Paine's distinction between strong and weak interactions within food webs has been used to model the interactions within at least one terrestrial food web. Teja Tscharntke (1992) has worked intensively on a food web associated with the wetland reed *Phragmites australis.* This reed grows in large stands along the shores of rivers and other wetlands. Tscharntke's study site was along the Elbe River near Hamburg in northwest Germany. Along the river, *Phragmites* is attacked by *Giraudiella inclusa,* a fly in the family Cecidomyidae, whose larvae develop within galls called "ricegrain" galls. At the study sites *Phragmites* is also attacked by *Archanara geminipuncta,* a moth in the family Noctuidae, whose larvae bore into the stems of *Phragmites.* Stem-boring by *A. geminipuncta* induces *Phragmites* to form side shoots, a response that provides additional sites for oviposition by the gall maker *G. inclusa.*

Tscharntke discovered that at least 14 species of parasitoid wasps attack *G. inclusa.* How can so many species attack a single host species and continue to coexist? Does this seem to violate the competitive exclusion principle (see chapter 10)? Tscharntke explains this apparent paradox by pointing out that each parasitoid species appears to specialize on attacking *G. inclusa* at different times and on different parts of *Phragmites.* In winter, blue tits, *Parus caeruleus,* move into stands of *Phragmites,* where they peck open the galls formed by *G. inclusa* and eat the larvae, causing mortality in this population as well as in its parasitoids.

Tscharntke represented these trophic interactions with a food web that captures the essential interactions among species in this community (fig. 14.5). Even though there are fewer interactions than in Winemiller's tropical fish webs (see fig. 14.4), Tscharntke's web still contains plenty of complexity. However, figure 14.5 focuses the reader on the most important interactions in the community by distinguishing between strong, weaker, and weakest interactions by representing this gradient in interaction strength by red (strong), blue (weak), or green (weakest) lines.

Figure 14.5 suggests that feeding by blue tits strongly influences the parasitoids *Aprostocetus calamarius* and *Torymus arundinis* and their host, *G. inclusa,* in large gall clusters on main shoots. The other series of strong interactions involves the parasitoids *Aprostocetus gratus* and *Platygaster quadrifarius,* which attack the *G. inclusa* that inhabit small gall clusters in side shoots of *Phragmites.* These side shoots are in turn stimulated by the stem-boring larvae of the moth *A. geminipuncta.* Notice that blue tits only weakly influence populations on this side of the web.

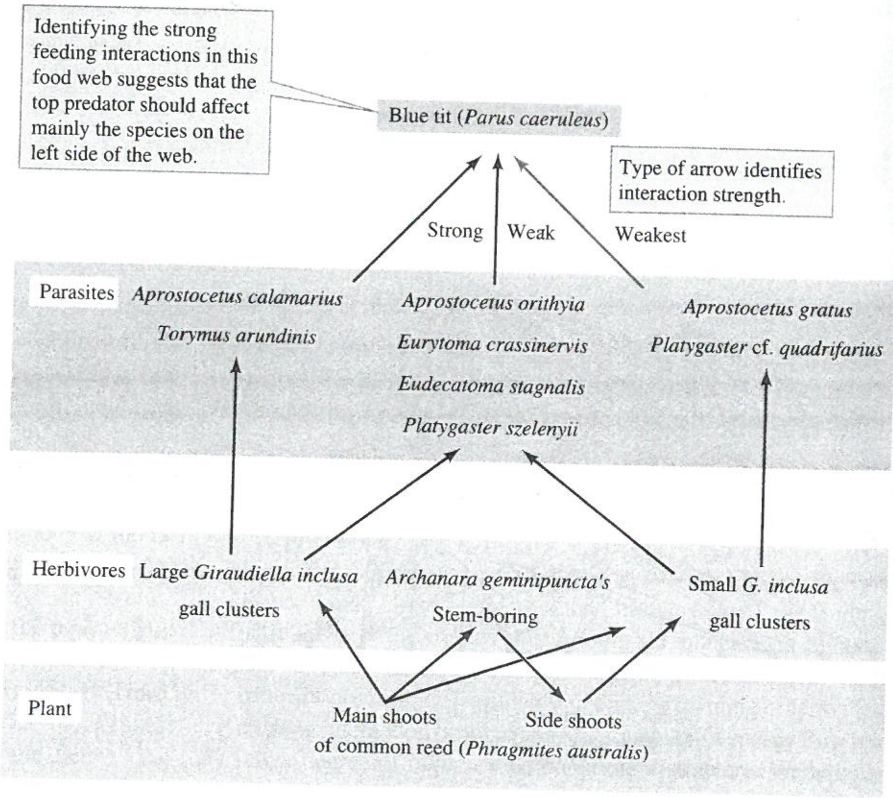
By distinguishing between weak and strong interactions, Tscharntke produced an easily understood food web to represent the study community. Identifying strong interactions allows us to determine which species may have the most significant influences on community structure. Those with substantial influence we now call **keystone species.**

Start

CASE HISTORIES:
keystone species

The feeding activities of a few keystone species may control the structure of communities.

Robert Paine (1966, 1969) proposed that the feeding activities of a few species have inordinate influences on community structure. He called these keystone species. Paine's keystone species hypothesis emerged from a chain of reasoning. First, he proposed that predators might keep prey populations below their carrying capacity. Next, he reasoned the potential for competitive exclusion would be low in populations kept below carrying capacity. Finally, he concluded that if keystone species reduce the likelihood of competitive exclusion, their activities would increase the number of species that could coexist in communities. In other words, Paine predicted that some predators may increase species diversity.



Identifying the strong feeding interactions in this food web suggests that the top predator should affect mainly the species on the left side of the web.

Type of arrow identifies interaction strength.

FIGURE 14.5 *Food web associated with* Phragmites australis *(data from Tscharntke 1992).*

Food Web Structure and Species Diversity

Paine began his studies by examining the relationship between overall species diversity within food webs and the proportion of the community represented by predators. He cited studies that demonstrated that as the number of species in marine zooplankton communities increases, the proportion that are predators also increases. For instance, the zooplankton community in the Atlantic Ocean over continental shelves includes 81 species, 16% of which are predators. In contrast, the zooplankton community of the Sargasso Sea contains 268 species, 39% of which are predators. Paine set out to determine if similar patterns occur in marine intertidal communities.

Paine described a food web from the intertidal zone at Mukkaw Bay, Washington, which lies in the north temperate zone at 49° N. This food web is typical of the rocky shore community along the west coast of North America (fig. 14.6).

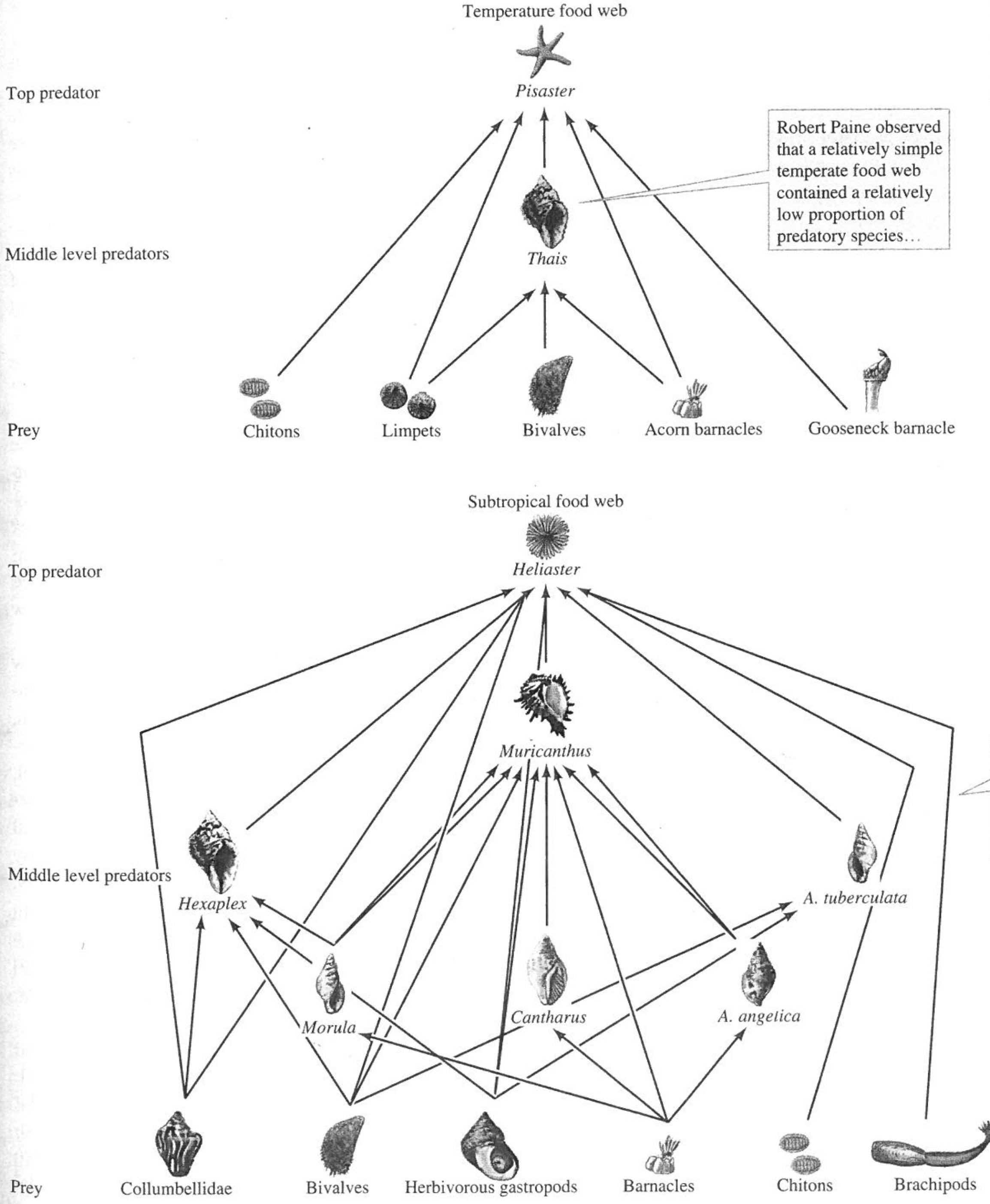


FIGURE 14.6
Roots of the keystone species hypothesis: does a higher proportion of predators in diverse communities indicate that predators contribute to higher species diversity?

Robert Paine observed that a relatively simple temperate food web contained a relatively low proportion of predatory species…

… while a diverse subtropical food web contained a higher proportion of predatory species.

The base of this food web consists of nine dominant intertidal invertebrates: two species of chitons, two species of limpets, a mussel, three species of acorn barnacles, and one species of goose-neck barnacle. Paine pointed out that *Pisaster* commonly consumes two other prey species in other areas, a snail and another bivalve, bringing the total food web diversity to 13 species. Ninety percent of the energy consumed by the middle-level predator, *Thais,* consists of barnacles. Meanwhile the top predator, *Pisaster,* obtains 90% of its energy from a mixture of chitons (41%), mussels (37%), and barnacles (12%).

Paine also described a subtropical food web (31° N) from the northern Gulf of California, a much richer web that included 45 species. However, like the food web at Mukkaw Bay, Washington, the subtropical web was topped by a single predator, the starfish *Heliaster kubinijii* (fig. 14.6). However, six predators occupy middle levels in the subtropical web, compared to one middle-level predator at Mukkaw Bay. Because four of the five species in the snail family Columbellidae are also predaceous, the total number of predators in the subtropical web is 11. These predators feed on the 34 species that form the base of the food web. Despite the presence of many more species in this subtropical web, the top predator, *Heliaster,* obtains most of its energy from sources similar to those used by *Pisaster* at Mukkaw Bay. *Heliaster* obtains 74% of its energy directly from a mixture of bivalves, herbivorous gastropods, and barnacles.

Paine found that as the number of species in his intertidal food webs increased, the proportion of the web represented by predators also increased, a pattern similar to that described by G. Grice and A. Hart (1962) when they compared zooplankton communities. As Paine went from Mukkaw Bay to the northern Gulf of California, overall web diversity increased from 13 species to 45 species, a 3.5-fold increase. However, at the same time, the number of predators in the two webs increased from 2 to 11, a 5.5-fold increase. According to Paine's predation hypothesis, this higher proportion of predators produces higher predation pressure on prey populations, which in turn promotes the higher diversity in the Gulf of California intertidal zone.

Does this pattern confirm Paine's predation hypothesis? No, it does not. First, Paine studied a small number of webs—not enough to make broad generalizations. Second, while the patterns described by Paine are consistent with his hypothesis, they may be consistent with a number of other hypotheses. To evaluate the keystone species hypotheses, Paine needed a direct experimental test.

Experimental Removal of Starfish

For his first experiment, Paine removed the top predator from the intertidal food web at Mukkaw Bay and monitored the response of the community. He chose two study sites in the middle intertidal zone that extended 8 m along the shore and 2 m vertically. One site was designated as a control and the other as an experimental site. He removed *Pisaster* from the experimental site and relocated them in another portion of the intertidal zone. Each week Paine checked the experimental site for the presence of *Pisaster* and removed any that might have colonized since his last visit.

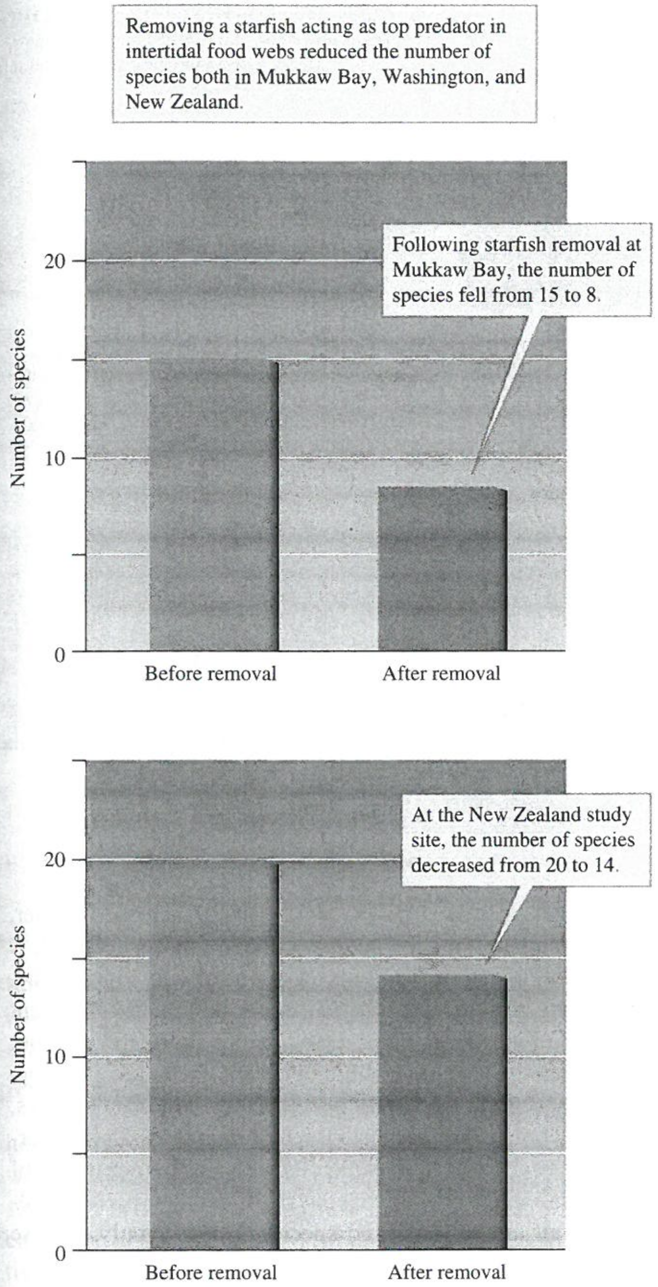
Paine followed the response of the intertidal community for 2 years. Over this interval, the diversity of intertidal invertebrates in the control plot remained constant at 15, while the diversity within the experimental plot declined from 15 to 8, a loss of 7 species. This reduction in species diversity supported Paine's keystone species hypothesis. However, if this reduction was due to competitive exclusion, what was the resource over which species competed?

As we saw in chapter 9, the most common limiting resource in the rocky intertidal zone is space. Within 3 months of removing *Pisaster* from the experimental plot, the barnacle *Balanus glandula* occupied 60% to 80% of the available space. One year after Paine removed *Pisaster, B. glandula* was crowded out by mussels, *Mytilus californianus,* and goose-neck barnacles, *Pollicipes polymerus.* Benthic algal populations also declined because of a lack of space for attachment. The herbivorous chitons and limpets also left, due to a lack of space and a shortage of food. Sponges were also crowded out and a nudibranch that feeds on sponges also left. After 5 years, the *Pisaster* removal plot was dominated by two species: the mussel, *M. californianus,* and the goose-neck barnacle, *P. polymerus.*

This experiment showed that *Pisaster* is a keystone species. When Paine removed it from his study plot, the community collapsed. However, did this one experiment demonstrate the general importance of keystone species in nature? To demonstrate this we need more experiments and observations across a wide variety of communities. Paine followed his work at Mukkaw Bay with a similar experiment in New Zealand.

The intertidal community along the west coast of New Zealand is similar to the intertidal community along the Pacific coast of North America. The top predator is a starfish, *Stichaster australis,* that feeds on a wide variety of invertebrates, including barnacles, chitons, limpets, and a mussel, *Perna canaliculus.* During 9 months following Paine's removal of the starfish, the number of species in the removal plot decreased from 20 to 14 and the coverage of the area by the mussel increased from 24% to 68%. As in Mukkaw Bay, the removal of a predaceous starfish produced a decrease in species richness and a significant increase in the density of a major prey species. Again, the mechanism underlying disappearance of species from the experimental plot was competitive exclusion due to competition for space.

These results show that intertidal communities thousands of kilometers apart that do not share any species of algae or genera of invertebrates are influenced by similar biological processes (fig. 14.7). This is reassurance to ecologists seeking general ecological principles. However, the two communities are not identical. The New Zealand intertidal


Removing a starfish acting as top predator in intertidal food webs reduced the number of species both in Mukkaw Bay, Washington, and New Zealand.

Following starfish removal at Mukkaw Bay, the number of species fell from 15 to 8.

At the New Zealand study site, the number of species decreased from 20 to 14.

FIGURE 14.7 *The effect of removing a top predator from two intertidal food webs (data from Paine 1966, 1971).*

community includes a large brown alga, *Durvillea antarctica,* that vigorously competes for space with the mussel *Perna.* The mussel *M. californianus* does not face such a competitive challenge in the North American intertidal zone.

In a second removal experiment, Paine removed both the starfish *Stichaster* and the large brown alga *Durvillea* from two different study plots. The result was far more dramatic than when Paine had removed the starfish only. After only 15 months, *Perna* dominated the study area and excluded nearly all other flora and fauna, covering 68% to 78% of the space in the two removal sites. Paine's studies in North America and New Zealand provide substantial support for the keystone species hypothesis. Many other studies quickly followed the lead taken by Paine's pioneering work.

STOP

Consumers' Effects on Local Diversity

~~Jane Lubchenko (1978) observed that previous studies had indicated that herbivores sometimes increase plant diversity, sometimes decrease plant diversity, and sometimes seem to do both. She proposed that to resolve these apparently conflicting results it would be necessary to understand (1) the food preferences of herbivores, (2) the competitive relationships among plant species in the local community, and (3) how competitive relationships and feeding preferences vary across environments. Lubchenko used these criteria to guide her study of the influences of an intertidal snail, *Littorina littorea,* on the structure of an algal community.~~

~~Lubchenko studied the feeding preferences of *Littorina* in the laboratory. Her experiments indicated that algae fell into low, medium, or high preference categories. Generally, highly preferred algae were small, ephemeral, and tender like the green algae, *Enteromorpha* spp., while most tough, perennial species like the red alga *Chondrus crispus* were never eaten or eaten only if the snail was given no other choice.~~

~~Lubchenko also studied variation in the abundance of algae and *Littorina* in tide pools. She found that tide pools with high densities of *Enteromorpha,* one of the snail's favorite foods, contained low densities ($4/m^2$) of snails. In contrast, pools with high densities of *Littorina* ($233–267/m^2$) were dominated by *Chondrus,* a species for which the snail shows low preference. Lubchenko reasoned that in the absence of *Littorina, Enteromorpha* competitively displaces *Chondrus.* She tested this idea by removing the *Littorina* from one of the pools in which they were present in high density and introducing them to a pool in which *Enteromorpha* was dominant. Lubchenko monitored a third pool with a high density of the snails as a control.~~

~~The results of Lubchenko's removal experiment were clear (fig. 14.8). While the relative densities of *Chondrus, Enteromorpha,* and other ephemeral algae remained relatively constant in the control pool, the density of *Enteromorpha* declined with the introduction of *Littorina.* Meanwhile, *Enteromorpha* quickly increased in density and came to dominate the pool from which Lubchenko had removed the snails. In addition, as the *Enteromorpha* population in this pool increased, the population of *Chondrus* declined. Lubchenko began another addition and removal experiment in two other pools in the fall to check for seasonal effects on feeding and competitive relations. This second removal experiment produced results almost identical to the first. Where *Littorina* were added, the *Enteromorpha* population declined, while the *Chondrus* population increased. Where the snails were removed, the *Chondrus* population declined, while the *Enteromorpha* population increased.~~

~~additions from the surrounding human population and consequent eutrophication of the lake (see chapter 3). However, as we shall see in chapter 15, predaceous fish like Nile perch can produce changes in ecosystem functioning that may in turn strongly influence populations and communities. Though we look for single causes of complex phenomena, ecological systems are affected by a complex interplay between biotic and abiotic factors. Some of these mutual influences will become more apparent in the next two chapters as we begin our discussion of the ecology of ecosystems.~~

Start

APPLICATIONS AND TOOLS:
humans as keystone species

People have long manipulated food webs both as a consequence of their own feeding activities and by introducing or deleting species from existing webs. In addition, many of these manipulations have focused on keystone species. Consequently, either consciously or unwittingly, people have, themselves, acted as keystone species in communities.

The Empty Forest: Hunters and Tropical Rain Forest Animal Communities

The current plight of the tropical rain forest is well known. However, Kent Redford (1992) points out that with few exceptions, most studies of human impact on the tropical rain forest have concentrated on direct effects of humans on vegetation, mainly on deforestation. Redford expands our view by examining the effects of humans on animals. The picture that emerges from this analysis is that humans have so reduced the population densities of rain forest animals in many areas that they no longer play their keystone roles in the system, a situation Redford calls "ecologically extinct."

Redford estimated that subsistence hunting, a major source of protein for many rural people, results in an annual death toll of approximately 14 million mammals and 5 million birds and reptiles within the Brazilian Amazon. He estimated further that commercial hunters, seeking skins, meat, and feathers, kill an additional 4 million animals annually. Consequently, the total take by hunters within the Brazilian Amazon is approximately 23 million individual animals. However, this figure underestimates the total number of animal deaths, since many wounded animals escape from hunters only to die. Including those fatally wounded animals that escape, Redford places the annual deaths within the Brazilian Amazon at approximately 60 million animals.

Hunters generally concentrate on a small percentage of larger bird and mammal species, however. For instance, Redford estimated that at Cocha Cashu Biological Station in Manu National Park, located in the Amazon River basin in eastern Peru, hunters concentrate on 9% of the 319 bird species and 18% of the 67 mammal species. Because hunters generally concentrate on the larger species, this small portion of the total species pool makes up about 52% of the total bird biomass and approximately 75% of the total mammalian biomass around Manu National Park (fig. 14.18).

As impressive as all these numbers are, there remains a critical question: Do hunters reduce the local densities of the birds and mammals they hunt? The answer is yes. Redford estimated that moderate to heavy hunting pressure in rain forests reduces mammalian biomass by about 80% to 93% and bird biomass by about 70% to 94%.

There may be cause for concern, however, that goes beyond the losses of these immense numbers of animals. As you might expect, many large rain forest mammals and birds may act as keystone species (fig. 14.19). If so, their decimation will have effects that ripple through the entire community. The first to suggest a keystone role for the large animals preferred by rain forest hunters was John Terborgh (1988), who presented his hypothesis in a provocative essay titled, "The Big Things That Run the World."

Terborgh's hypothesis has been supported by a variety of studies. He observed that in the absence of pumas and

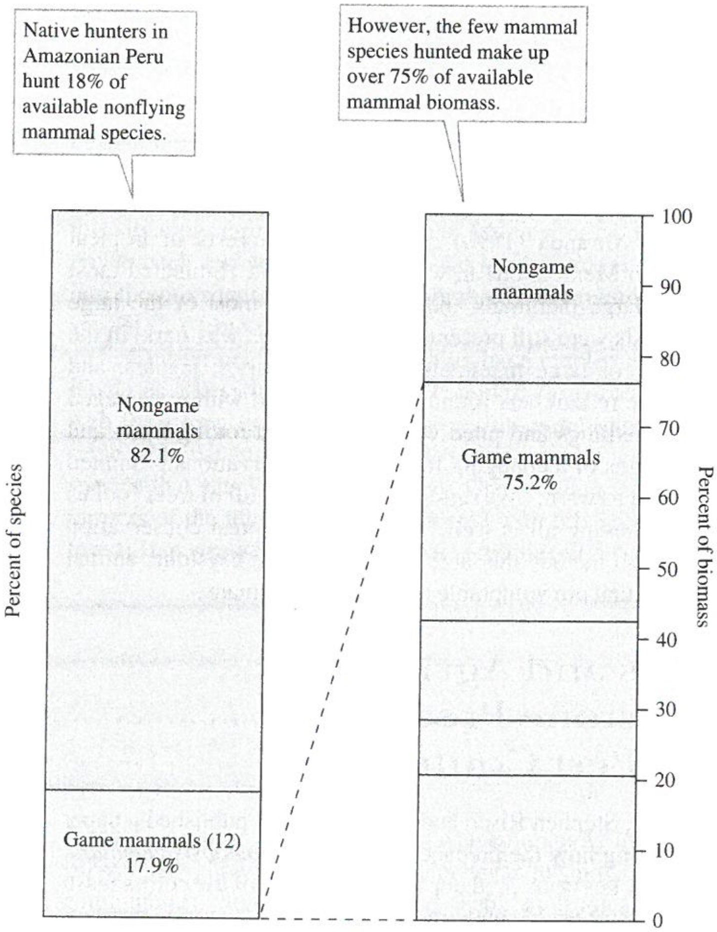


FIGURE 14.18 *Highly selective hunting by Amazonian natives (data from Redford 1992).*

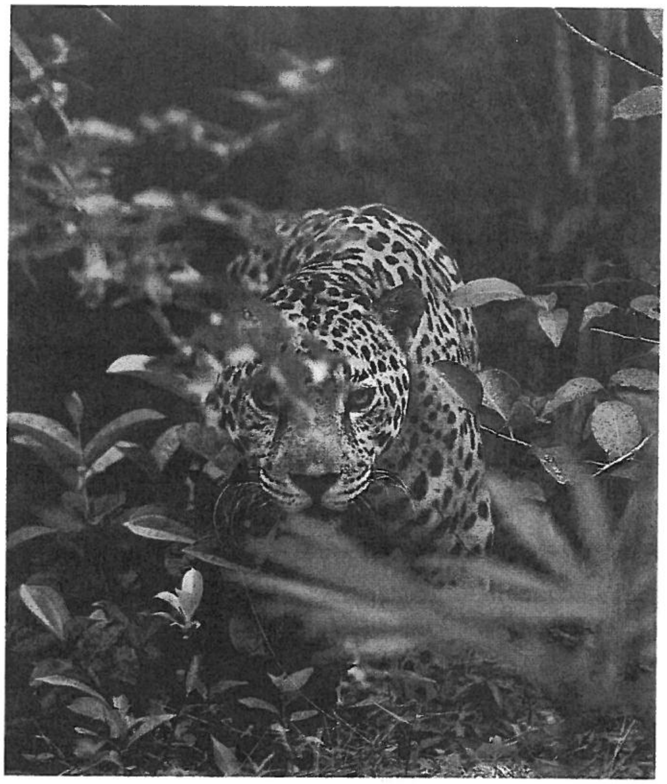
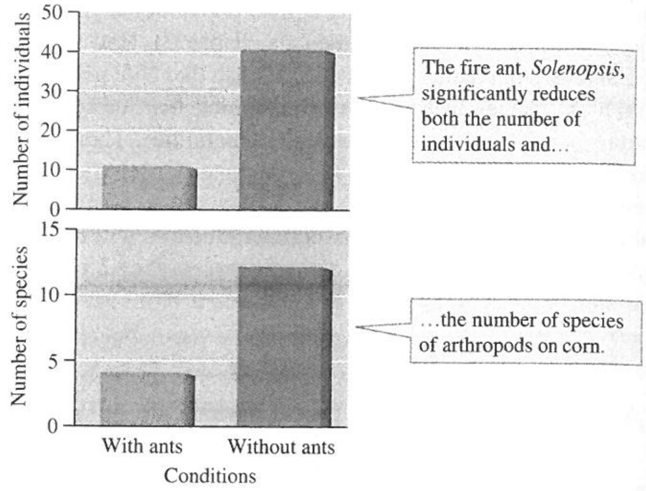


FIGURE 14.19 *Large predators such as this jaguar may act as keystone species in tropical rain forests.*

jaguars on Barro Colorado Island, Panama, medium-sized mammal species are over 10 times more abundant than in areas still supporting populations of these large cats. R. Dirzo and A. Miranda (1990) compared two forests in tropical southern Mexico, one in which hunting had eliminated most of the large mammals and one in which most of the large mammals were still present. The comparison was stark. In the absence of large mammals such as peccaries, jaguars, and deer, the researchers found forests carpeted with undamaged plant seedlings and piled with uneaten and rotting fruits and nuts, signs of a changing forest. Such observations prompted Redford to warn, "We must not let a forest full of trees fool us into believing all is well." Tropical rain forest conservation must also include the large, and potentially keystone, animal species that are vulnerable to hunting by humans.

Ants and Agriculture: Keystone Predators for Pest Control

In 1982, Stephen Risch and Ronald Carroll published a paper describing how the predaceous fire ant, *Solenopsis geminata,* acts as a keystone predator in the food web of the corn-squash agroecosystem in southern Mexico. While "natural enemies" had been used to control insect pests for some time, Risch and Carroll put these efforts into a community context. They drew conceptual parallels between biological control of insects with natural enemies and studies of the influences of keystone species, citing studies of the influences of herbivores on plant communities and the effects of predators on intertidal communities. In their own experiments, Risch and Carroll demonstrated how predation by *Solenopsis* in the corn-squash agroecosystem reduces the number of arthropods and the arthropod diversity (fig. 14.20). This study showed how *Solenopsis* could act as a keystone species to the benefit of the agriculturist.



The fire ant, *Solenopsis,* significantly reduces both the number of individuals and...

...the number of species of arthropods on corn.

FIGURE 14.20 *Effect of* Solenopsis geminata *on the arthropod populations on corn (data from Risch and Carroll 1982).*

The conceptual breakthrough represented by the work of Risch and Carroll is impressive. However, their work had been anticipated, 1,700 years earlier, by farmers in southern China. H. Huang and P. Yang (1987) cite Ji Han, who, in A.D. 304, wrote "Plants and Trees of the Southern Regions" in which he included the following:

> The Gan (mandarin orange) is a kind of orange with an exceptionally sweet and delicious taste . . . In the market, the natives of Jiao-zhi [southeastern China and North Vietnam] sell ants stored in bags of rush mats. The nests are like thin silk. The bags are all attached to twigs and leaves, which, with the ants inside the nests, are for sale. The ants are reddish-yellow in color, bigger than ordinary ants. In the south, if the Gan trees do not have this kind of ant, the fruits will be damaged by many harmful insects and not a single fruit will be perfect.

Now, 17 centuries after the observations of Ji Han, we know this ant as the citrus ant, *Oecophylla smaragdina.* The use of this ant to control herbivorous insects in citrus orchards was unknown outside of China until 1915. In 1915, Walter Swingle, a plant physiologist who worked for the U.S. Department of Agriculture, was sent to China to search for varieties of oranges resistant to citrus canker, a disease that was devastating citrus groves in Florida. While on this trip, Swingle came across a small village where the main occupation of the people was growing ants for sale to orange growers. The ant was the same one described by Ji Han in A.D. 304.

FIGURE 14.21 *While pests in this North American orange orchard are controlled mainly by chemical insecticides, weaver ants have been used to control insect pests of orange orchards in China for over 17 centuries.*

Oecophylla is one of the weaver ants, which use silk to construct a nest by binding leaves and twigs together. These ants spend the night in their nest. During the day, the ants spread out over the home tree as they forage for insects. Farmers place a nest in a tree and then run bamboo strips between trees so that the ants can have access to more than one tree. The ants will eventually build nests in adjacent trees and can colonize an entire orchard.

The ants harvest protein and fats when they gather insects from their home tree, but they have other needs as well. They also need a source of liquid and carbohydrates, and they get these materials by cultivating Homoptera, known as soft-scale insects or mealy bugs, which produce nectar. The ants and soft-scale insects have a mutualistic relationship in which the ants transport the insects from tree to tree and protect them from predators. In return the ants consume the nectar produced by the soft-scale insects. Because of this mutualism with the soft-scale insect, which can itself be a serious pest of citrus, several early agricultural scientists expressed skepticism that *Oecophylla* would be an effective agent for pest control in citrus. They suggested that the use of this ant could produce infestations by soft-scale insects.

Despite these criticisms, all Chinese citrus growers interviewed insisted that *Oecophylla* is effective at pest control and that the damage caused by soft-scale insects is minor. Research done by Yang appears to have solved this apparent contradiction. Comparing orange trees treated with chemical insecticides to those protected by *Oecophylla,* Yang recorded higher numbers of soft-scale insects in the trees tended by ants. However, these higher numbers did not appear to cause serious damage to the orange trees. When Yang inspected the soft-scale insects closely, he found that they were heavily infested with the larvae of parasitic wasps. He also found that the ants did not reduce populations of lacewing larvae and ladybird beetles, predators that feed on soft-scale insects. Huang and Yang concluded that *Oecophylla* is effective at pest control because while it attacks the principal, larger pests of citrus, it does not reduce populations of other predators that attack the smaller pests of citrus, such as soft-scale insects, aphids, and mites (fig. 14.21).

The association between *Oecophylla* and citrus trees seems similar to that between ants and acacias (see chapter 12). There is a difference, however. Humans maintain *Oecophylla* as a substantial component of the food web in citrus orchards. Not only have specialized farmers historically cultivated and distributed the ants, *Oecophylla* must also be protected from the winter cold. The ant cannot survive the winter in southeast China in orange trees. Consequently, farmers must generally provide shelter and food for the ants during winter.

The labor and expense of maintaining these ants through the winter may be reduced by mixed plantings of orchard trees. Farmers in Shajian village in the Huaan district of southeast China have successfully maintained *Oecophylla* over the winter in mixed plantings of orange and pomelo trees. During winter the ants are mostly in pomelo trees, which are larger and have thicker foliage than orange trees, characteristics that reduce cooling rates on winter nights. In this situation, farmers do not have to add new nests of *Oecophylla* each spring. Gradually, the ant has become integrated into the mixed citrus and pomelo orchards and requires little special care from the farmers.

The farmers of southeast China have employed *Oecophylla* as a keystone species in a complex citrus-based food web for a long time. However, the results would not be the same with just any ant species. The citrus growers required a species that acts in a particular way. One wonders how long farmers of the region had experimented with this species before Ji Han wrote his account of their activities in A.D. 304.

SUMMARY CONCEPTS

Stop.

A food web summarizes the feeding relations in a community. The earliest work on food webs concentrated on simplified communities in areas such as the Arctic islands. However, researchers such as Charles Elton (1927) soon found that even these so-called simple communities included very complex feeding relations. The level of food web complexity increased substantially, however, as researchers began to study complex communities. Studies of the food webs of tropical freshwater fish communities revealed highly complex networks of trophic interaction that persisted even in the face of various