

# 12

## *Predation and Herbivory*



## 12 Predation and Herbivory

- *Case Study: Snowshoe Hare Cycles*
- Predation and Herbivory
- Adaptations
- Effects on Communities
- Population Cycles
- *Case Study Revisited*
- *Connections in Nature: From Fear to Hormones to Demography*

## Case Study: Snowshoe Hare Cycles



200 years of Hudson's Bay Company records document cycles of abundance of lynx and snowshoe hares.

## Case Study: Snowshoe Hare Cycles

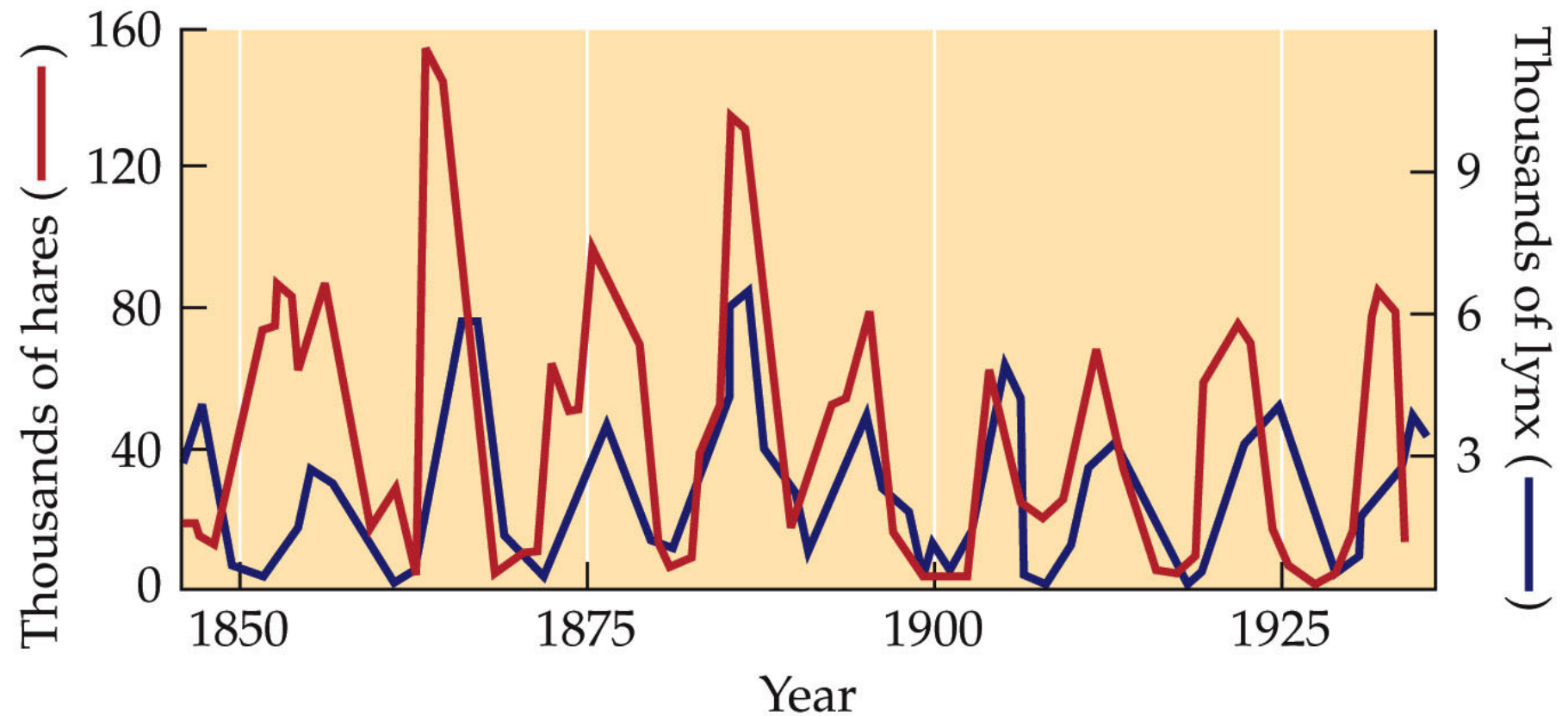
In the early 1900s, wildlife biologists used these records to graph the cycles of abundance of the lynx and hares.

This stimulated over 80 years of research on what drives the cyclic fluctuations in hare populations.

Hare populations also rise and fall in synchrony across broad regions of Canada.

Figure 12.2 A Hare Population Cycles and Reproductive Rates

(A)

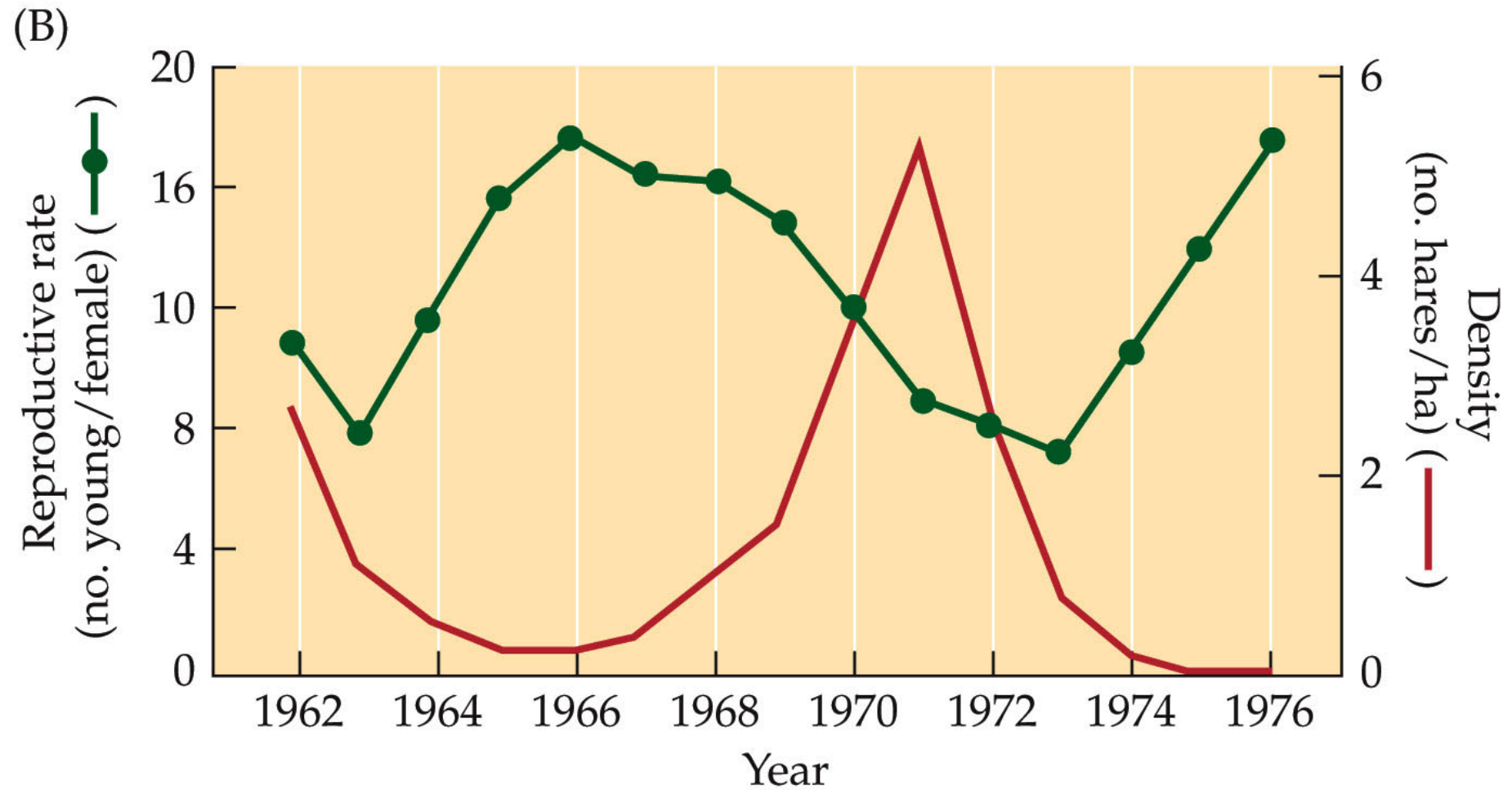


## Case Study: Snowshoe Hare Cycles

Population studies revealed that hare reproductive rates reach highest levels several years before hare density reaches a maximum. Then they decrease, reaching the lowest levels 2–3 years after hare density peaks.

Hare survival rates show a similar pattern.

Figure 12.2 B Hare Population Cycles and Reproductive Rates





## Case Study: Snowshoe Hare Cycles

Several hypotheses have been suggested to explain the changes in hare birth and survival rates.

1. Food supplies can become limiting when hare population density is high.

But some declining hare populations do not lack food; and the experimental addition of food does not prevent hare populations from declining.



## Case Study: Snowshoe Hare Cycles

2. Predation by lynx and other predators can explain the drop in survival rates as hare numbers decline. But it can't explain:

- Hare birth rates drop during the decline phase of the cycle.
- Hare numbers sometimes rebound slowly after predator numbers plummet.
- The physical condition of hares worsens as hares decrease in number.

## Introduction

Over half the species on Earth obtain energy by feeding on other organisms, in a variety of types of interactions.

All are **exploitation**—a relationship in which one organism benefits by feeding on, and thus directly harming, another.

## Introduction

- **Herbivore**—eats the tissue or internal fluids of living plants or algae.
- **Predator**—kills and eats other organisms, referred to as *prey*.
- **Parasite**—lives in or on another organism (its *host*), feeding on parts of the it. Usually they don't kill the host.
- Some parasites (*pathogens*) cause disease.

## Figure 12.3 Three Ways to Eat Other Organisms

(A)



(B)



(C)



## Introduction

Not all organisms fit neatly into these categories.

For example, some predators such as wolves also eat berries, nuts, and leaves.

**Parasitoids** are insects that lay an egg on or in another insect host. After hatching, larva remain in the host, which they eat and usually kill. Are they unusual parasites or unusual predators?



Figure 12.4 Are Parasitoids Predators or Parasites?



## Predation and Herbivory

**Concept 12.1: Most predators have broad diets, whereas a majority of herbivores have relatively narrow diets.**

Predators and herbivores share some similarities, but there are also differences.

Often, herbivores do not kill the food organisms as predators do, but there are exceptions.



## Predation and Herbivory

Some predators forage throughout their habitat in search of food.

Others are **sit-and-wait predators**, remaining in one place and attacking prey that move within striking distance.

These include sessile animals, such as barnacles, and carnivorous plants.

## Predation and Herbivory

Predators tend to concentrate their efforts in areas that yield abundant prey.

Example: Wolf packs follow seasonal migrations of elk herds.

Sit-and-wait predators such as spiders relocate from areas where prey are scarce to areas where prey are abundant.

## Predation and Herbivory

Most predators eat a broad range of prey species, without showing preferences.

Specialist predators do show a preference (e.g., lynx eat more hares than would be expected based on hare abundance).

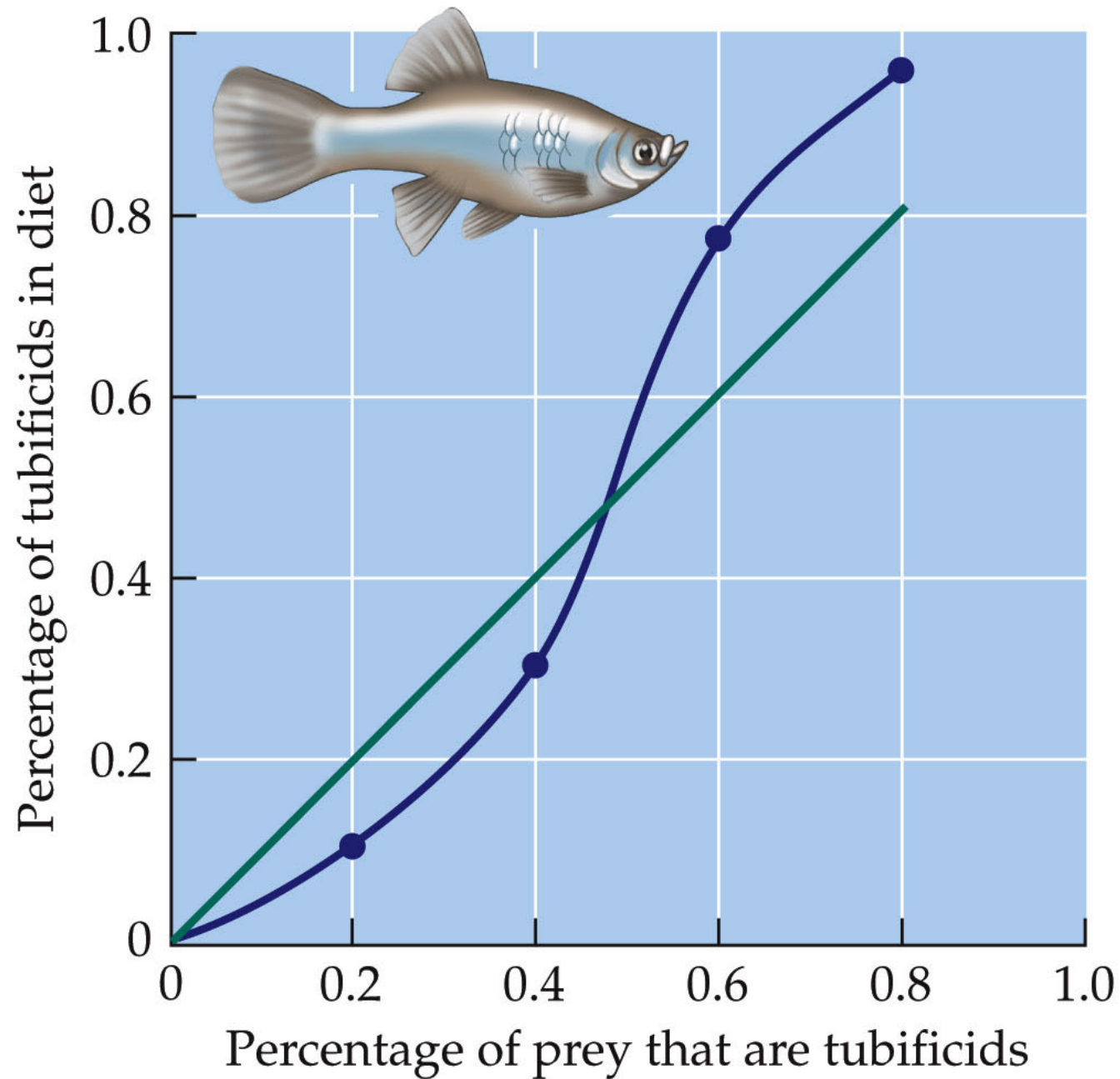
## Predation and Herbivory

Some predators concentrate foraging on whatever prey is most abundant.

When researchers provided guppies with two kinds of prey, the guppies ate disproportionate amounts of whichever prey was most abundant.

These predators tend to switch from one prey type to another.

Figure 12.5 A Predator That Switches to the Most Abundant Prey



## Predation and Herbivory

Switching may occur because the predator forms a search image of the most common prey type and orients toward that prey.

Or, learning enables it to become increasingly efficient at capturing the most common prey.

In some cases switching is consistent with optimal foraging theory.

## Predation and Herbivory

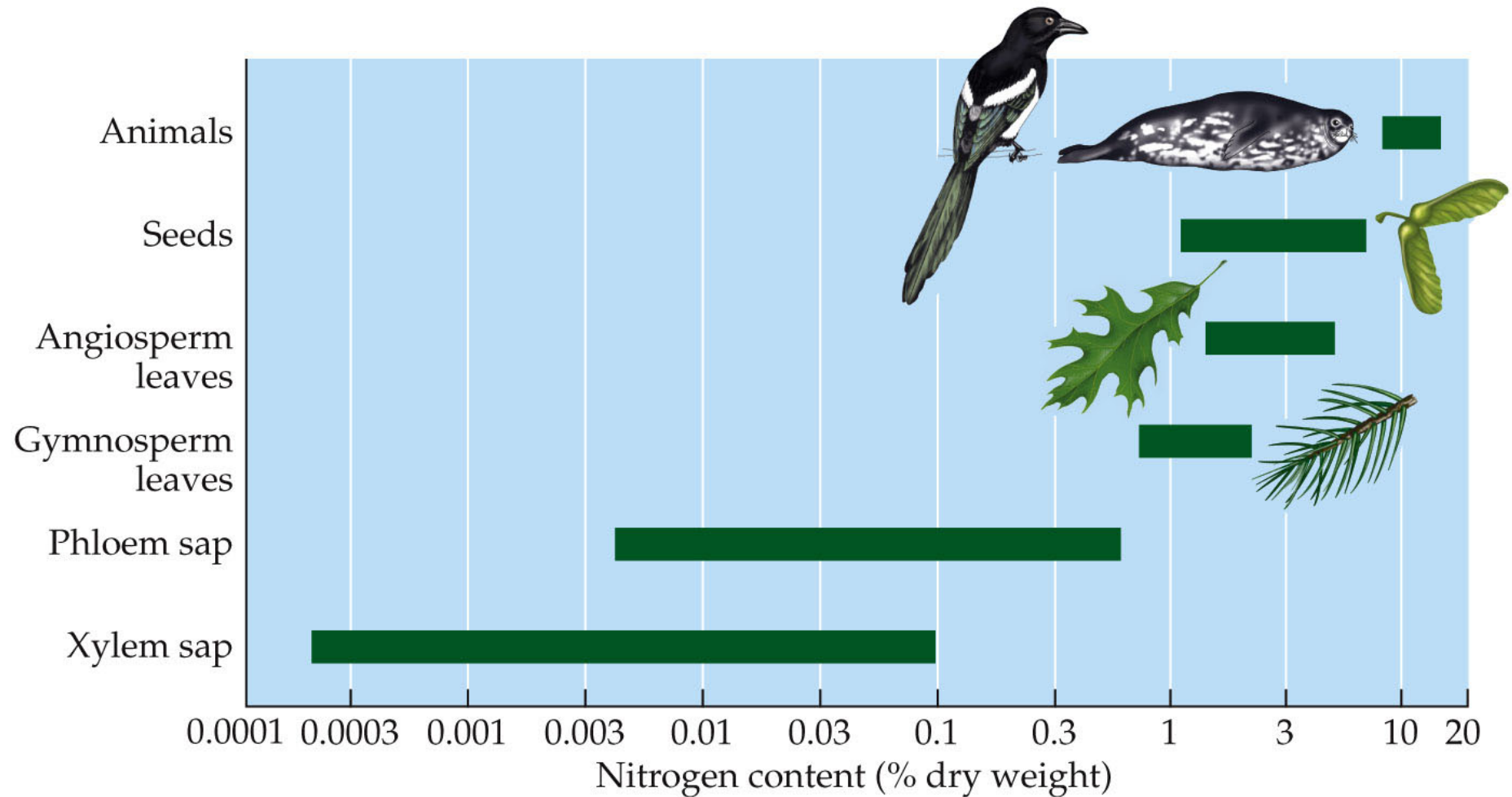
Herbivores can be grouped based on what part of a plant they feed on.

Large herbivores may eat all aboveground parts, but most specialize on particular plant parts.

Leaves are the most common part eaten. They are often the most nutritious part of the plant.



Figure 12.6 The Nitrogen Content of Plant Parts Varies Considerably



## Predation and Herbivory

Leaf-eating herbivores can reduce the growth, survival, or reproduction of their food plants.

Belowground herbivores can also have an impact. A 40% reduction in growth was observed in bush lupine plants after 3 months of herbivory by root-killing ghost moth caterpillars.

## Predation and Herbivory

Herbivores that eat seeds can impact reproductive success.

Some herbivores feed on the fluids of plants, by sucking sap, etc. For example, lime aphids did not reduce aboveground growth in lime trees but the roots did not grow that year, and a year later, leaf production dropped by 40% (Dixon 1971).

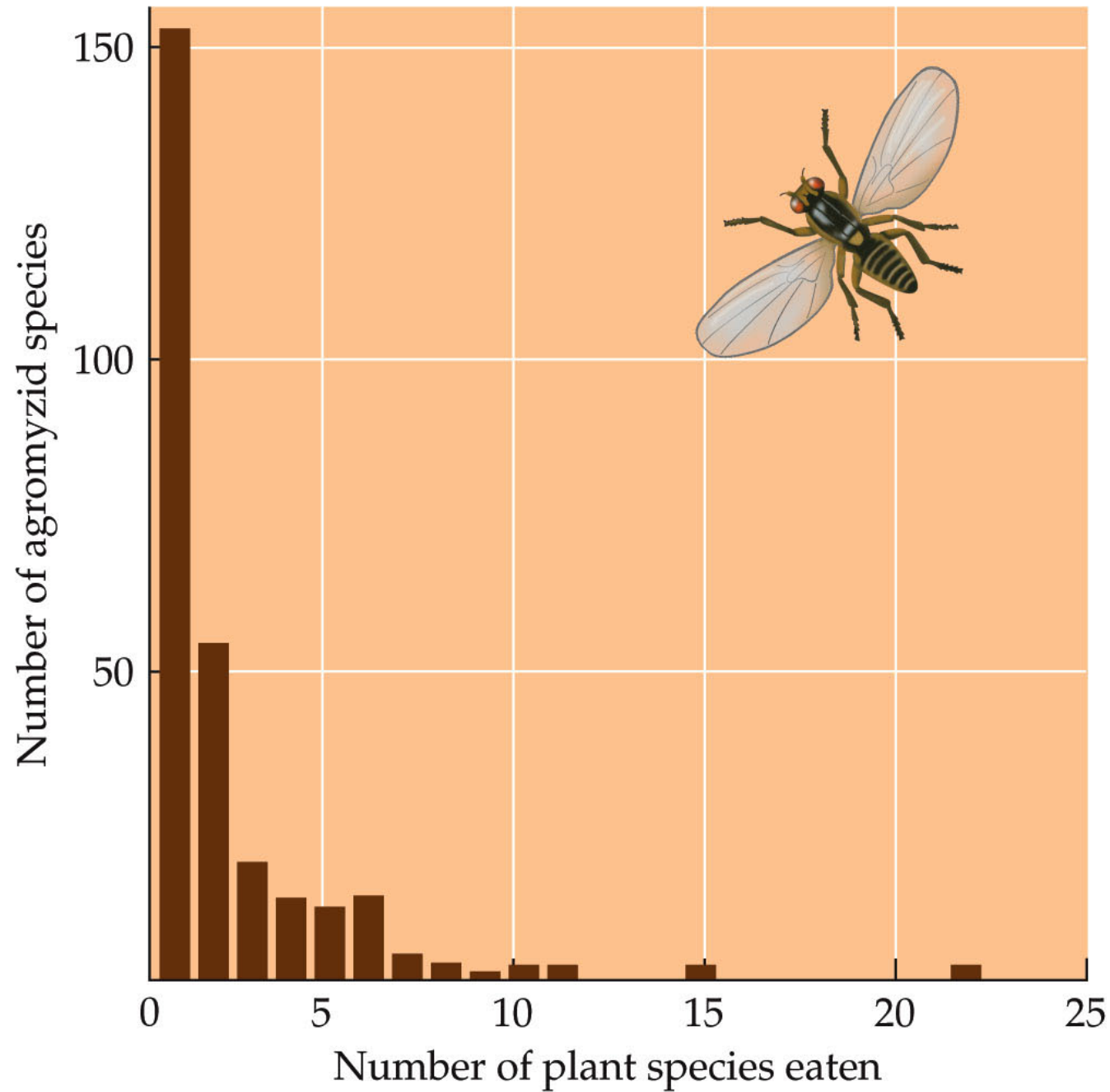
## Predation and Herbivory

Most herbivores feed on a narrow range of plant species.

Many are insects; most feed on only one or a few plant species.

An example is species of agromyzid flies, whose larvae are leaf miners, and feed on only one or a few plant species.

Figure 12.7 Most Agromyzid Flies Have Narrow Diets



## Predation and Herbivory

Some herbivores (e.g., grasshoppers) feed on a wide range of species

Large browsers, such as deer, often switch from one tree or shrub species to another.

## Predation and Herbivory

The golden apple snail is a voracious generalist, capable of removing all the large plants from wetlands; the snail then survives by eating algae and detritus.



## Adaptations

**Concept 12.2: Organisms have evolved a wide range of adaptations that help them capture food and avoid being eaten.**

Life changed radically with the appearance of the first macroscopic predators roughly 530 million years ago.

Before that time, the seas were dominated by soft-bodied organisms.

## Adaptations

Within a few million years, many herbivores had evolved defenses, such as body armor and spines.

The increase in prey defenses occurred because predators exert strong selection pressure on their prey: If prey are not well defended, they die.

Herbivores exert similar selection pressure on plants.

## Adaptations

Physical defenses include large size (e.g., elephants), rapid or agile movement (gazelles), and body armor (snails, anteater).

(A)



Figure 12.8 A Adaptations to Escape Being Eaten.

# Adaptations

Other species contain toxins. They are often brightly colored, as a warning—**aposematic coloration**. Predators learn not to eat them.

(B)



Figure 12.8 B Adaptations to Escape Being Eaten.

## Adaptations

Other prey species use mimicry as a defense.

**Crypsis**—the prey is camouflaged, or resembles its background.

Others may resemble another species that is fierce or toxic; predators that have learned to avoid the toxic species will avoid the mimic species as well.

Figure 12.8 C, D Adaptations to Escape Being Eaten

(C)



(D)





# Adaptations

(E)



Some species use behavior—such as foraging less in the open; or keeping lookouts for predators.

Figure 12.8 E Adaptations to Escape Being Eaten.

## Adaptations

Sometimes there is a trade-off between behavioral and physical defenses.

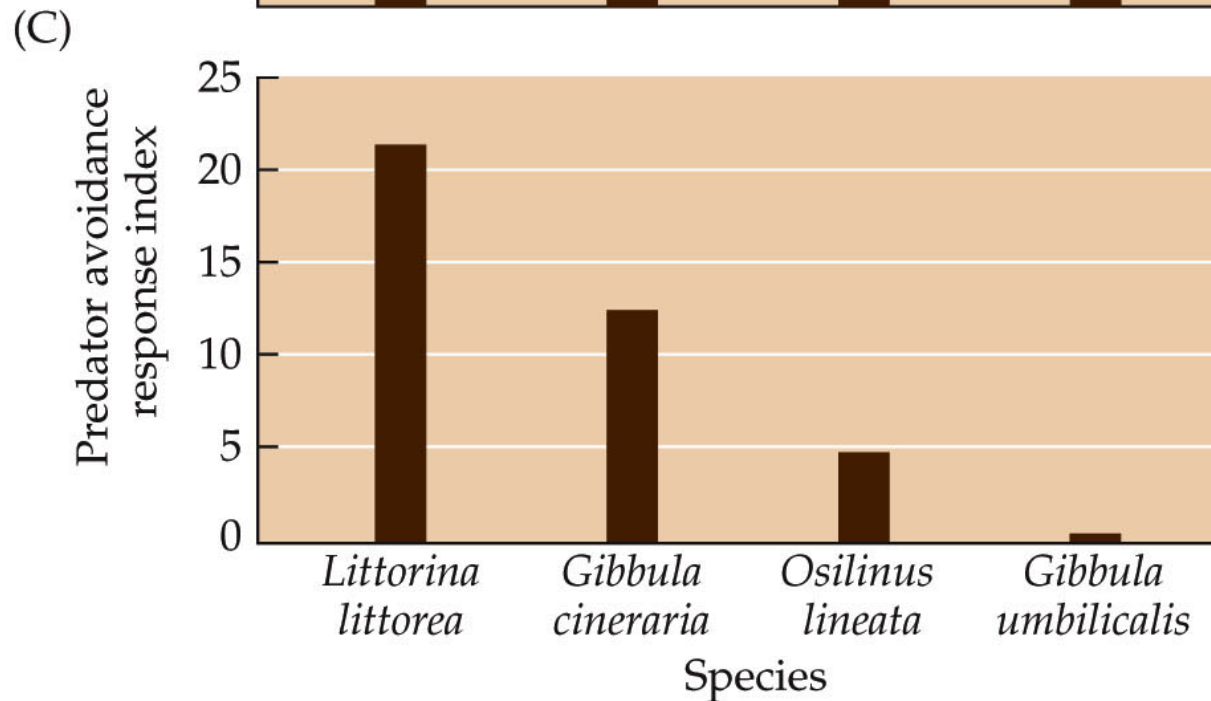
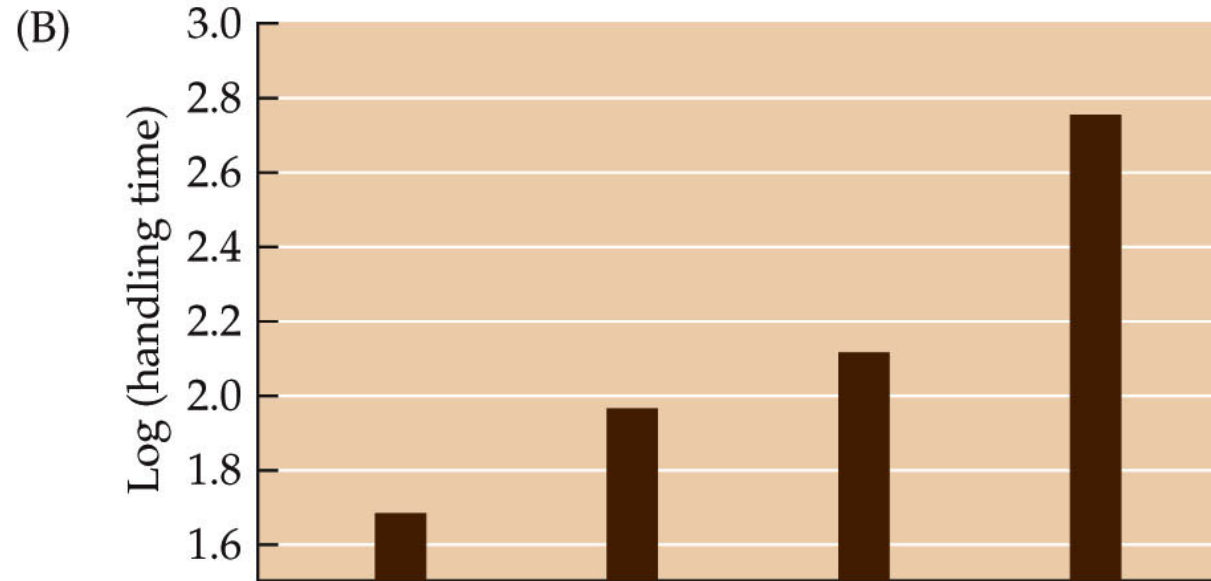
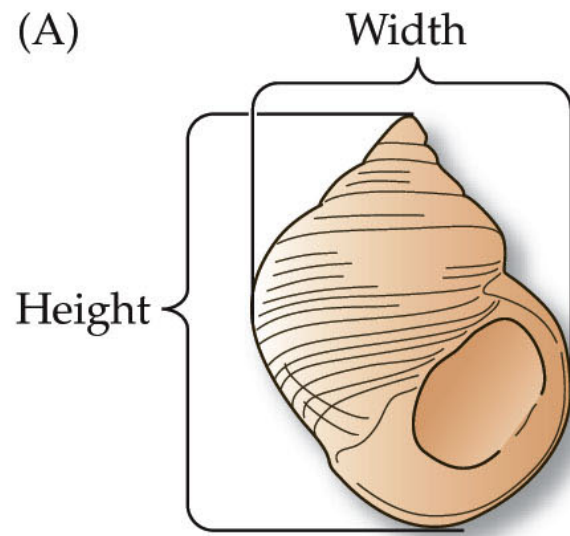
Example: Crabs use their powerful claws to crush snail shells.

Snails have evolved defenses, including thicker shells and reduced shell aspect ratio (ratio of shell height to width).

Some snails can detect crab odors and retreat when crabs are present.



Figure 12.9 A Trade-off in Snail Defenses against Crab Predation



## Adaptations

Cotton et al. (2004) studied four snail species and their crab predator.

The snail shells were of equal thickness, but one species was easily crushed because it had higher aspect ratio (tall and narrow), making it easier to grip and handle.

This species had the strongest behavioral response, seeking refuge quickly.

## Adaptations

Plants also have defenses.

Some produce huge numbers of seeds in some years and hardly any in other years (called *masting*). The plants hide (in time) from seed-eating herbivores, then overwhelm them by sheer numbers.

In some bamboos, bouts of mass flowering may be up to 100 years apart.

## Adaptations

Other defenses include producing leaves at times of the year when herbivores are scarce.

**Compensation**—growth responses that allow the plant to compensate for, and thus tolerate, herbivory. Removal of plant tissue stimulates new growth.

## Adaptations

Removal of leaves can decrease self-shading, resulting in increased plant growth.

Removal of apical buds may allow lower buds to open and grow.

When *exact compensation* occurs, herbivory causes no net loss of plant tissue.

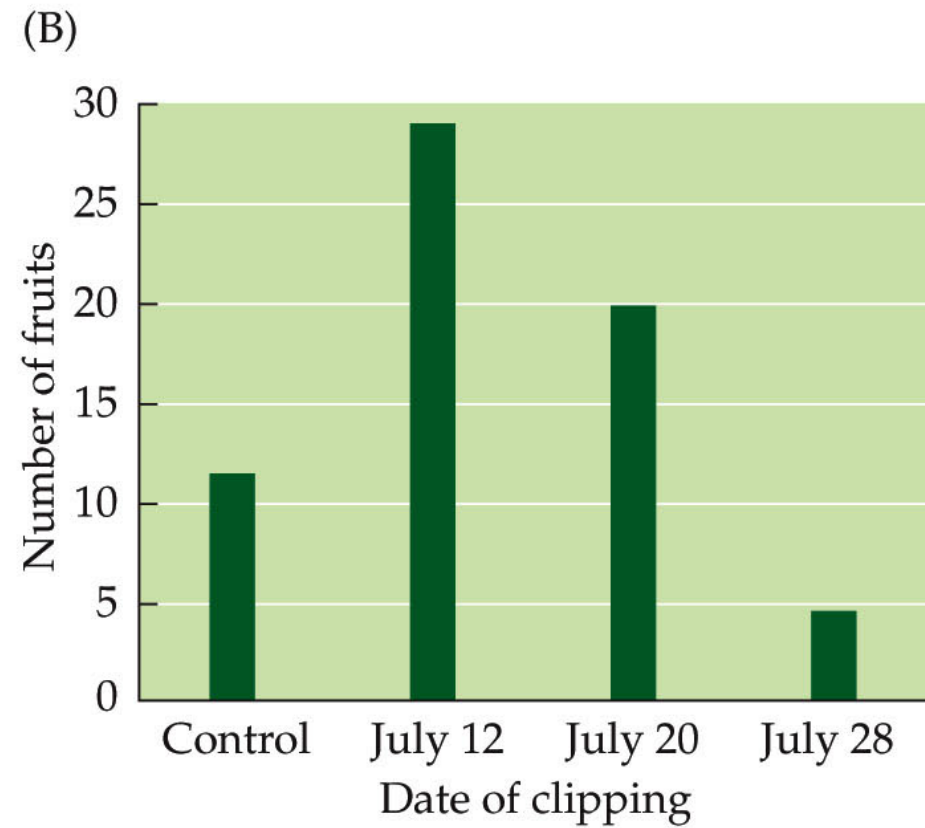
## Adaptations

For some plants, herbivory can be a benefit in some circumstances.

In field gentians, herbivory early in the growing season results in compensation, but later in the season it does not.

If too much material is removed, or there are not enough resources for growth, compensation cannot occur.

Figure 12.10 Compensating for Herbivory



## Adaptations

Plants have an array of structural defenses, including tough leaves, spines and thorns, saw-like edges, and pernicious (nearly invisible) hairs that can pierce the skin.

**Secondary compounds** are chemicals that reduce herbivory. Some are toxic to herbivores, others attract predators or parasitoids that will attack the herbivores.



## Adaptations

Some plants produce secondary compounds all the time.

**Induced defenses** are stimulated by herbivore attack. This includes secondary compounds and structural mechanisms. Example: some cacti increase spine production after they have been grazed on.

## Adaptations

Induced defenses have been studied in wild tobacco plants.

The seeds germinate after fires, and the plants live 3 years or less. Thus, populations appear and disappear from the landscape, and herbivory is unpredictable.

## Adaptations

The tobacco plants have two induced defenses:

- Toxic secondary compounds that deter herbivores directly.
- Compounds that deter herbivores indirectly by attracting predators and parasitoids.

## Adaptations

Kessler et al. (2004) used “gene silencing” to develop three varieties in which one of three genes was disabled.

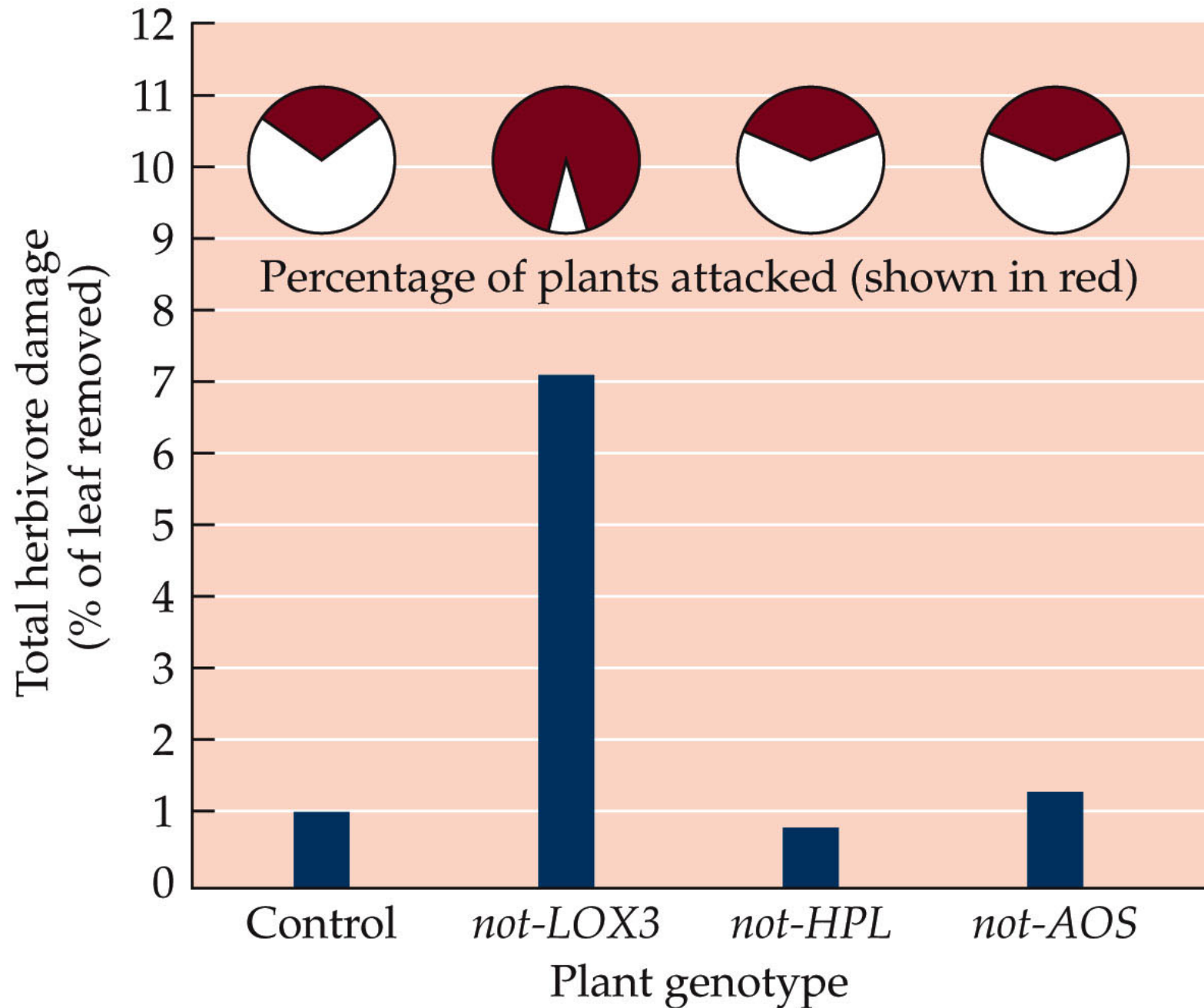
The three genes are part of a chemical pathway thought to control the induction of both direct (toxins) and indirect (attractants) defenses.

## Adaptations

The *not-LOX3* variety suffered much more damage from herbivores than either control plants or the other two experimental varieties.

Also, a greater variety of herbivores could feed on these plants than on the others.

Figure 12.11 Herbivores Damage Plants Lacking an Induced-Defense Gene



## Adaptations

These results showed that changes in a single gene can alter both the level of herbivory and the community of herbivores.

It also showed the power of combining molecular genetic techniques with ecological field experiments and being able to examine the effects of particular genes in a natural setting.

# Adaptations

Improvement in defense adaptations exert strong selection pressure on predators and herbivores.

For any defense mechanism of a prey species, there is usually a predator with a countervailing offense.

Example: Cryptic prey may be detected by smell or touch instead of sight.



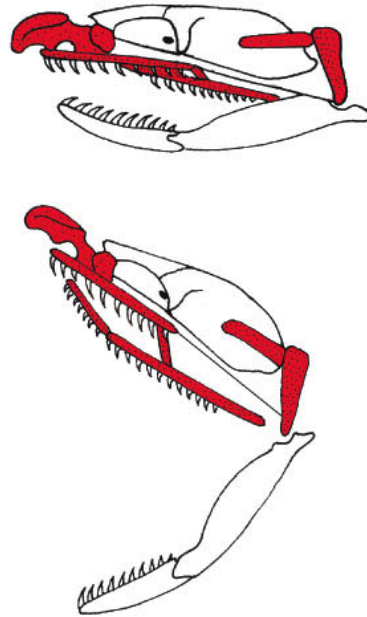
## Adaptations

Predators may have unusual physical features for prey capture.

Example: Most snakes can swallow prey that are larger than their heads.

The bones of a snake's skull are not rigidly attached to one another, which allows the snake to open its jaws to a seemingly impossible extent.

Figure 12.12 How Snakes Swallow Prey Larger Than Their Heads



## Adaptations

Some predators subdue prey with poisons (e.g., spiders).

Some use mimicry, blending into their environment so that prey are unaware of their presence.

Some have inducible traits (e.g., a ciliate that adjusts its size to match the size of the available prey).

## Adaptations

Some predators detoxify or tolerate prey chemical defenses.

The garter snake, *Thamnophis sirtalis*, is the only predator known to eat the toxic rough-skinned newt.

In some populations, the newt skin has large amounts of tetrodotoxin (TTX), an extremely potent neurotoxin.

Figure 12.13 A Nonvenomous Snake and Its Lethal Prey



## Adaptations

Garter snakes produce no poisons themselves, but some populations are resistant to the poisons of their prey.

Resistant garter snakes are protected from TTX, but there are costs associated with the ability to eat toxic newts.

Resistant garter snakes move more slowly than less-resistant individuals.

## Adaptations

After swallowing a toxic newt, the snake can't move for 7 hours. During this time it is vulnerable to predation and may suffer heat stress.

The newt and the snake may be locked in an evolutionary arms race: In populations where the newt has evolved to produce more TTX, the snake has evolved to tolerate the higher concentrations of the toxin.

## Adaptations

Plant defenses can also be overcome by herbivores.

Many have digestive enzymes that allow them to tolerate plant toxins. This can provide an abundant food source that other herbivores can't eat.



## Adaptations

Some tropical plants in the genus *Bursera* produce toxic sticky resins and store them in canals in leaves and stems.

If an insect herbivore chews through one of the canals, the resin squirts from the plant under high pressure to repel or even kill the insect.

Figure 12.14 Plant Defense and Herbivore Counterdefense

(A)



(B)



## Adaptations

Some tropical beetles in the genus *Blepharida* have evolved an effective defense (Becerra 2003).

They chew slowly through the leaf veins where the resin canals are located, releasing the pressure so gradually that the resin does not squirt from the plant.

## Adaptations

Some *Bursera* species produce a complex set of 7–12 toxins, some of which differ considerably in chemical composition.

Only a small subgroup of *Blepharida* beetles can detoxify all of these compounds and eat the plants.

These beetles diversified during the last 5–19 million years, roughly in synchrony with the plants they feed on.

## Effects on Communities

**Concept 12.3: Predation and herbivory affect ecological communities greatly, in some cases causing a shift from one community type to another.**

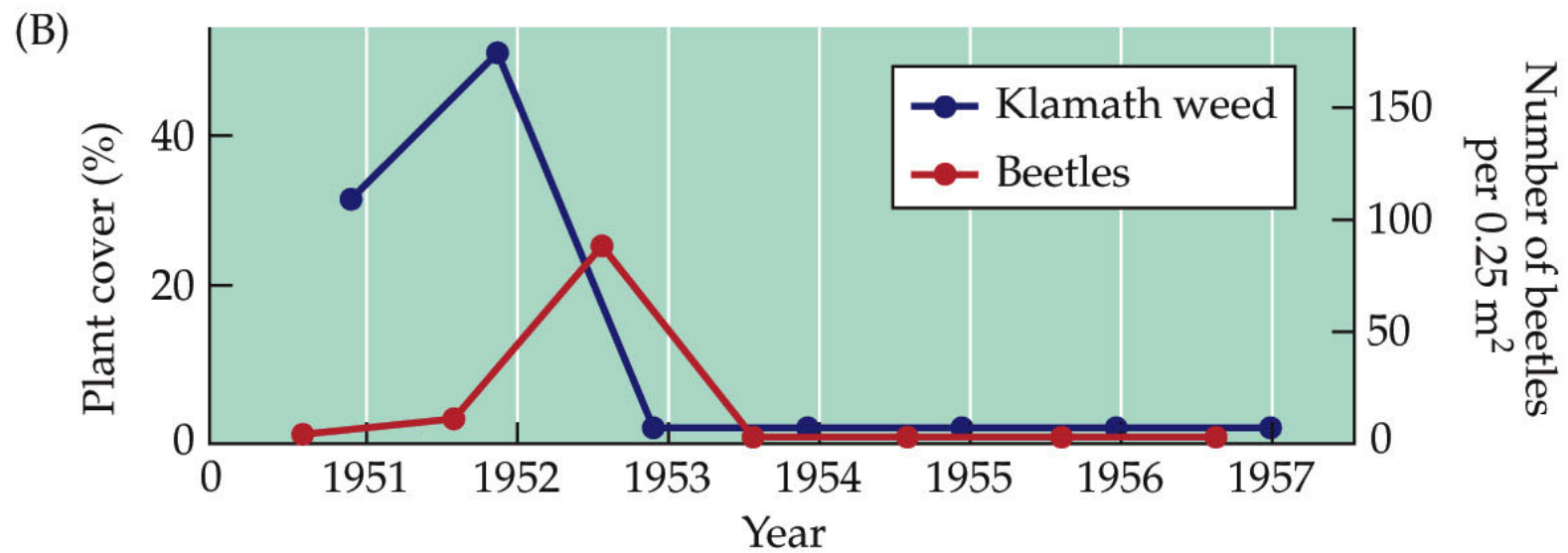
All exploitative interactions have the potential to reduce the growth, survival, or reproduction of the organisms that are eaten.

## Effects on Communities

Klamath weed is an introduced plant that is poisonous to livestock. It infested about 4 million acres of rangeland in the western U.S.

A leaf-feeding beetle (*Chrysolina quadrigemina*) rapidly reduced the density of this weed.

Figure 12.15 A Beetle Controls a Noxious Rangeland Weed



## Effects on Communities

Predators and parasitoids can also have dramatic effects.

Introductions of wasps that prey on crop-eating insects can decrease their densities by 97.5% to 99.7%, reducing the economic damage caused by the pests.



## Effects on Communities

Predators and herbivores can change the outcome of competition, thereby affecting distribution or abundance of competitor species.

If the presence of a predator or herbivore decreases performance of the top competitor, the inferior competitor may increase in abundance.

## Effects on Communities

Paine (1974) removed starfish predators from a rocky intertidal zone, which led to the local extinction of all large invertebrates but one, a mussel.

When the starfish predator was present, inferior competitors were able to persist.

## Effects on Communities

Predators can decrease the distribution and abundance of their prey.

Schoener and Spiller (1996) studied the effects of *Anolis* lizard predators on their spider prey in the Bahamas.

On 12 islands, four had lizards naturally, four had lizards introduced for the study, and four had no lizards (control).

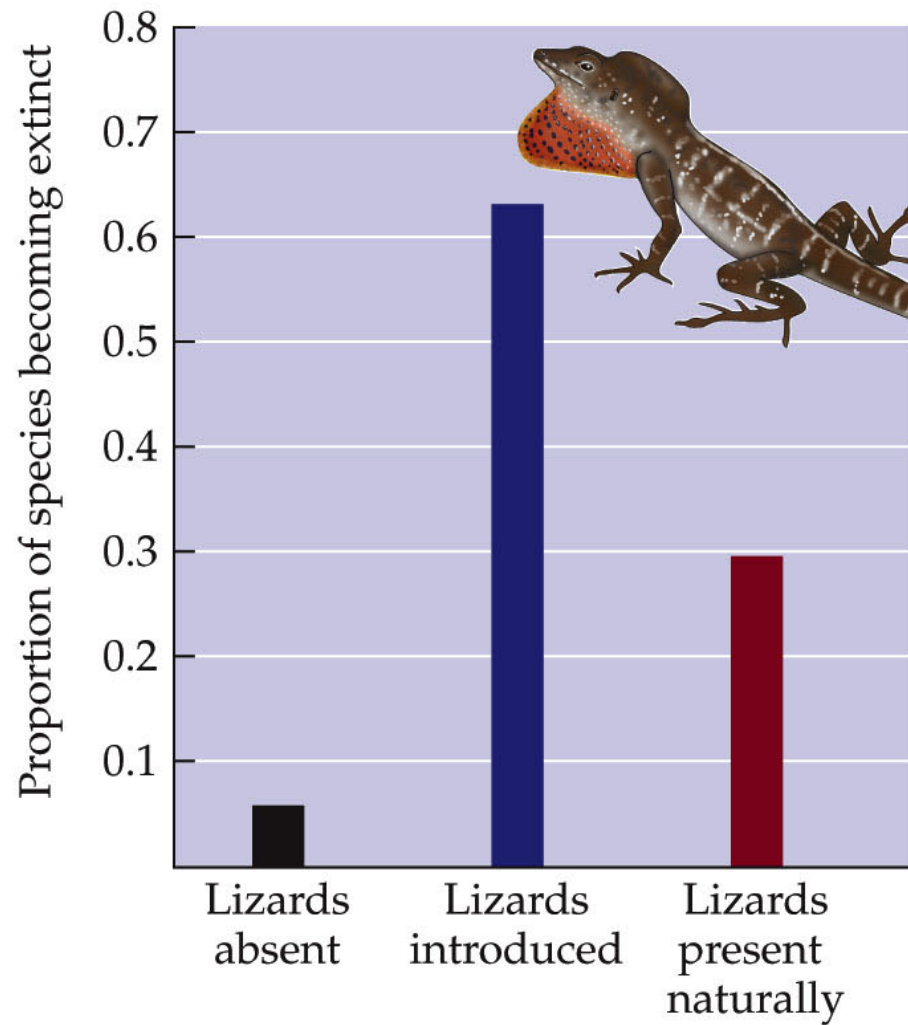
## Effects on Communities

The introduced lizards greatly reduced the distribution and abundance of their spider prey.

The proportion of spider species that went extinct was 13 times higher on islands where lizards were introduced.

Density of spiders was about 6 times higher on islands without lizards.

Figure 12.16 Lizard Predators Can Drive Their Spider Prey to Extinction



## Effects on Communities

Introduction of lizards reduced the density of both common and rare spider species: Most rare species went extinct.

Similar results have been obtained for beetles eaten by rodents and grasshoppers eaten by birds.

## Effects on Communities

Herbivores can decimate food plants.

Lesser snow geese (*Chen caerulescens*) can benefit the salt marshes of northern Canada where they summer, because they fertilize the nitrogen-poor soil with their feces.

The plants grow rapidly after low to intermediate levels of grazing by geese.

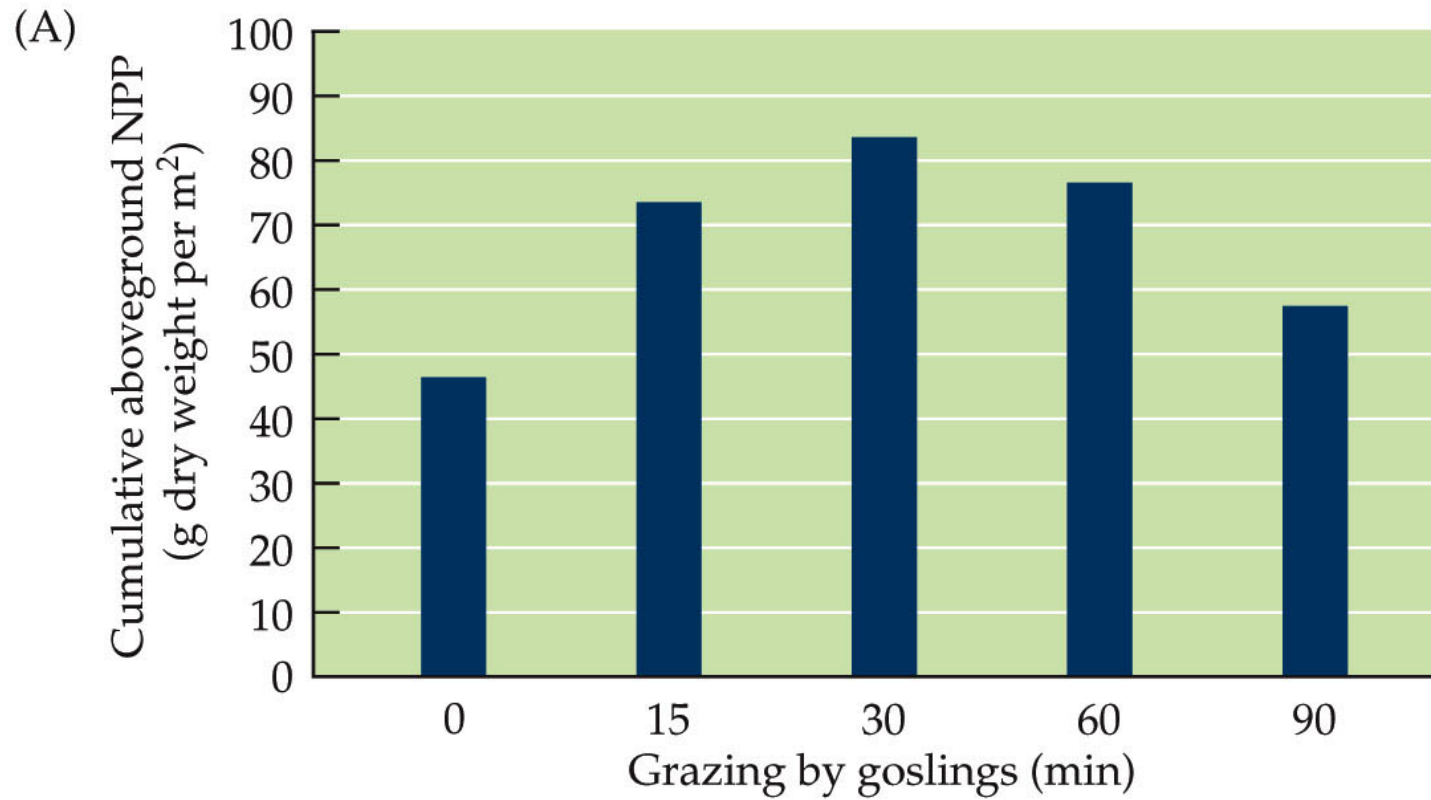
## Effects on Communities

But around 1970, lesser snow goose densities increased exponentially; probably because of increased crop production near their overwintering sites.

At high densities, the geese completely removed the vegetation, drastically changing distribution and abundance of marsh plant species.



Figure 12.17 Snow Geese Can Benefit or Decimate Marshes



## Effects on Communities

Predators can reduce diversity of prey species (e.g., the lizards and spiders), but in some cases, a predator that suppresses a dominant competitor can (indirectly) increase diversity (e.g., the starfish and mussels).

Predators can also alter communities by affecting transfer of nutrients from one ecosystem to another.

## Effects on Communities

Arctic foxes were introduced to some of the Aleutian Islands around 1900.

These introductions reduced seabird density by 100-fold, which reduced the amount of guano which fertilizes plants on the islands.

The guano transfers nitrogen and phosphorus from the ocean to the land.

## Effects on Communities

With less guano, dwarf shrubs and herbaceous plants increased in abundance at the expense of grasses.

The introduction of foxes had the unexpected effect of transforming the community from grassland to tundra (Croll et al. 2005).

## Effects on Communities

Herbivores can also have large effects.

Darwin observed that Scotch fir trees rapidly replaced heath when areas were enclosed to prevent grazing by cattle.

Heathlands that were grazed had many small fir seedlings, kept browsed down by the cattle. Thus, the very existence of the heath community in that area depended on herbivory.

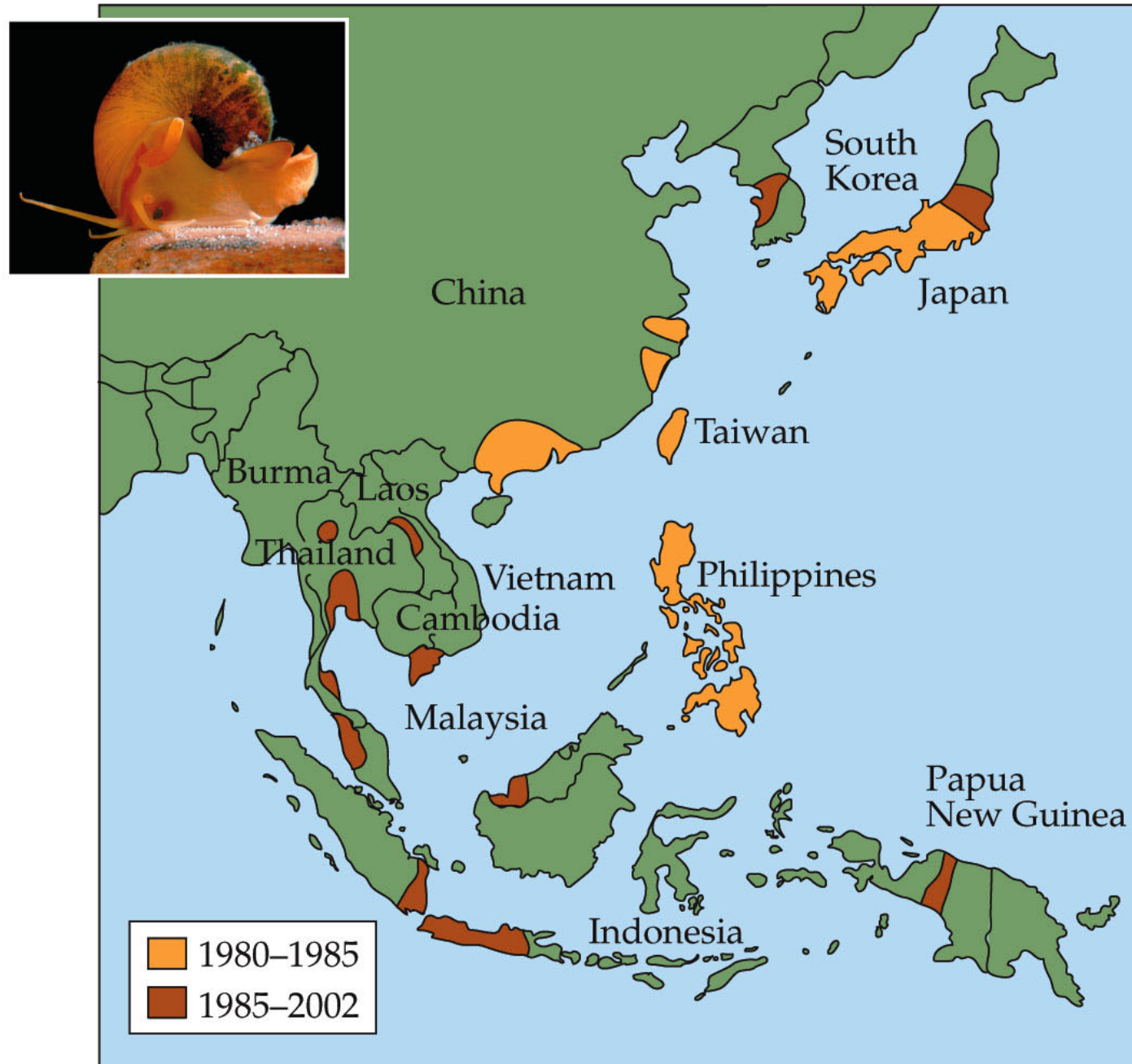
## Effects on Communities

The golden apple snail was introduced from South America to Taiwan in 1980.

The snail escaped from cultivation and spread rapidly through Southeast Asia.

The snail eats aquatic plants, but if they aren't available, it can eat algae and detritus.

Figure 12.18 The Geographic Spread of an Aquatic Herbivore



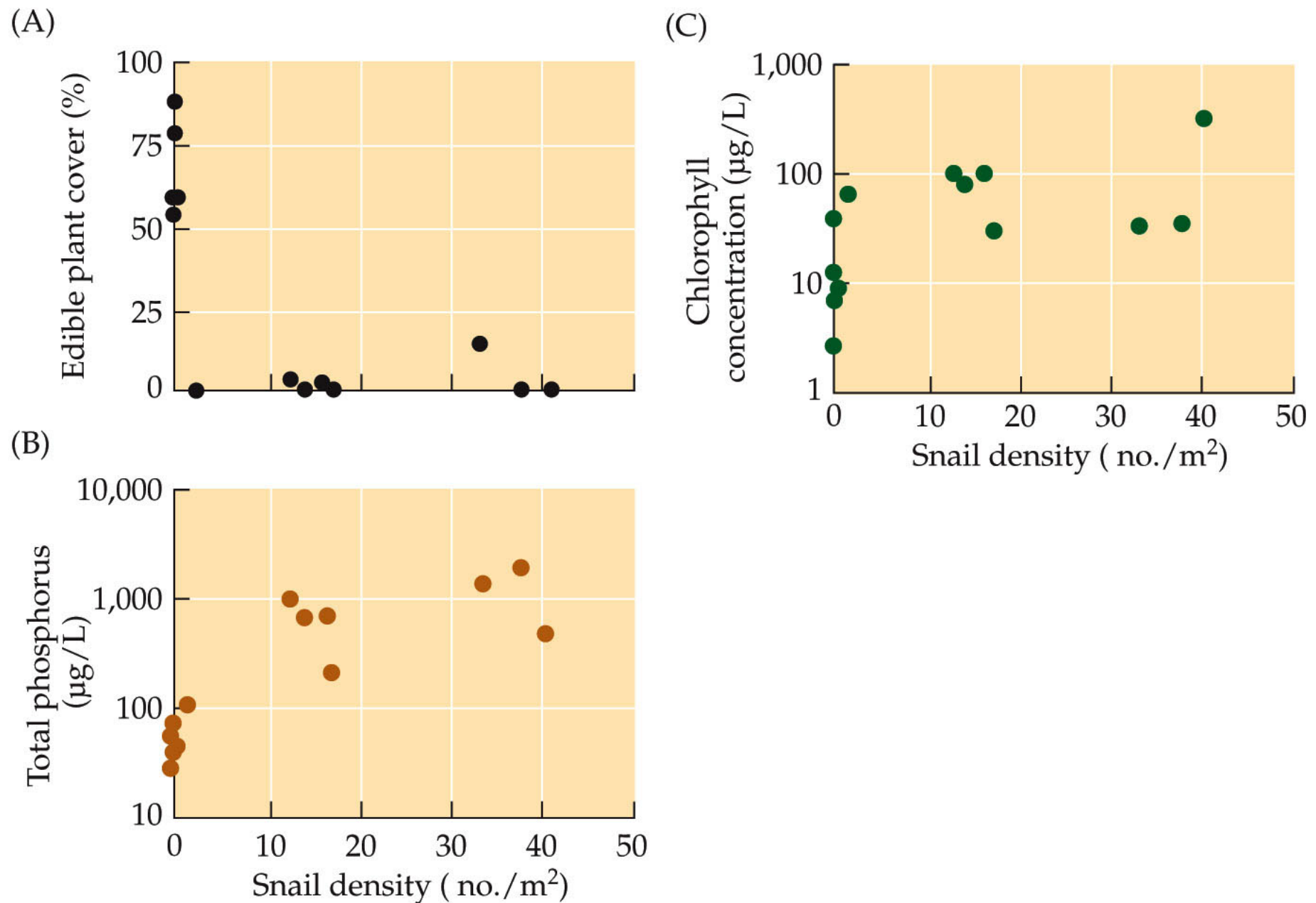
## Effects on Communities

Wetland communities with high snail densities were characterized by few plants, high nutrient concentrations, and high densities of algae (Carlsson et al. 2004).

To test the influence of the snail, enclosures with water hyacinth and 0, 2, 4, or 6 snails were constructed.



Figure 12.19 A Snail Herbivore Alters Aquatic Communities



## Effects on Communities

Where snails were present, water hyacinth biomass decreased, but increased in the 0-snail enclosure.

Phytoplankton and net primary productivity increased in enclosures with snails.

## Effects on Communities

Both studies show that the golden apple snail causes a complete shift from wetlands with clear water and many plants to wetlands with turbid water, few plants, high nutrients, and high algal densities.

The snails affect plants directly by feeding on them, and also release nutrients in their feces that stimulate phytoplankton growth.

## Population Cycles

**Concept 12.4: Population cycles can be caused by feeding relations, such as a three-way interaction between predators, herbivores, and plants.**

A specific effect of exploitation can be population cycles.

Lotka and Volterra evaluated these effects mathematically in the 1920s.

## Population Cycles

The Lotka–Volterra predator–prey model:

$$\frac{dN}{dt} = rN - aNP$$

$$\frac{dP}{dt} = f aNP - dP$$

## Population Cycles

$$\frac{dN}{dt} = rN - aNP$$

$N$  = Number of prey

$P$  = Number of predators

$r$  = Population growth rate

$a$  = Capture efficiency

## Population Cycles

When  $P = 0$ , the prey population grows exponentially.

With predators present ( $P \neq 0$ ), the rate of prey capture depends on how frequently they encounter each other ( $NP$ ), and efficiency of prey capture ( $a$ ).

The overall rate of prey removal is  $aNP$ .

## Population Cycles

$$\frac{dP}{dt} = f a N P - dP$$

$N$  = Number of prey

$P$  = Number of predators

$d$  = Death rate

$a$  = Capture efficiency

$f$  = Feeding efficiency



## Population Cycles

If  $N = 0$ , predator population decreases exponentially at death rate  $d$ .

When prey are present ( $N \neq 0$ ), individuals are added to the prey population according to number of prey killed ( $aNP$ ), and the feeding efficiency with which prey are converted to predator offspring ( $f$ ).

## Population Cycles

Zero population growth isoclines can be used to determine what happens to predator and prey populations over long periods of time.

Prey population decreases if  $P > r/a$ ; it increases if  $P < r/a$ .

Predator population decreases if  $N < d/fa$ ; it increases if  $N > d/fa$ .

Combining these reveals that predator and prey populations tend to cycle.

Figure 12.20 A, B, C Predator–Prey Models Produce Population Cycles

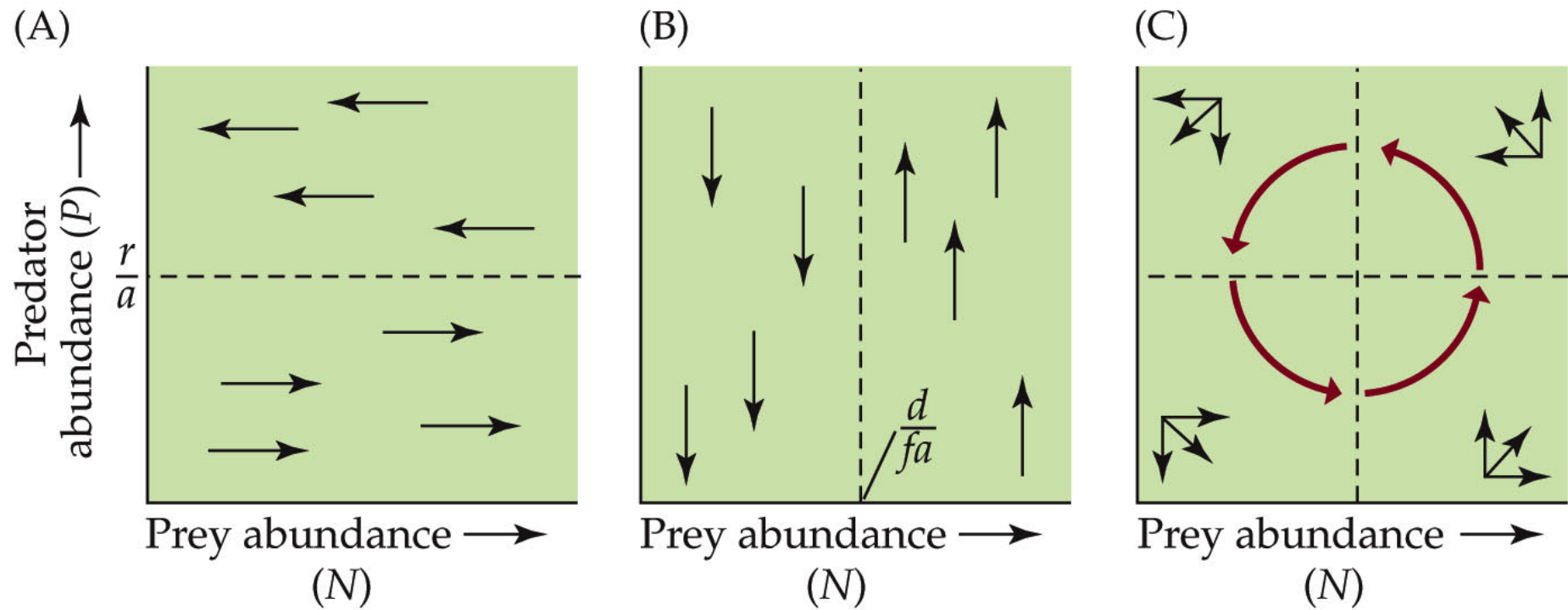
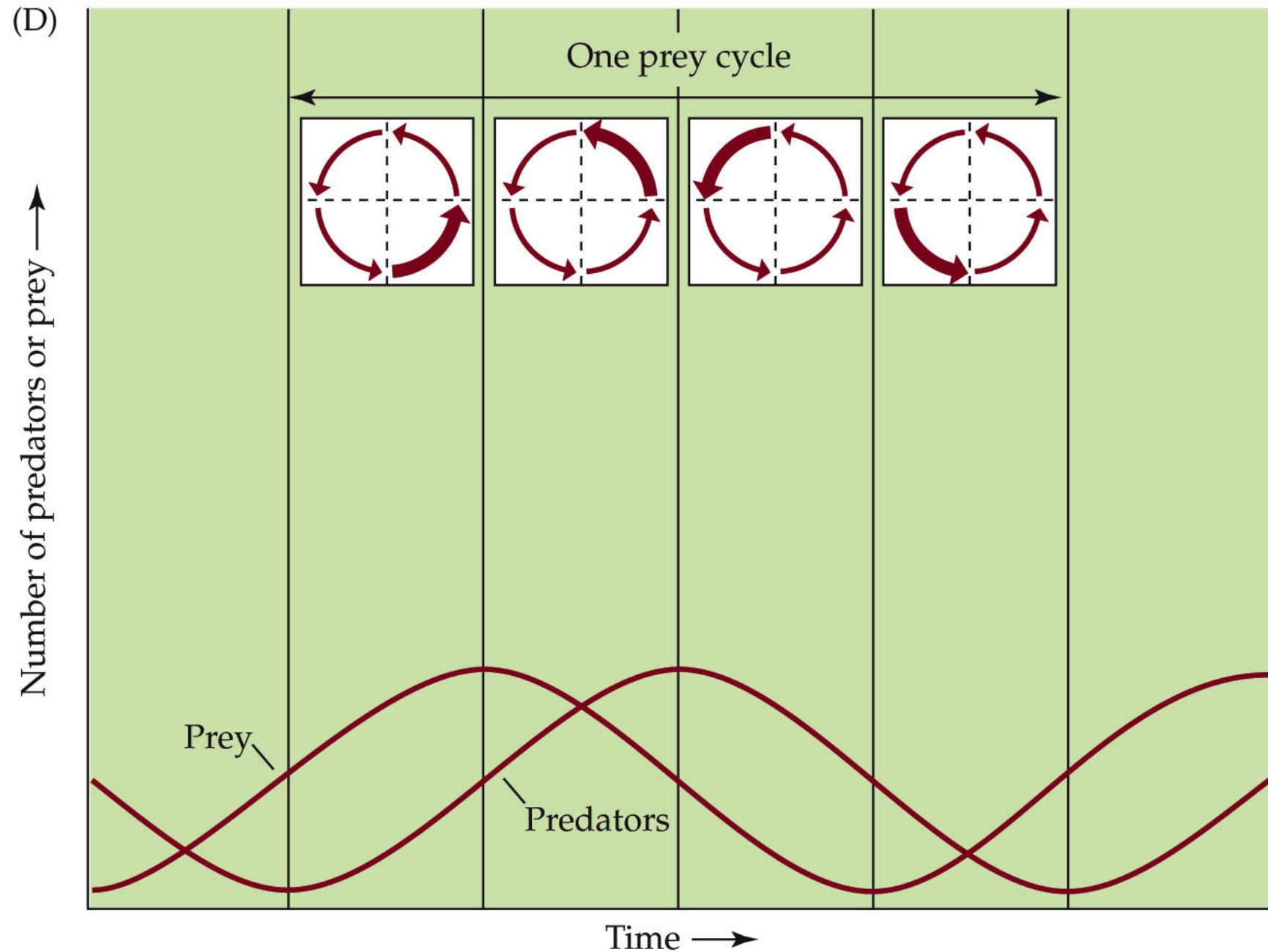


Figure 12.20 D Predator–Prey Models Produce Population Cycles



## Population Cycles

The Lotka–Volterra predator–prey model suggests that predator and prey populations have an inherent tendency to cycle.

It also has an unrealistic property: The amplitude of the cycle depends on the initial numbers of predators and prey.

More complex models don't show this dependence on initial population size.

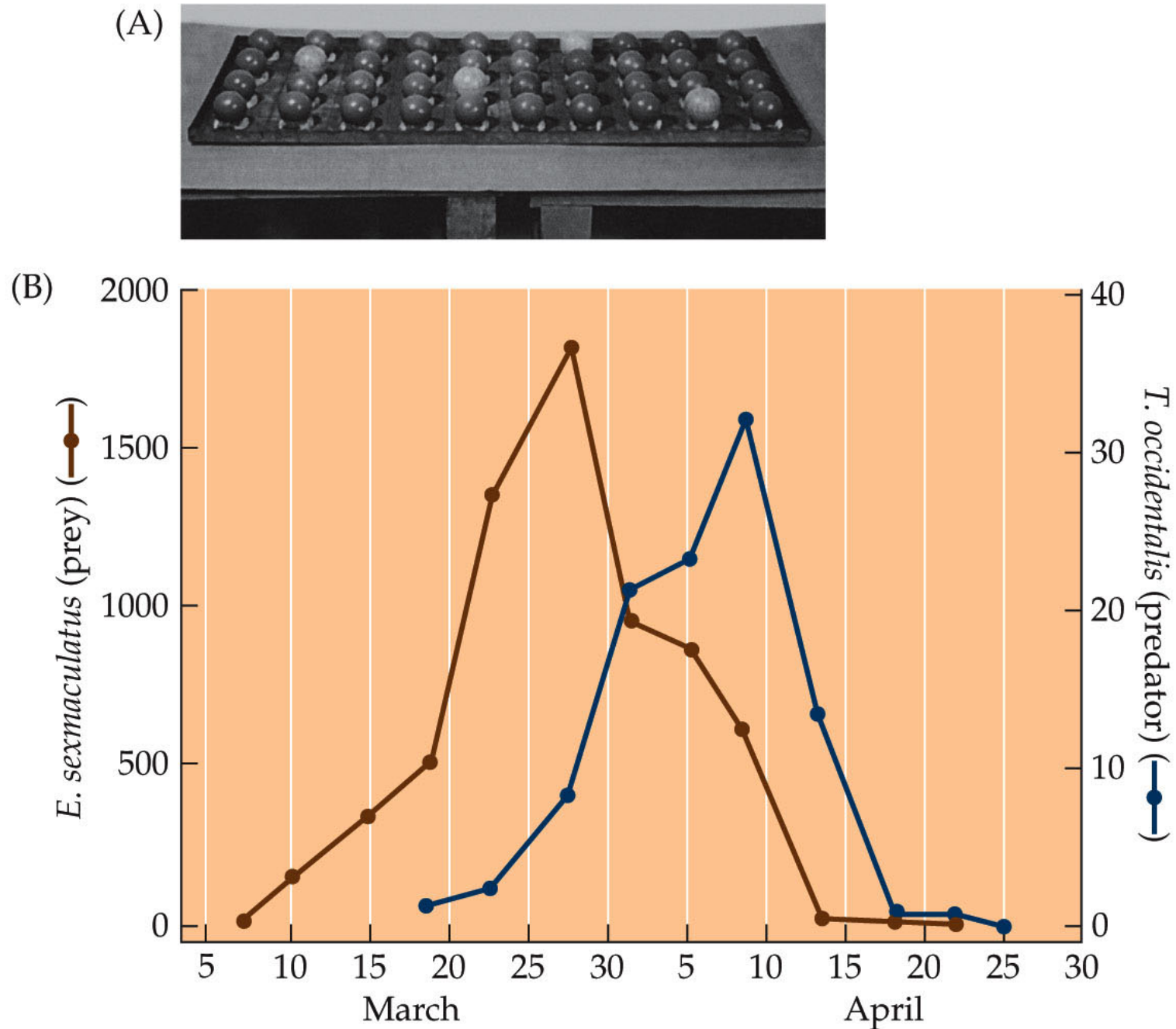
## Population Cycles

Population cycles are difficult to achieve in the laboratory.

In Huffaker's (1958) experiments with a predatory mite that eats the herbivorous six-spotted mite, both populations went extinct.

When prey are easy for predators to find, predators typically drive prey to extinction, then go extinct themselves.

Figure 12.21 In a Simple Environment, Predators Drive Prey to Extinction



## Population Cycles

Huffaker observed that the prey persisted longer if the oranges they fed on were widely spaced—presumably because it took the predators more time to find their prey.

He tested this in another experiment with more complex habitat.



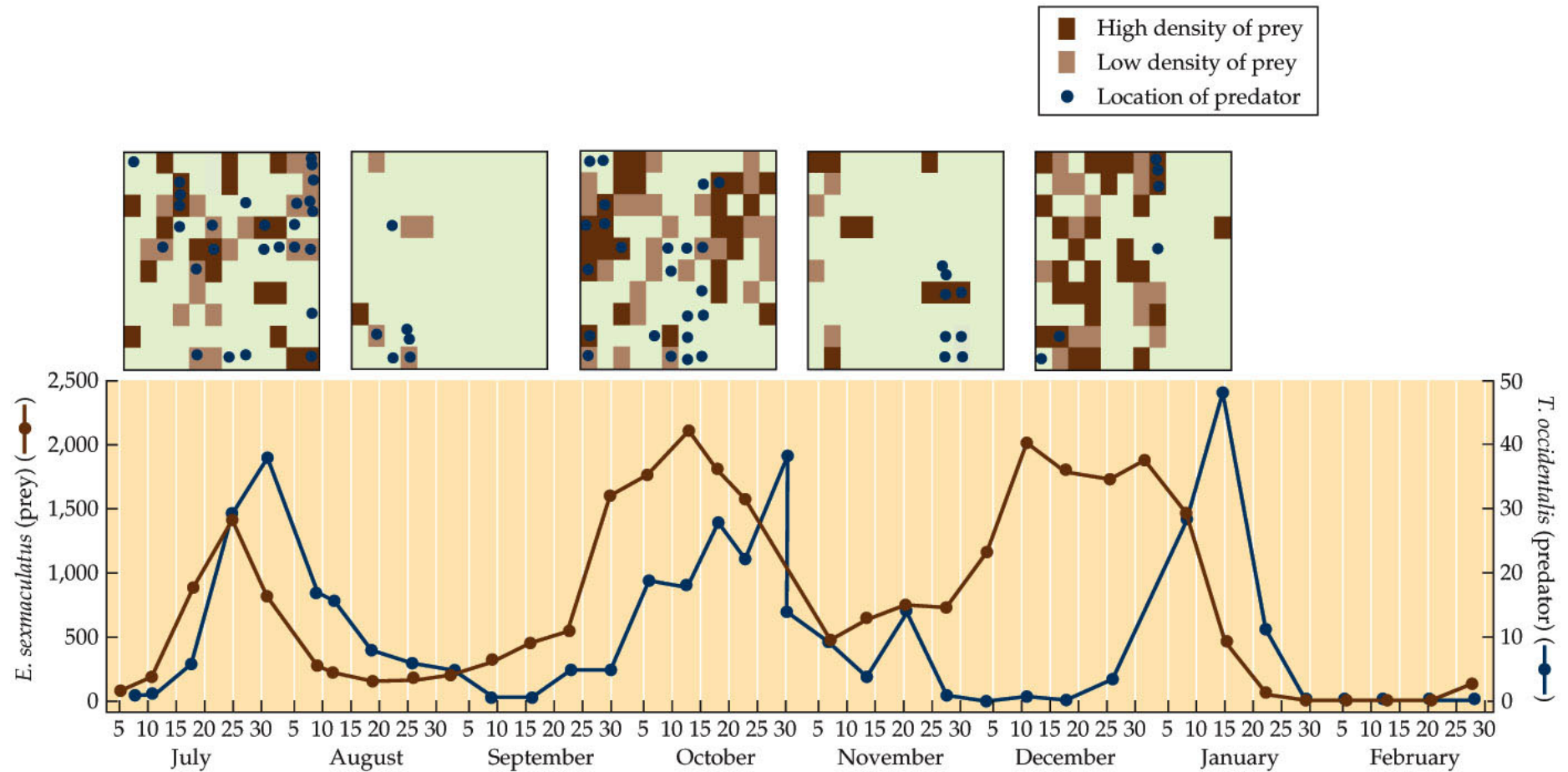
## Population Cycles

Strips of Vaseline were added that partially blocked movement of the predatory mites.

Small wooden posts were placed in the oranges, allowing the herbivorous mites to spin a silken thread and float on air currents over the Vaseline barriers.

Under these conditions, both populations persisted, and cycles resulted.

Figure 12.22 Predator–Prey Cycles in a Complex Habitat



## Population Cycles

The herbivores could disperse to unoccupied oranges, where their numbers increased.

Once predators found an orange with six-spotted mites, they ate them all, and both prey and predator numbers on that orange dropped.

But some six-spotted mites dispersed to other oranges, where they increased until they were discovered by the predators.

## Population Cycles

Many studies have shown that predators influence population cycles of prey.

But it is not the only factor. Food supplies for herbivores can also play a role, as well as social interactions.

Population cycles often seem to be caused by three-way feeding relationships: predators, prey, and the prey's food supply (e.g., plants).

## Population Cycles

In natural populations, many factors can prevent predators from driving prey to extinction, including habitat complexity and limited predator dispersal (Huffaker's mites), switching behavior in predators (the guppies in Figure 12.5), and spatial refuges (areas where predators cannot hunt effectively).

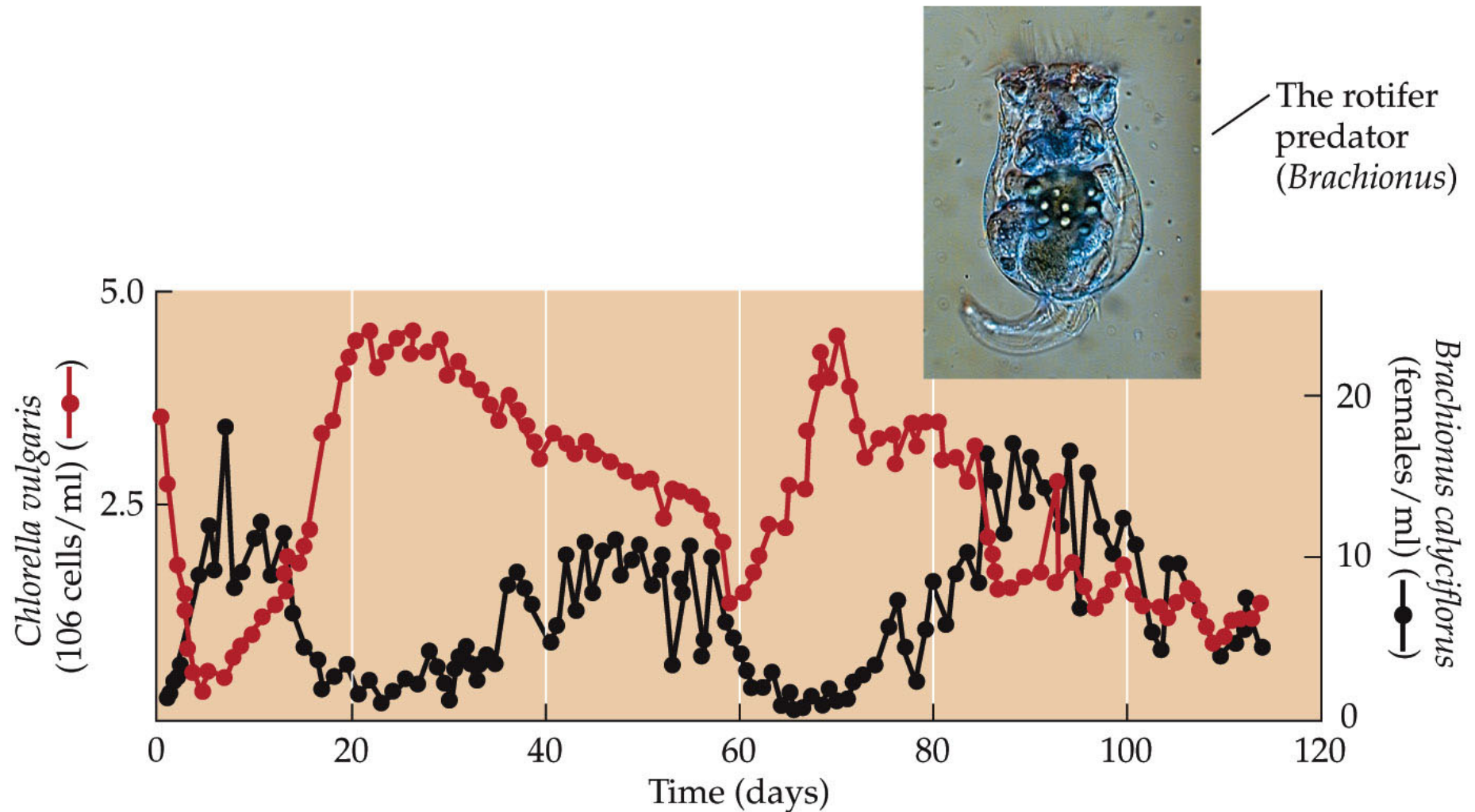
Evolution can also influence predator–prey cycles.

## Population Cycles

In experiments with a rotifer predator and algal prey species, Hairston et al. found that populations cycled, but not synchronously.

Predator populations peaked when prey populations reached their lowest levels, and vice-versa.

Figure 12.23 Evolution Causes Unusual Population Cycles



# Population Cycles

They suggested four possible mechanisms:

1. Rotifer egg viability increases with prey density.
2. Algal nutritional quality increases with nitrogen concentrations.
3. Accumulation of toxins alters algal physiology.
4. The algae might evolve in response to predation.



## Population Cycles

These hypotheses were tested in two ways (Yoshida et al. 2003):

1. Data were compared with mathematical models. Only the model that included evolution in the prey population provided a good match to their data.

## Population Cycles

2. They manipulated the ability of the prey population to evolve by using a single algal genotype.

When the prey could not evolve, typical predator–prey cycles resulted.

When the prey could evolve (multiple genotypes), the cycles became asynchronous.

## Population Cycles

Algal genotypes that were most resistant to predators were poor competitors.

When predator density is high, resistant genotypes increase in number, then predator numbers decrease.

When predator density is low, the resistant genotype is outcompeted by other genotypes and they increase in number. Then the predator population increases.

## Case Study Revisited: Snowshoe Hare Cycles

Neither the food supply hypothesis nor the predation hypothesis alone can explain hare population cycles.

But they can be explained by combining the two hypotheses, and adding more realism to the models.

## Case Study Revisited: Snowshoe Hare Cycles

An experiment used seven  $1 \times 1$  km blocks of forest in the Canadian wilderness (Krebs et al. 1995):

- Food was added to two blocks (+Food).
- An electric fence was used to exclude predators from one block (–Predators).
- One block had added food and no predators (+Food/–Predators).

## Case Study Revisited: Snowshoe Hare Cycles

Survival rates and densities of hares in each block of forest were monitored for an 8-year period.

Compared with controls, hare densities were higher in all three treatments.

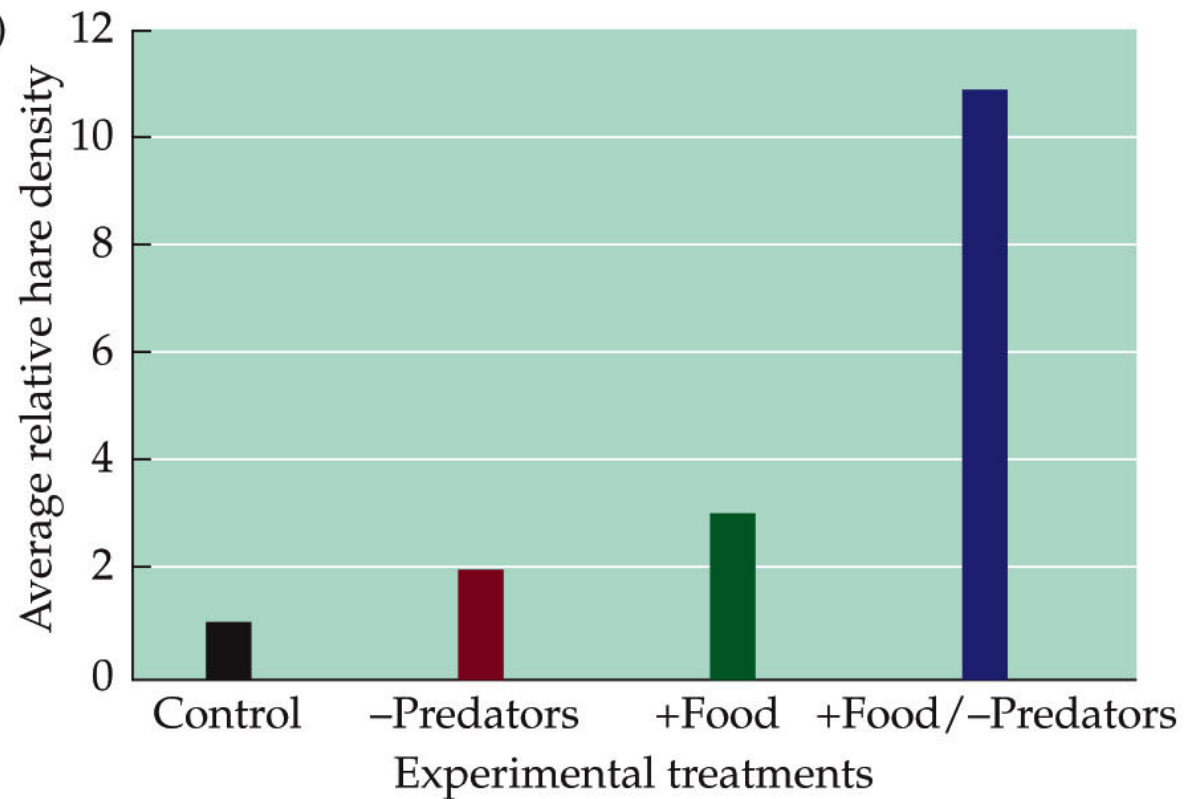
In the +Food/–Predators block, hare densities were 11 times higher than controls, suggesting that both factors influence hare cycles.

Figure 12.24 Both Predators and Food Influence Hare

(A)



(B)



## Case Study Revisited: Snowshoe Hare Cycles

This was supported by a mathematical model of feeding relationships across three levels: Vegetation, hares, and predators (King and Schaffer 2001).

There was reasonably good agreement between the model and the field experiment results.



Figure 12.25 A Vegetation–Hare–Predator Model Predicts Hare Densities Accurately (Part 1)

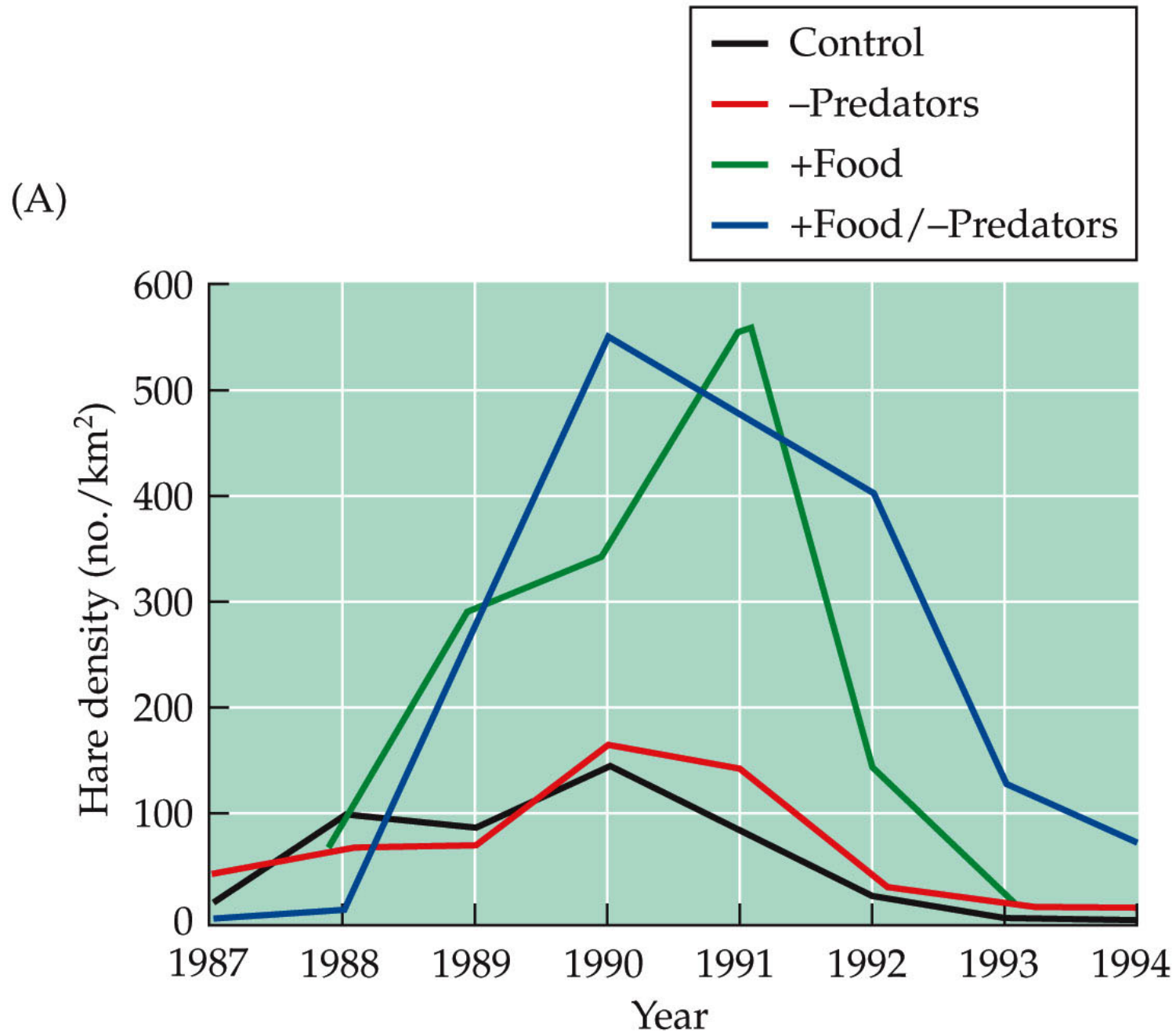
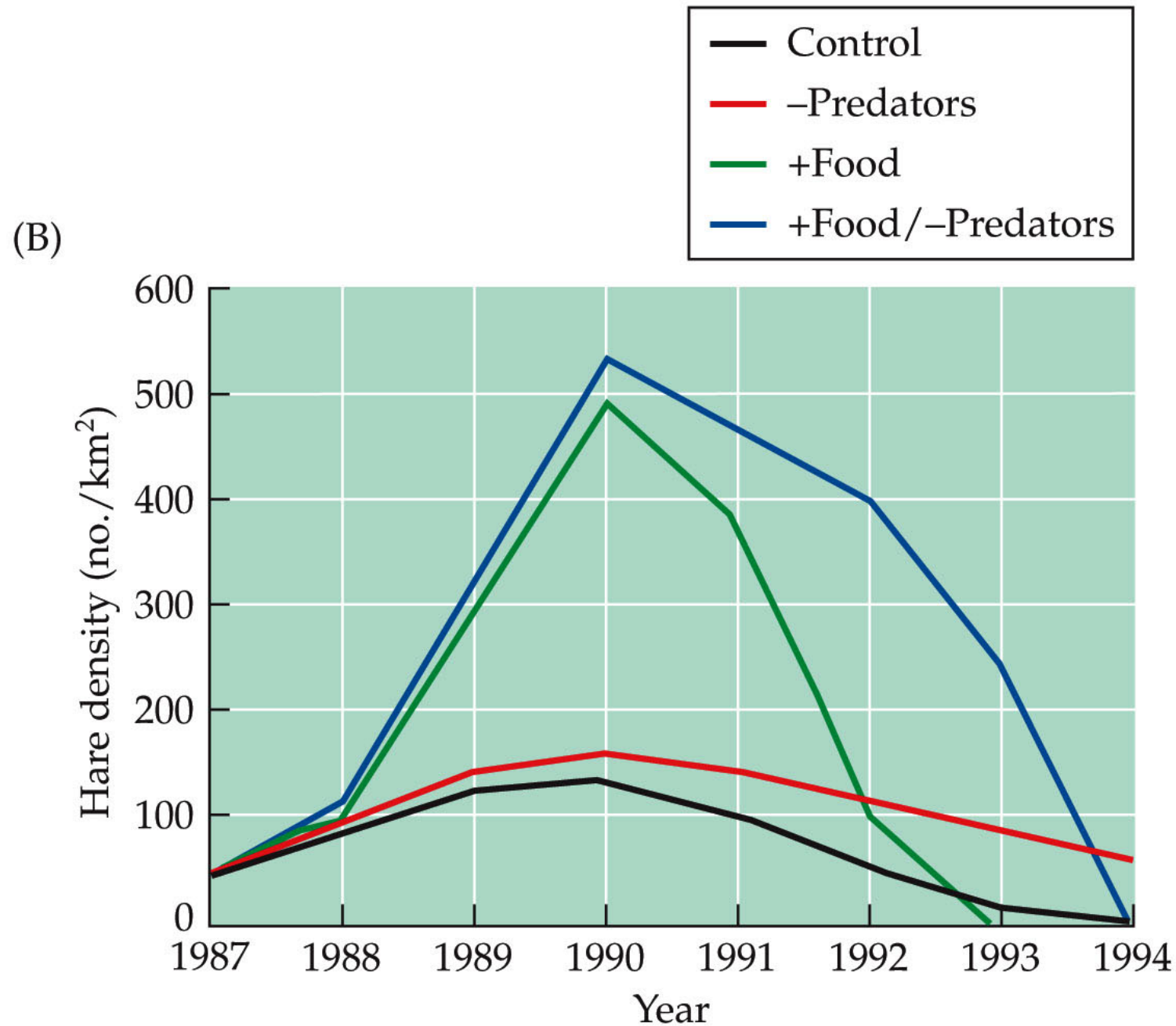


Figure 12.25 A Vegetation–Hare–Predator Model Predicts Hare Densities Accurately (Part 2)



## Case Study Revisited: Snowshoe Hare Cycles

We still do not have a complete understanding of factors that cause hare populations to cycle in synchrony across broad regions.

Lynx can move long distances from areas with few prey to areas with abundant prey; their movements might be enough to cause geographic synchrony in hare cycles.

## Case Study Revisited: Snowshoe Hare Cycles

Large geographic regions in Canada experience a similar climate.

Within these regions, lynx and hare cycles are similar to one another. The reason for this synchrony also remains to be determined.

## Case Study Revisited: Snowshoe Hare Cycles

In the Krebs et al. experiment, the hare cycle continued in the +Food/–Predators block.

One possible reason is that the fences did not exclude all predators, such as birds of prey.

Another possible reason is stress caused by the fear of predator attack.

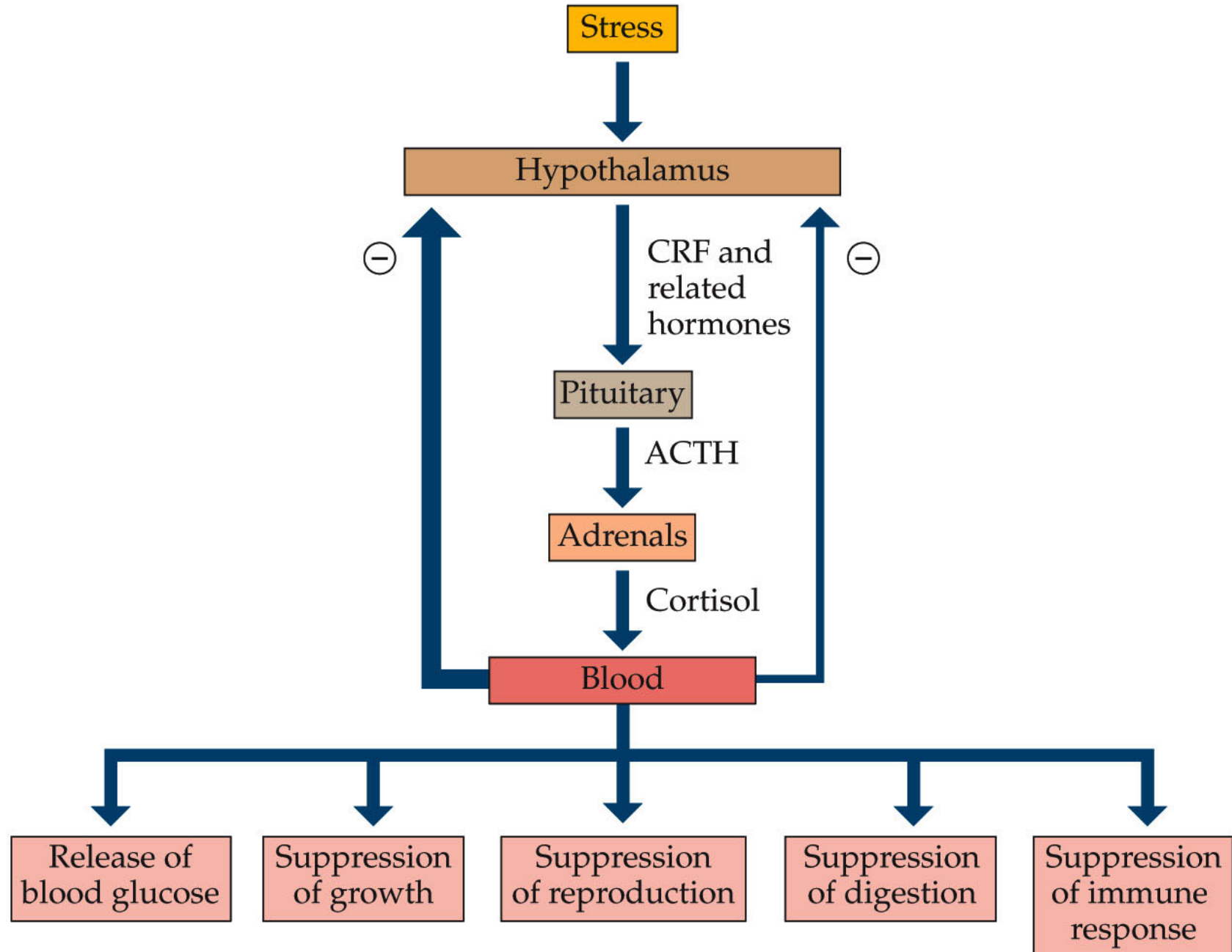
## Connections in Nature: From Fear to Hormones to Demography

Predators can alter prey behavior, and may also influence prey physiology.

Boonstra et al. (1998) tested the effects of fear on prey populations.

The “fight-or-flight” response to stress works by mobilizing energy and directing it to the muscles, and by suppressing functions not essential for immediate survival.

Figure 12.26 The Stress Response



## Connections in Nature: From Fear to Hormones to Demography

This response works well for immediate or acute stress, such as attack by a predator.

The response is short-lived, shut down by negative feedbacks.

For chronic stress however, the response is maintained for long periods.



## Connections in Nature: From Fear to Hormones to Demography

The long-term effects can influence growth and reproduction and susceptibility to disease.

Collectively, this reduces survival rate.

When predators are abundant, it seems reasonable to assume that hares are under chronic stress.

## Connections in Nature: From Fear to Hormones to Demography

Boonstra et al. measured hormone levels and immune responses of hares exposed to high versus low numbers of predators.

In the decline phase of the hare cycle (many predators), cortisol and blood glucose levels increased, reproductive hormones decreased, and overall body condition worsened.

## Connections in Nature: From Fear to Hormones to Demography

Laboratory studies suggest that the conditions experienced by hares as they mature can influence their reproductive success for years to come.

Chronic stress from predation may explain the drop in birth rate during the decline phase, and also why hare numbers sometimes rebound slowly after predators decline.