ators and perpetrators of epidemics in nature are extensive, people tend to condemn all other predators without ascertaining whether these predators are actually detrimental to human interests. The idea that "the only good hawk is a dead hawk" is a most uncritical generalization.

A way to be objective is to consider predation, parasitism, herbivory, and allelopathy from the population and community levels of organization, rather than from the individual level. Predators, parasites, and grazers certainly kill or injure the individuals that they feed or secrete toxic chemicals on, and they depress, in some measure at least, the growth rate of their target populations or reduce the total population size. But does this mean that these populations would be healthier without consumers or inhibitors? From the long-term, coevolutionary viewpoint, are predators the sole beneficiaries of the association? As pointed out in the discussion of population regulation (Chapter 6), predators and parasites help keep herbivorous insects at a low density so they will not destroy their own food supply and habitat. In Chapter 3, we discussed how animal herbivores and plants have evolved an almost mutualistic (+ +) relationship.

Deer populations are often cited as examples of populations that tend to irrupt when predator pressure is reduced. The Kaibab deer herd, as originally described by Leopold (1943) on the basis of estimates by Rasmussen (1941), allegedly increased from 4000 (on 700,000 acres on the north side of the Grand Canyon in Arizona) in 1907 to 100,000 in 1924, coincident with a predator removal campaign organized by the U.S. government. Caughley (1970) reexamined this case and concluded that although there is no question that the deer did increase, overgraze, and then decline, there is doubt about the extent of the overpopulation, and there is no evidence that it was due solely to the removal of predators. Cattle and fire may also have played a part. Caughley believed that irruptions of ungulate populations are more likely to result from changes in habitat or food quality, which enable the population to "escape" from the usual mortality control.

One thing is clear: the most violent irruptions occur when a species is introduced into a new area, where there are both unexploited resources and a lack of negative interactions. The population explosion of rabbits introduced into Australia is a well-known example among the thousands of cases of severe oscillations that result when species with high biotic potential are introduced into new areas. An interesting sequel to the attempts to control the irruption of rabbits by introducing a disease organism has provided evidence for group selection in a parasite-host system (as discussed in Section 3).

The most important generalization is that negative interactions become less negative with time if the ecosystem is sufficiently stable and spatially diverse to allow reciprocal adaptations. Parasite-host or predator-prey populations introduced into experimental microcosms or mesocosms usually oscillate violently, with a certain probability of extinction. Pimentel and Stone (1968), for example, have shown experimentally (Fig. 7-6) that violent oscillations occur when a host, such as the house fly (*Musca domestica*) and a parasitic wasp (*Nasonia vitripennis*) are first placed together in a limited culture system. When individuals selected from cultures that had managed to survive the violent oscillations for two years were then reestablished in new cultures, it was evident that through genetic selection, an ecological homeorhesis had evolved in which both populations could now coexist in a much more stable equilibrium.

In the real world of humans and nature, time and circumstances may not favor spective hosts or prey, the effect is moderate, neutral, or even beneficial from the long-term viewpoint; and (2) that newly acquired parasites or predators are the most damaging. In fact, a list of the diseases, parasites, and insect pests that cause the greatest loss in agriculture or forestry would include mostly species that have recently been introduced into a new area, such as the chestnut blight, or that have acquired a new host or prey. The European corn ear worm (*Helicoverpa zea*), the gypsy moth (*Lymantria dispar*), the Japanese beetle (*Popillia japonica*), and the Mediterranean fruit fly (*Ceratitis capitata*) are just a few introduced insect pests that belong to this category. The lesson, of course, is to avoid introducing new potential pests and to avoid, wherever possible, the stressing of ecosystems with poisons that destroy useful as well as pest organisms. Much the same principle applies to severe human diseases: the most feared are the newly acquired. For a recent discussion regarding the introduction of new predators and pathogens on resident species at the community, metacommunity, and global levels, see M. A. Davis (2003). Simberloff (2003) described the need for more population biological research in order to control introduced species based on sound ecological theory.

Of special interest are organisms intermediate between predators and parasites —for example, the so-called parasitic or *parasitoid* insects. These organisms often can consume the entire individual prey, as does the predator, yet they have the host specificity, high biotic potential, and small size of the parasite. Entomologists have propagated some of these organisms artificially, using them to control insect pests. In general, attempts to make similar use of large, unspecialized predators have not been successful. For example, the mongoose (*Herpestes edwardsi*) introduced in the Caribbean Islands to control rats in sugarcane fields has more severely reduced ground-nesting birds than rats. If the predator is small, is specialized in its choice of prey, and has a high biotic potential, control can be effective.

Most general theories proposed to explain the trophic structure of plant communities pay little attention to the potentially profound influence of insect herbivores. Indeed, most theories of trophic interactions and community regulation suggest that insect herbivory will have little influence on terrestrial vegetation, particularly on net primary production (see, for example, Hairston et al. 1960; Oksanen 1990). Many ar-

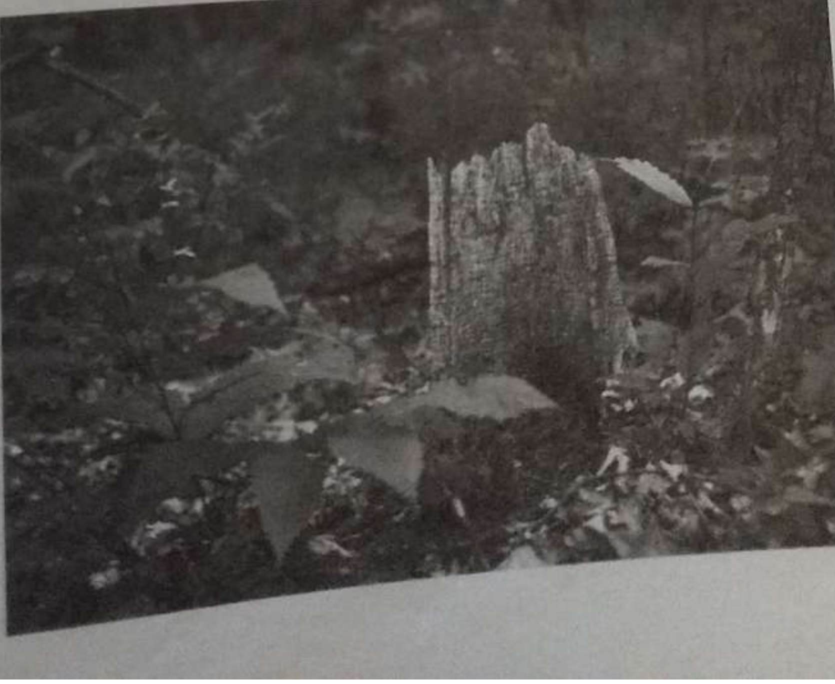

Figure 7-7. Results of the chestnut blight in a southern Appalachian region, illustrating the extreme effect that a parasitic organism (fungus, *Endothia parasitica*) introduced from the Old World had on a newly acquired host (American chestnut tree, *Castanea dentata*).

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Courtesy of Walter Carson

Figure 7-8. The plot on the left was sprayed with insecticide for eight years and is dominated by a dense stand of the goldenrod *Solidago altissima*. Surrounding plots were left as unsprayed controls. This photograph was taken two years after an outbreak of the chrysomelid beetle *Microrhopala vittata* defoliated numerous stems of *S. altissima*. These outbreaks occur every 5–15 years and typically exert a strong influence on standing crop biomass (after W. P. Carson and Root 2000).

gue that predators and parasites keep insect herbivores from causing major damage to their host plants in terrestrial communities (Strong et al. 1984; Spiller and Schoener 1990; Bock et al. 1992; Marquis and Whelan 1994; Dial and Roughgarden 1995) and that insect herbivores typically consume only a small amount of the available net primary production (Hairston et al. 1960; Strong, Lawton, et al. 1984; Crawley 1989; Root 1996; Price 1997).

A different view holds that insects only damage or consume a small amount of their host plants because most plant species are well defended or have low nutritional value (Hartley and Jones 1997). Lawton and McNeil (1979) suggested that herbivorous insects are caught between the interacting forces of predators and parasites on the one hand and unpalatable or low-quality plants on the other. Regardless of which view one holds, the conclusion is the same: herbivorous insects will have a negligible influence on plant community structure, composition, and productivity (Pacala and Crawley 1992). Pacala and Crawley (1992) concluded that "herbivores often have little effect on communities," although later Crawley (1997) noted that there was an insufficient number of studies of insect herbivory from which to generalize.

More recently, however, it has been found that the removal of arthropods can also cause significant changes in community structure and function. Studies by V. K. Brown (1985) and W. P. Carson and Root (1999) have demonstrated that the exclusion of herbivorous insects with insecticides causes major changes in flowering frequency and plant species composition in old-field communities. W. P. Carson and Root (2000) demonstrated that insect herbivores could have a very strong top-down effect on plant communities, but this occurred primarily during insect outbreaks. Using insecticide-treated and control plots, they examined the long-term (10-year) effects of suppressing insects on the structure and diversity of an old field dominated by the goldenrod *Solidago altissima* (Fig. 7-8). An outbreak of the chrysomelid beetle *Microrhopala vittata*, which specializes on *S. altissima*, occurred during the experiment and persisted for several years. The damage caused by this outbreak dramatically reduced the biomass, density, height, survivorship, and reproduction of *S. altissima*. Herbivore exclusion caused the formation of dense stands of goldenrods with a twofold increase in both standing crop biomass and litter. The understory in these dense stands had significantly lower plant abundance, species richness, flowering shoot production and light levels; these conditions persisted for years following the outbreak. Thus, *M. vittata* functioned as a keystone species. Furthermore, insect herbivory indirectly increased the abundance of invading trees, thereby increasing the rate of succession by speeding up the transition of this old field to a tree-dominated stage.

W. P. Carson and Root (2000) argued that insect outbreaks may be extremely important in community dynamics, but for the most part are ignored in theories of community regulation. The observations (1) that native phytophagous herbivores periodically irrupt (pulse) and reduce the abundance and vigor of dominant plant species; (2) that these outbreaks may occur more readily in dense or lush concentrations of their hosts; and (3) that an outbreak may occur more than once during the life span of a long-lived host, suggest that insect outbreaks may play a very important role in plant community regulation and dynamics.

As manipulators of ecosystems, human beings are slowly learning how to be a prudent predator (when and how much biomass to harvest without damaging the system or relationship). The problem can be approached experimentally by setting up test populations in microecosystems. In one such experimental model, shown in Figure 7-9, guppies (*Lebistes reticulatus*) were used to mimic a commercial fish population being exploited by humans. As shown, the maximum sustained yield was obtained when *one third* of the population was harvested during each reproductive period, which reduced the equilibrium density to slightly less than half the unexploited one. Within the limits of the experiment, these ratios tended to be independent of the carrying capacity of the system, which was varied at three levels by manipulating the food supply.

One-species models often prove to be oversimplifications, because they do not account for competing species that may respond to the reduced density of the harvested species by increasing their own density and using up food or other resources

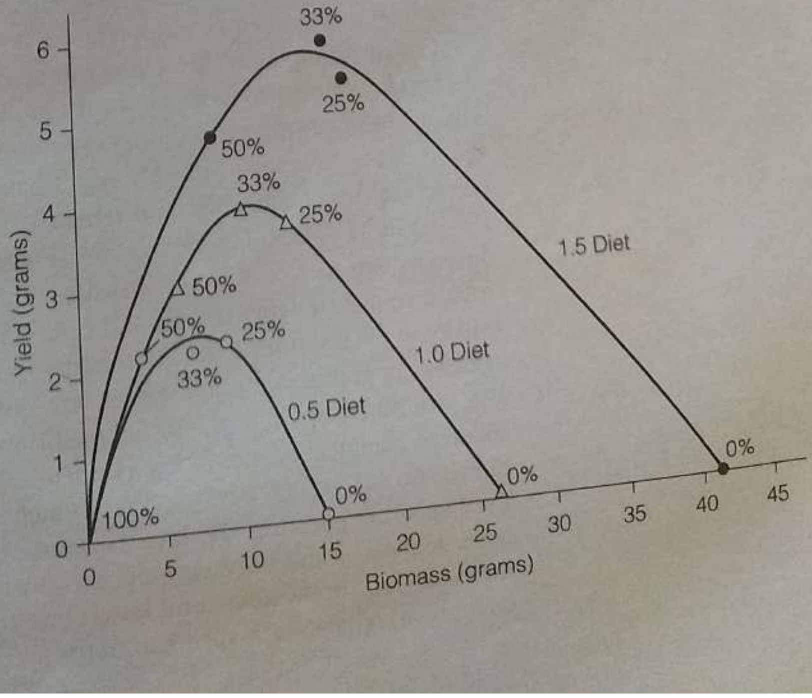

Figure 7-9. Biomass and yield in test populations of the guppy (*Lebistes reticulatus*) exploited at different rates (shown as percentage removal per reproductive period) at three different diet levels. The highest yields were obtained when about one third of the population was harvested per reproductive period and mean biomass was reduced to less than half that of the unexploited population (yield curves skewed to the left) (after Silliman 1969).