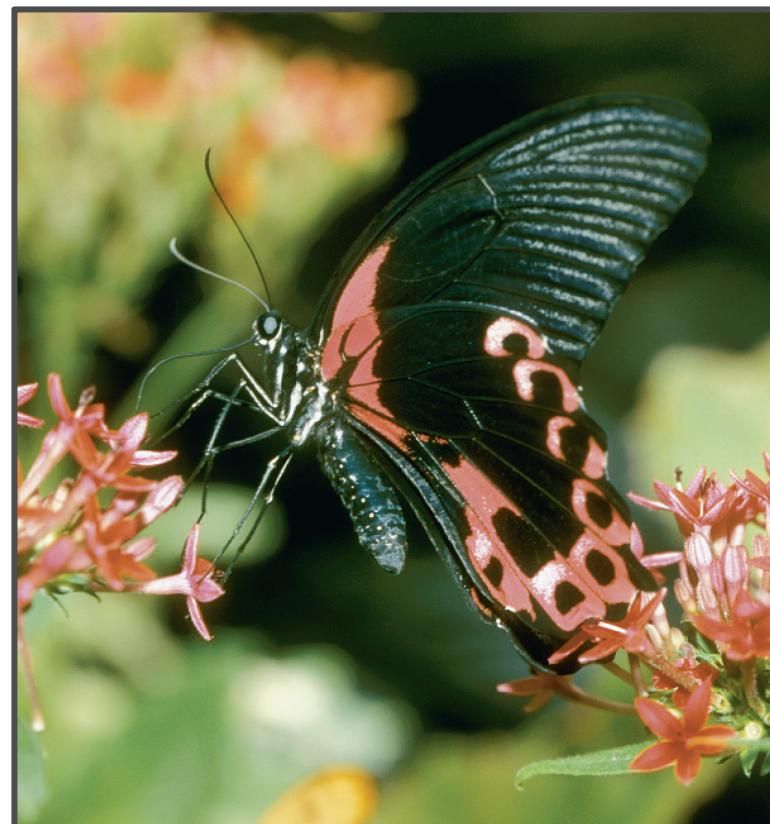


FIGURE 13.10B Species of Swallowtail Butterflies Have Both Mimetic and Cryptic Forms

PLANT-HERBIVORE INTERACTIONS

13.11 Plants show immediate and long-term reactions to herbivory

Unlike animals, plants do not possess many of the same options for avoiding their predators, the herbivores. Plants are not mobile, so they cannot escape from herbivores. They have no behavioral mechanisms for avoiding herbivores. However, this does not mean that plants are at the mercy of herbivores. Two major strategies employed by plants to defend against herbivory are (1) to be resistant to herbivores, and (2) to tolerate the damage caused by herbivores. Plants often defend themselves against herbivores by making toxic chemical compounds that cause herbivores to completely avoid feeding on the plant. An alternative to resistance is tolerance. Plants may still be able to produce flowers and seeds, even after herbivores have removed substantial portions of their leaf area. As we shall see, it may not be possible for a plant to both defend itself and be tolerant of herbivory.

Tolerance and **resistance** are both aspects of plant defense. Resistant plants will show little or no reduction in fitness or the ability to reproduce as a consequence of herbivore attack. **Tolerance** is a relative measure of the fitness reduction caused by a particular level of damage from herbivores. The greater the tolerance, the smaller the fitness reduction. The difference between the fitness of a plant damaged by herbivory and an undamaged plant is called **compensatory ability**. The smaller this difference, the greater the tolerance. In some cases this difference may actually be positive; that is, the plant's fitness is greater after herbivory. For different genotypes of the plant *Asclepias* (Figure 13.11A), compensatory ability increases with increasing root-to-shoot biomass ratio. This means that plants that store more energy in their roots

are better able to reproduce after herbivore damage, perhaps because of their ability to replace lost biomass from the energy reserves in their roots.

Other plants tolerate herbivory due to structural aspects of the plants. For instance, wild tomatoes are better able to tolerate herbivory damage than domesticated tomatoes are. This is because the canopy structure of wild tomatoes can better exploit light resources after damage than can the canopies of the domesticated tomato.

As with many life-history traits, the abilities to resist herbivory and tolerate herbivory appear to trade off. The production of defensive chemical compounds is likely to be energetically costly and thus compromises a plant's ability to tolerate damage from herbivores. Kirk Stowe (1998) selected for high levels of toxic mustard glycosides in the wild mustard, *Brassica rapa*. He did this by employing the classic procedures of artificial selection. He then compared the ability of these high-level defense plants to tolerate herbivory of specific levels. Compared to control plants, which were not selected for resistance, and plants that were selected for low levels of glycosides, the plants with high levels of glycosides showed greater declines in fitness with increasing herbivory levels (Figure 13.11B). These experiments demonstrate that resistance comes with a cost—reduced tolerance.

Herbivory may have effects on the entire herbivore community, because many plants will produce defensive chemicals in response to herbivore damage. Robert Denno and colleagues (2000) have studied this phenomenon in two species of planthoppers, *Prokelisia marginata* and *P. dolus*.

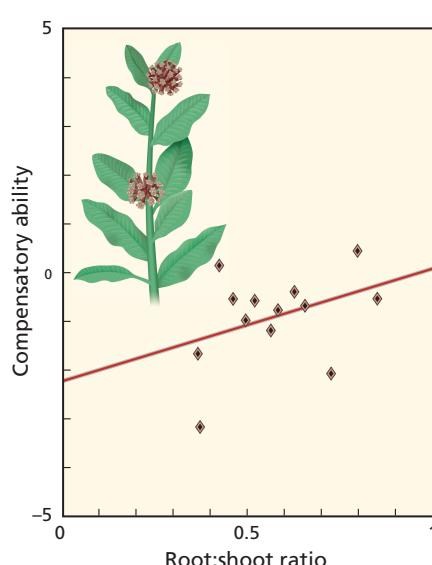


FIGURE 13.11A The compensatory ability of *Asclepias syriaca* becomes greater as more resources are stored in roots; for example, the root-to-shoot ratio becomes greater.

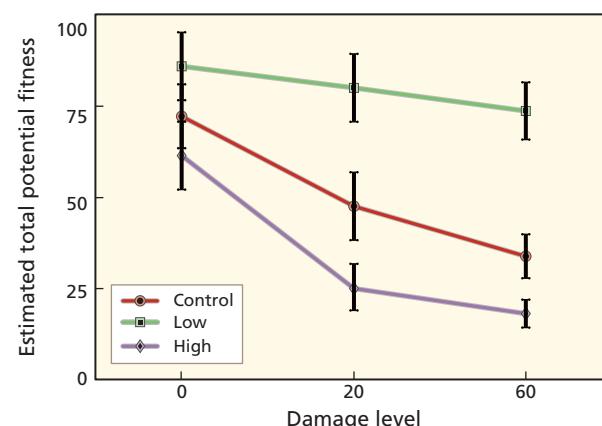


FIGURE 13.11B The wild mustard, *Brassica rapa*, can defend itself against herbivory by producing toxic mustard-oil glycosides, or glucosinolates. Plants selected for high levels of chemical defense show a greater reduction in fitness than do either controls or lines selected for low levels of defense, when they are actually damaged by herbivory. This study shows that high levels of defense have a cost in reduced tolerance.



The development time and adult size of female *P. marginata* were determined in three experimental treatments (Figure 13.11C). In one case, the control—host plant—was fresh and not previously exposed to either planthopper. An intraspecific competition treatment allowed *P. marginata* to feed first on the host plant. Then, that plant material was given to experimental *P. marginata*, whose development time and size were measured. This type of intraspecific competition increased the development time and decreased

adult size (Figure 13.11C). The interspecific competition treatment allowed host plants to be fed on by *P. dolus* first, and then the plants were fed on by *P. marginata*. Interspecific competition increased development time to about the same extent that intraspecific competition did. However, adult size was more severely affected by interspecific competition. The overall results suggest that herbivory has direct effects on the plant community and indirect effects on other intraspecific and interspecific competitors. 

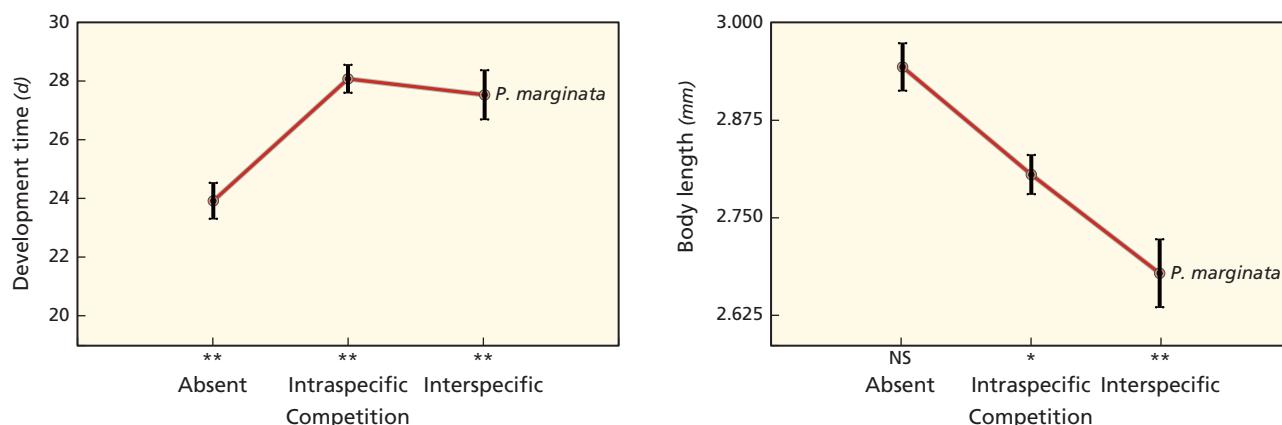
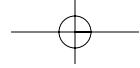


FIGURE 13.11C Development Time and Size of Female Planthoppers Following Three Experimental Competition Treatments In the *absent* treatment, planthoppers fed on fresh material. In the *intraspecific* treatment, planthoppers fed on plants previously fed upon by other members of the same species. In the *interspecific* treatment, planthoppers fed on plants previously fed on by members of a different species. Previous feeding has negative effects on both development time and body size. The effect on body size is most pronounced when there is interspecific competition.





13.12 Herbivores employ various offensive strategies to overcome plant defenses

Many defenses mounted by plants to ward off herbivores are quite effective. However, this does not mean that herbivores will not adapt to these defenses. In fact, we can think of herbivores as employing a variety of offensive mechanisms to exploit host plants. These offensive mechanisms may be any behavioral, physiological, or morphological trait that increases the performance and reproductive success on host plants. Some of these offensive mechanisms can be classified as less aggressive than others in the sense that they do not inflict direct damage on the plants.

For instance, herbivores faced with suboptimal food may simply eat more. This may be accomplished by eating more frequently, or by eating larger amounts per meal. Alternatively, herbivores may vary their diet to obtain their required calories and nutrition.

Slightly more aggressive mechanisms of herbivore offense include various physiological and morphological adaptations. Many of the toxic compounds produced by plants will be detoxified by enzymes that are part of the cytochrome P-450 system. The importance of these enzymes was demonstrated by Anurag Agrawal and colleagues (2002) on a species of spider mite (*Tetranychus urticae*) that feeds on a variety of host plants.

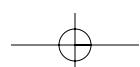
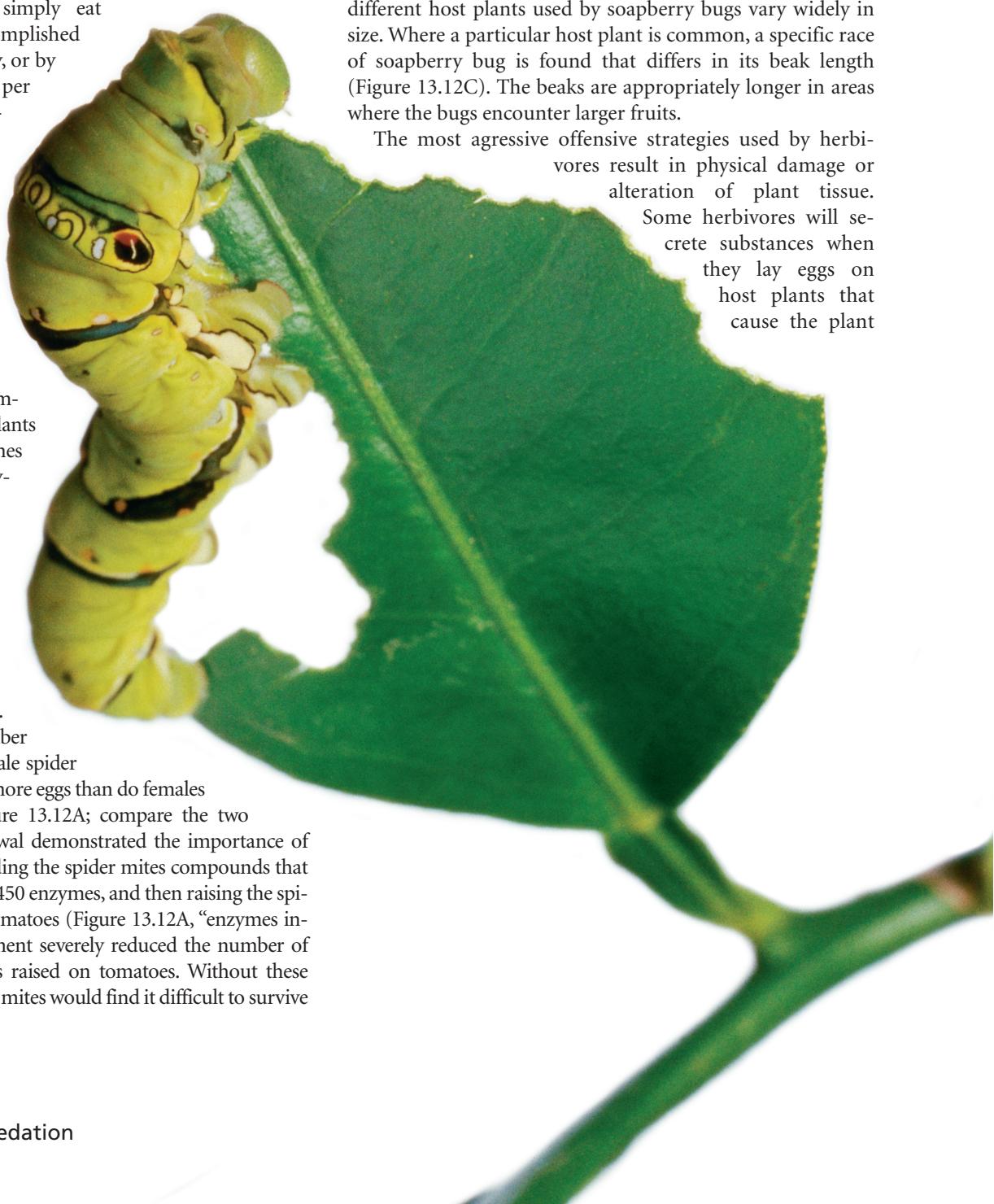
Tomatoes produce a number of toxic compounds. Female spider mites raised on beans lay more eggs than do females raised on tomatoes (Figure 13.12A; compare the two control treatments). Agrawal demonstrated the importance of the P-450 enzymes by feeding the spider mites compounds that inhibited the protective P-450 enzymes, and then raising the spider mites on beans and tomatoes (Figure 13.12A, “enzymes inhibited” bars). This treatment severely reduced the number of eggs produced by females raised on tomatoes. Without these protective enzymes, spider mites would find it difficult to survive on tomatoes.

Herbivores may also sequester toxic compounds in their own cells. The herbivore then gains the benefits of these toxins for protection against their own predators. The variety of sequestered compounds is large and includes cannabinoids, cardenolides, cocaine, and mustard oils.

Herbivores may also evolve morphological traits to better exploit host plants. Soapberry bugs live on a variety of host plants (Figure 13.12B). The bugs have long, tubular beaks used for feeding. The bug inserts its beak through the outer coat of the fruit until it pierces the seed coat. The bug then liquefies the seed and sucks up its contents. The fruits of the different host plants used by soapberry bugs vary widely in size. Where a particular host plant is common, a specific race of soapberry bug is found that differs in its beak length (Figure 13.12C). The beaks are appropriately longer in areas where the bugs encounter larger fruits.

The most aggressive offensive strategies used by herbivores result in physical damage or alteration of plant tissue.

Some herbivores will secrete substances when they lay eggs on host plants that cause the plant



to produce new plant tissue, called a gall (Figure 13.12D). These structures surround the developing larvae and usually provide access to nutrients within the gall. In addition, the gall may serve as protection from pathogens, predators, and parasites.

Some herbivores cut the large veins at the base of plant leaves. These veins serve as canals to transport plant-defensive chemicals. If the insect then feeds on leaf material beyond the veins, it will avoid the harmful effects of the plant's chemical defenses.

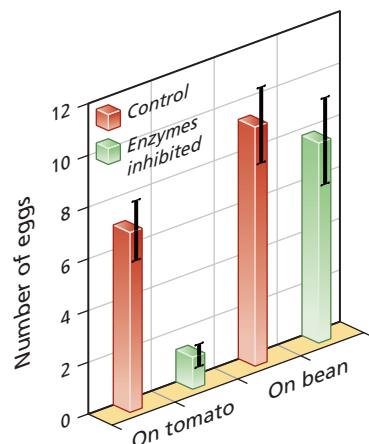


FIGURE 13.12A Number of Eggs Laid by Spider Mites Raised on Either Tomato or Bean Plants The two control treatments show that the spider mites do better on beans, because the tomato produces toxic compounds that the spider mites must detoxify. When the detoxification enzymes are inhibited, the performance of the mites is more severely affected on tomato, indicating the importance of these enzymes for using tomatoes as a host plant.

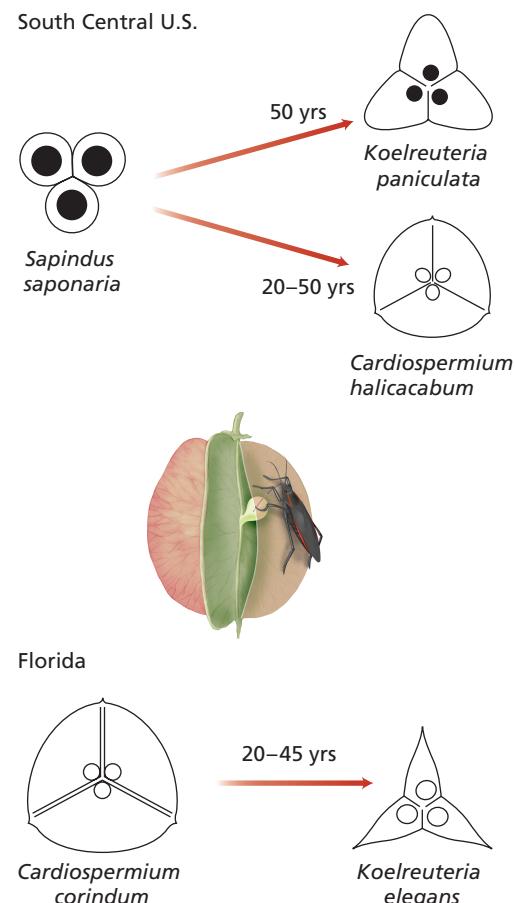


FIGURE 13.12B The soapberry bug feeds on a variety of host plants whose fruits vary widely in size. Different races of soapberry bugs are found on each of these host plants, with different-sized beaks that appear to have evolved in response to the host plant morphology.

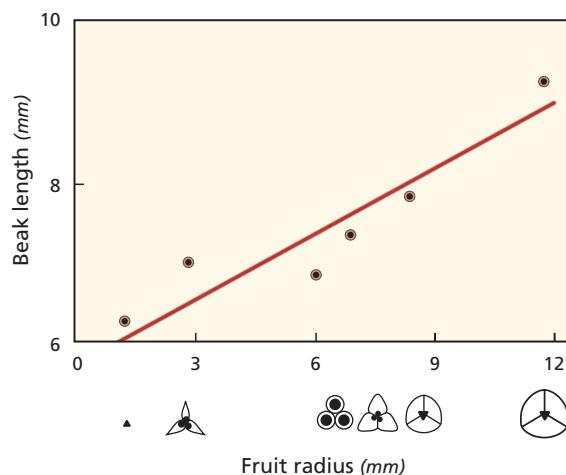
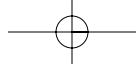


FIGURE 13.12C Beak Length of the Local Soapberry Bug as a Function of the Diameter of Fruit on Its Host Plant



FIGURE 13.12D The bumps on these maple leaves are maple bladder gall.



SUMMARY

1. Many natural populations of predators and prey show pronounced cycles.
2. One of the first and simplest models of predator-prey dynamics was developed by Vito Volterra and Alfred Lotka. This model produces cycles, but they are not stable and thus unlike the cycles of real populations.
3. The Lotka-Volterra predator-prey model can be made more realistic by including density-dependent prey growth and predator satiation.
4. The behavior of predators can be evaluated by comparing it to models of optimal behavior. Although ecologists have conflicting ideas about which properties of behavior should be optimal, two candidates are optimizing energy gain per unit of time spent foraging and minimizing time spent foraging.
5. Birds like wagtails and great tits appear to adjust their diets in a manner consistent with the maximization of energy return.
6. Prey may escape predators by avoiding any one of the stages of predation: encounter, detection, identification, approach, subjugation, or consumption.
7. Some prey sequester toxic or distasteful compounds that effectively dissuade many predators from eating them. These species are often conspicuously colored to warn predators.
 - a. Different species that employ these defenses may evolve similar warning coloration. These Müllerian mimics each benefit from their effects on common predators.
 - b. Some species evolve to look very similar to distasteful species, even though they lack that type of protection. These Batesian mimics thereby benefit from the protection afforded by the truly distasteful species.
8. Plants show a variety of adaptations to herbivores, including resistance and tolerance. Plants that evolve high levels of resistance may become less tolerant of herbivore damage.
9. Herbivores have a variety of offensive options to make them better at using plant resources. These mechanisms include behavioral changes, morphology, physiology, and active destruction or alteration of plant tissue.

REVIEW QUESTIONS

1. Why do the rises and declines of lynx always follow the rise and decline of hares?
2. Why is it likely that the cycles resulting from the Lotka-Volterra predator-prey model are not a complete explanation of predator-prey cycles in nature?
3. Why should the numbers of prey captured by predators eventually level off at very high prey densities?
4. Suppose a predator can choose from two prey that are equally nutritious. Prey A takes 0.9 hour to handle, and prey B takes 1 hour. The encounter rates per hour are 3 for prey A and 2 for prey B. If the predator minimizes the time spent capturing and consuming prey, should it choose a diet of just prey A, or should it choose both species? Explain your choice.
5. Give two examples of how prey avoid predators.
6. What is the difference between Müllerian and Batesian mimicry?
7. Under what conditions do we expect Müllerian and Batesian mimicry to evolve?
8. What is the difference between plant resistance to herbivores and plant tolerance of herbivores?
9. What evidence suggests that high resistance may lower tolerance?
10. What is meant by herbivore offense? Give three examples.

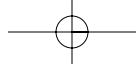
KEY TERMS

aposematic coloration
Batesian mimics
community
compensatory ability
cryptic coloration

functional response
handling time
herbivores
host and parasite
Lotka-Volterra predator-prey equations

Müllerian mimics
predation
prey
resistance

satiated
tolerance
waiting time



FURTHER READINGS

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