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CHAPTER 7

Invasive species

Daniel Simberloff

An invasive species is one that arrives (often with human assistance) in a habitat it had not previously occupied, then establishes a population and spreads autonomously. Species invasions are one of the main conservation threats today and have caused many species extinctions. The great majority of such invasions are by species introduced from elsewhere, although some native species have become invasive in newly occupied habitats (see Box 7.1). In some areas of the world—especially islands (see Box 7.2)—introduced species comprise a large proportion of all species. For instance, for the Hawaiian islands, almost half the plant species, 25% of insects, 40% of birds, and most freshwater fishes are introduced, while the analogous figures for Florida are 27% of plant species, 8% of insects, 5% of birds, and 24% of freshwater fishes. Not all introduced species become invasive, however. Many plant species imported as ornamentals persist in

Box 7.1 Native invasives
Daniel Simberloff

Although the great majority of invasive species are introduced, occasionally native plant species have become invasive, spreading rapidly into previously unoccupied habitats. These invasions fall into two categories, both involving human activities. In the first, a native species that is rather restricted in range and habitat is supplemented with introductions from afar that have new genotypes, and the new genotypes, or recombinants involving the new genotypes, become invasive. An example in North America is common reed (*Phragmites australis*), which was present for at least thousands of years and is probably native, but which spread widely, became much more common, and began occupying more habitats beginning in the mid- nineteenth century. This invasion is wholly due to the introduction of Old World genotypes at that time, probably in soil ballast (Saltonstall 2002). Similarly, reed canarygrass (*Phalaris arundinacea*), native to North America but previously uncommon, became highly invasive in wetland habitats with the introduction of European genotypes as a forage crop in the 19th century (Lavergne and Molofsky 2007).

The second category of native invasives arises from human modification of the environment. For instance, in western Europe, the grass *Elymus athericus*, previously a minor component of high intertidal vegetation, began spreading seaward because of increased nitrogen in both aerial deposition and runoff, and it now occupies most of the intertidal in many areas (Valéry *et al.* 2004). The plant apparently uses the nitrogen to increase its tolerance or regulation of salt. In various regions of the western United States, Douglas fir (*Pseudotsuga menziesii*) and several other tree species have invaded grasslands and shrublands as a result of fire suppression, increased grazing by livestock, or both. Natural fire had precluded them, and when fire was suppressed, livestock served the same role (Simberloff 2008). By contrast, Virginia pine (*Pinus virginiana*) in the eastern United States

continues

Box 7.1 (Continued)

invaded serpentine grasslands when fires were suppressed and long-time grazing practices were restricted (Thiet and Boerner 2007).

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Box 7.2 Invasive species in New Zealand
Daniel Simberloff

Many islands have been particularly afflicted by introduced species, even large islands such as those comprising New Zealand (Allen and Lee 2006). New Zealand had no native mammals, except for three bat species but now has 30 introduced mammals. Among these, several are highly detrimental to local fauna and/or flora. The Australian brushtail possum (*Trichosurus vulpecula*; Box 7.2 Figure) now numbers in the millions and destroys broadleaved native trees, eating bird eggs and chicks as well. Pacific and Norway rats are also devastating omnivores that particularly plague native birds. Introduced carnivores—the stoat (*Mustela erminea*), weasel (*M. nivalis*), ferret (*M. furo*), and hedgehog (*Erinaceus europaeus*) —are all widespread and prey on various combinations of native birds, insects, skinks, geckos, and an endemic reptile (*Sphenodon punctatus*). Many ungulates have been introduced, of which European red deer (*Cervus elaphus*) is most numerous. Trampling and grazing by ungulates has greatly damaged native vegetation in some areas. Feral pigs (*Sus scrofa*) are now widespread in forest and scrub habitats, and their rooting causes erosion, reduces populations of some plant species, and changes nutrient cycling by mixing organic and mineral layers of the soil. Of 120 introduced bird species, 34 are established. To some extent they probably compete with native birds and prey on native invertebrates, but their impact is poorly studied and certainly not nearly as severe as that of introduced mammals. European brown trout (*Salmo trutta*) are widely established and have caused the local extirpation of a number of fish species.

Among the estimated 2200 established introduced invertebrate species in

Box 7.2 Figure Brushtail possum. Photograph by Rod Morris.

continues

Box 7.2 (Continued)

New Zealand, German wasps (*Vespula germanica*) and common wasps (*V. vulgaris*) have probably had the most impact, especially by monopolizing the honeydew produced by native scale insects that had supported several native bird species, including the kaka (*Nestor meridionalis*), the tui (*Prosthemadera novaeseelandiae*), and the bellbird (*Anthornis melanura*).

About 2100 species of introduced plants are now established in New Zealand, outnumbering native species. Several tree species introduced about a century ago are now beginning to spread widely, the lag caused by the fact that trees have long life cycles. Most of the introduced plants in New Zealand, including trees, invade largely or wholly when there is some sort of disturbance, such as land-clearing or forestry. However, once established, introduced plants have in some instances prevented a return to the original state after disturbance stopped. New Zealand also has relatively few nitrogen-fixing plant species, and even these have been outcompeted by introduced nitrogen-fixers such as gorse (*Ulex europaeus*), Scotch broom (*Cytisus scoparius*), and tree lupine (*Lupinus arboreus*). As in other areas (see above), in parts of New Zealand these nitrogen-fixers have, by fertilizing the soil, favored certain native species over others and have induced an invasional meltdown by allowing other introduced plant species to establish.

Given the enormous number of introduced species invading New Zealand and the many sorts of impacts these have generated, it is not surprising that New Zealand enacted the first comprehensive national strategy to address the entire issue of biological invasions, the Biosecurity Act of 1993.

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gardens with human assistance but cannot establish in less modified habitats. The fraction of introduced species that establish and spread is a matter under active research, but for some organisms it can be high. For example, half of the freshwater fish, mammal, and bird species introduced from Europe to North America or vice-versa have established populations, and of these, more than half became invasive (Jeschke and Strayer 2005).

Invasive species can produce a bewildering array of impacts, and impacts often depend on context; the same introduced species can have minimal effects on native species and ecosystems in one region but can be devastating somewhere else. Further, the same species can affect natives in several different ways simultaneously. However, a good way to begin to understand the scope of the threat posed by biological invasions is to classify the main types of impacts.

7.1 Invasive species impacts

7.1.1 Ecosystem modification

The greatest impacts of invasive species entail modifying entire ecosystems, because such modifications are likely to affect most of the originally resident species. Most obviously, the physical structure of the habitat can be changed. For instance, in Tierra del Fuego, introduction of a few North American beavers (*Castor canadensis*) in 1946 has led to a population now over 50 000, and in many areas they have converted forests of southern beech (*Nothofagus* spp.) to grass- and sedge-dominated meadows (Lizarralde *et al.* 2004). In the Florida Everglades, introduced Australian paperbark (*Melaleuca quinquenervia*) trees have effected the opposite change, from grass- and sedge-dominated prairies to nearly monospecific paperbark forests (Schmitz *et al.* 1997). In parts of Hawaii, Asian and American mangrove species have replaced beach communities of herbs and small shrubs with tall mangrove forests (Allen 1998).

Introduced plant species can modify an entire ecosystem by overgrowing and shading out native species. South American water hyacinth (*Eichhornia crassipes*) now covers parts of Lake Victoria in Africa (Matthews and Brand 2004a), many lakes and rivers in the southeastern United States (Schardt 1997), and various waterbodies in Asia and Australia (Matthews and Brand 2004b), often smothering native submersed vegetation. Vast quantities of rotting water hyacinth, and consequent drops in dissolved oxygen, can also affect many aquatic animal species. Similar overgrowth occurs in the Mediterranean Sea, where *Caulerpa taxifolia* (Figure 7.1), an alga from the tropical southwest Pacific Ocean, replaces seagrass meadows over thousands of hectares, greatly changing the animal community (Meinesz 1999).

A new species of cordgrass (*Spartina anglica*) arose in England in the late nineteenth century by hybridization between a native cordgrass and an introduced North American species. The new species invaded tidal mudflats and, trapping much more sediment, increased elevation and converted mudflats to badly drained, dense salt marshes with different animal species (Thompson 1991). The hybrid species was later introduced to New Zealand and the state of Washington with similar impacts.

Introduced species can change entire ecosystems by changing the fire regime (see Chapter 9). The invasion of the Florida Everglades by Australian paperbark trees, noted above, is largely due to the fact that paperbark catches fire easily and produces hotter fires than the grasses and sedges it replaces. The opposite transformation, from forest to grassland, can also be effected by a changed fire regime. In Hawaii, African molassesgrass (*Melinis minutiflora*) and tropical American tufted beardgrass (*Schizachyrium condensatum*) have replaced native-dominated woodland by virtue of increased fire frequency and extent (D'Antonio and Vitousek 1992).

Introduced plants can change entire ecosystems by modifying water or nutrient regimes. At Eagle Borax Spring in California, Mediterranean salt cedars (*Tamarix* spp.) dried up a large marsh (McDaniel *et al.* 2005), while in Israel, Australian eucalyptus trees were deliberately introduced to drain swamps (Calder 2002). By fertilizing nitrogen-poor sites, introduced nitrogen-fixing plants can favor other exotic species over natives. On the geologically young, nitrogen-poor volcanic island of Hawaii, firetree (*Morella faya*), a nitrogen-fixing shrub from the Azores, creates conditions that favor other introduced species that previously could not thrive in the low-nutrient

Figure 7.1 *Caulerpa taxifolia*. Photograph by Alex Meinesz.

soil and disfavor native plants that had evolved to tolerate such soil (Vitousek 1986).

Pathogens that eliminate a previously dominant plant can impact an entire ecosystem. In the first half of the twentieth century, Asian chestnut blight (*Cryphonectria parasitica*) ripped through eastern North America, effectively eliminating American chestnut (*Castanea dentata*), a tree that had been common from Georgia through parts of Canada and comprised at least 30% of the canopy trees in many forests (Williamson 1996). This loss in turn led to substantial structural changes in the forest, and it probably greatly affected nutrient cycling, because chestnut wood, high in tannin, decomposes slowly, while the leaves decompose very rapidly (Ellison *et al.* 2005). Chestnut was largely replaced by oaks (*Quercus* spp.), which produce a recalcitrant litter. Because this invasion occurred so long ago, few of its effects were studied at the time, but it is known that at least seven moth species host-specific to chestnut went extinct (Opler 1978). Such pathogens are also threats to forest industries founded on introduced species as well as natives, as witness the vast plantations in Chile of North American Monterrey pine (*Pinus radiata*) now threatened by recently arrived *Phytophthora pinifolia* (Durán *et al.* 2008).

7.1.2 Resource competition

In Great Britain, the introduced North American gray squirrel (*Sciurus carolinensis*) forages for nuts more efficiently than the native red squirrel (*Sciurus vulgaris*), leading to the decline of the latter species (Williamson 1996). The same North American gray squirrel species has recently invaded the Piedmont in Italy and is spreading, leading to concern that the red squirrel will also decline on the mainland of Europe as it has in Britain (Bertolino *et al.* 2008). The house gecko (*Hemidactylus frenatus*) from Southeast Asia and parts of Africa has invaded many Pacific islands, lowering insect populations that serve as food for native lizards, whose populations have declined in some areas (Petren and Case 1996).

7.1.3 Aggression and its analogs

The red imported fire ant (*Solenopsis invicta*) from southern South America has spread through the southeastern United States and more recently has invaded California. It attacks other ant species it encounters, and in disturbed habitats (which comprise much of the Southeast) this aggression has caused great declines in populations of native ant species (Tschinkel 2006). The Argentine ant (*Linepithema humile*), also native to South America, similarly depresses populations of native ant species in the United States by attacking them (Holway and Suarez 2004). The Old World zebra mussel (*Dreissena polymorpha*; Figure 7.2), spreading throughout much of North America, threatens the very existence of a number of native freshwater bivalve species, primarily by settling on them in great number and suturing their valves together with byssal threads, so that they suffocate or starve (Ricciardi *et al.* 1998). Although plants do not attack, they have an analogous ability to inhibit other species, by producing or sequestering chemicals. For example, the African crystalline ice plant (*Mesembryanthemum crystallinum*) sequesters salt, and when leaves fall and decompose, the salt remains in the soil, rendering it inhospitable to native plants in California that cannot tolerate such high salt concentrations (Vivrette and Muller 1977). Diffuse knapweed (*Centaurea diffusa*) from Eurasia and spotted knapweed (*C. stoebe*) from Europe are both major invaders of rangelands in the American West. One reason they dominate native range plants in the United States is that they produce

Figure 7.2 Zebra mussel. Photograph by Tony Ricciardi.

root exudates that are toxic to native plants (Callaway and Ridenour 2004). An invasive introduced plant can also dominate a native species by interfering with a necessary symbiont of the native. For instance, many plants have established mutualistic relationships with arbuscular mycorrhizal fungi, in which the fungal hyphae penetrate the cells of the plants' roots and aid the plants to capture soil nutrients. Garlic mustard (*Alliaria petiolata*) from Europe, Asia, and North Africa is a highly invasive species in the ground cover of many North American woodlands and floodplains. Root exudates of garlic mustard, which does not have mycorrhizal associates, are toxic to arbuscular mycorrhizal fungi found in North American soils (Callaway *et al.* 2008).

7.1.4 Predation

One of the most dramatic and frequently seen impacts of introduced species is predation on native species. Probably the most famous cases are of mammalian predators such as the ship rat (*Rattus rattus*), Norway rat (*R. norvegicus*), Pacific rat (*R. exulans*), small Indian mongoose (*Herpestes auropunctatus*), and stoat (*Mustela erminea*) introduced to islands that formerly lacked such species. In many instances, native bird species, not having evolved adaptations to such predators, nested on the ground and were highly susceptible to the invaders. Introduced rats, for example, have caused the extinction of at least 37 species and subspecies of island birds throughout the world (Atkinson 1985). The brown tree snake (*Boiga irregularis*; Figure 7.3), introduced to Guam from New Guinea in cargo after World War II, has caused the extinction or local extirpation of nine of the twelve native forest bird species on Guam and two of the eleven native lizard species (Lockwood *et al.* 2007). For these native species, an arboreal habitat was no defense against a tree-climbing predator. Another famous introduced predator that has wreaked havoc with native species is the Nile perch (*Lates niloticus*), deliberately introduced to Lake Victoria in the 1950s in the hope that a fishery would be established to provide food and jobs to local communities (Pringle 2005). Lake Victoria is home of one of the great evolutionary species radiations, the hundreds of species of cichlid fishes. About half of them are now extinct because of predation by the perch, and several others are maintained only by captive rearing (Lockwood *et al.* 2007).

Many predators have been deliberately introduced for "biological control" of previously introduced species (see below), and a number of these have succeeded in keeping populations of the target species at greatly reduced levels. For instance, introduction of the Australian vedalia

Figure 7.3 Brown tree snake. Photograph by Gad Perry.

ladybeetle (*Rodolia cardinalis*) in 1889 controlled Australian cottony-cushion scale (*Icerya purchasi*) on citrus in California (Caltagirone and Doutt 1989). However, some predators introduced for biological control have attacked non-target species to the extent of causing extinctions. One of the worst such disasters was the introduction of the rosy wolf snail (*Euglandina rosea*), native to Central America and Florida, to many Pacific islands to control the previously introduced giant African snail (*Achatina fulica*). The predator not only failed to control the targeted prey (which grows to be too large for the rosy wolf snail to attack it) but caused the extinction of over 50 species of native land snails (Cowie 2002). The small Indian mongoose, implicated as the sole cause or a contributing cause in the extinction of several island species of birds, mammals, and frogs, was deliberately introduced to all these islands as a biological control agent for introduced rats (Hays and Conant 2006). The mosquitofish (*Gambusia affinis*) from Mexico and Central America has been introduced to Europe, Asia, Africa, Australia, and many islands for mosquito control. Its record on this score is mixed, and there is often evidence that it is no better than native predators at controlling mosquitoes. However, it preys on native invertebrates and small fishes and in Australia is implicated in extinction of several fish species (Pyke 2008).

7.1.5 Herbivory

Introduced herbivores can devastate the flora of areas lacking similar native species, especially on islands. Goats (*Capra aegagrus hircus*) introduced to the island of St. Helena in 1513 are believed to have eliminated at least half of ~100 endemic plant species before botanists had a chance to record them (Cronk 1989). European rabbits (*Oryctolagus cuniculus*) introduced to islands worldwide have devastated many plant populations, often by bark-stripping and thus killing shrubs and seedling and sapling trees. Rabbits also often cause extensive erosion once vegetation has been destroyed (Thompson and King 1994). Damage to forests and crop plants by introduced herbivores is often staggering. For instance, the South American cassava mealybug (*Phenacoccus manihoti*), invading extensive cassava-growing parts of Africa, often destroys more than half the crop yield (Norgaard 1988), while in the United States, the Russian wheat aphid (*Diuraphis noxia*) caused US$600 million damage in just three years (Office of Technology Assessment 1993). In forests of the eastern United States, the European gypsy moth (*Lymantria dispar*) caused a similar amount of damage in only one year (Office of Technology Assessment 1993). In high elevation forests of the southern Appalachian Mountains, the Asian balsam woolly adelgid (*Adelges piceae*) has effectively eliminated the previously dominant Fraser fir tree (Rabenold *et al.* 1998), while throughout the eastern United States the hemlock woolly adelgid (*A. tsugae*) is killing most hemlock trees, which often formed distinct moist, cool habitats amidst other tree species (Ellison *et al.* 2005).

Plant-eating insects have been successful in many biological control projects for terrestrial and aquatic weeds. For instance, in Africa's Lake Victoria, a massive invasion of water hyacinth was brought under control by introduction of two South American weevils, *Neochetina eichhorniae* and *N. bruchi* (Matthews and Brand 2004a); these have also been introduced to attack water hyacinth in tropical Asia (Matthews and Brand 2004b). The South American alligatorweed flea beetle (*Agasicles hygrophila*) has minimized the invasion of its South American host plant (*Alternanthera philoxeroides*) in Florida (Center *et al.* 1997) and contributed greatly to its control in slow-moving water bodies in Asia (Matthews and Brand 2004b). A particularly famous case was the introduction of the South American cactus moth (*Cactoblastis cactorum*) to Australia, where it brought a massive invasion of prickly pear cactus (*Opuntia* spp.) under control (Zimmermann *et al.* 2001). In probably the first successful weed biological control project, a Brazilian cochineal bug (*Dactylopius ceylonicus*) virtually eliminated the smooth prickly pear (*Opuntia vulgaris*) from India (Doutt 1964). In 1913, the same insect was introduced to South Africa and effectively eliminated the same plant (Doutt 1964).

However, occasionally, biological control introductions of herbivorous insects have devastated non-target native species. The same cactus moth introduced to Australia was introduced to control pest prickly pear on the island of Nevis in the West Indies. From there, it island-hopped through the West Indies and reached Florida, then spread further north and west. In Florida, it already threatens the very existence of the native semaphore cactus (*O. corallicola*), and there is great concern that this invasion, should it reach the American Southwest and Mexico, would not only threaten other native *Opuntia* species but also affect economically important markets for ornamental and edible *Opuntia* (Zimmermann *et al.* 2001). The Eurasian weevil (*Rhinocyllus conicus*), introduced to Canada and the United States to control introduced pest thistles, attacks several native thistles as well (Louda *et al.* 1997), and this herbivory has led to the listing of the native Suisun thistle (*Cirsium hygrophilum* var. *hygrophilum*) on the U.S. Endangered Species List (US Department of the Interior 1997). In each of these cases of herbivorous biological control agents threatening natives, the introduced herbivore was able to maintain high numbers on alternative host plants (such as the targeted hosts), so decline of the native did not cause herbivore populations to decline.

7.1.6 Pathogens and parasites

Many introduced plant pathogens have modified entire ecosystems by virtually eliminating dominant plants. The chestnut blight was discussed above. A viral disease of ungulates, rinderpest, introduced to southern Africa from Arabia or India in cattle in the 1890s, attacked many native ungulates, with mortality in some species reaching 90%. The geographic range of some ungulate species in Africa is still affected by rinderpest. Because ungulates often play key roles in vegetation structure and dynamics, rinderpest impacts affected entire ecosystems (Plowright 1982).

Of course, many introduced diseases have affected particular native species or groups of them without modifying an entire ecosystem. For instance, avian malaria, caused by *Plasmodium relictum capristranoae*, introduced with Asian birds and vectored by previously introduced mosquitoes, contributed to the extinction of several native Hawaiian birds and helps restrict many of the remaining species to upper elevations, where mosquitoes are absent or infrequent (Woodworth *et al.* 2005). In Europe, crayfish plague (*Aphanomyces astaci*), introduced with the North American red signal crayfish (*Pacifastacus lenusculus*; Figure 7.4 and Plate 7) and also vectored by the subsequently introduced Lousiana crayfish

Figure 7.4 North American red signal crayfish (right) and a native European crayfish (*Astacus astacus*). Photograph by David Holdich.

(*Procambarus clarkii*), has devastated native European crayfish populations (Goodell *et al.* 2000). The European fish parasite *Myxosoma cerebralis*, which causes whirling disease in salmonid fishes, infected North American rainbow trout (*Oncorhynchus mykiss*) that had been previously introduced to Europe and were moved freely among European sites after World War II. Subsequently, infected frozen rainbow trout were shipped to North America, and the parasite somehow got into a trout hatchery in Pennsylvania, from which infected rainbow trout were shipped to many western states. In large areas of the West, most rainbow trout contracted the disease and sport fisheries utterly collapsed (Bergersen and Anderson 1997). Introduced plant parasites can greatly damage agriculture. For example, parasitic witchweed (*Striga asiatica*) from Africa reached the southeastern United States after World War II, probably arriving on military equipment. It inflicts great losses on crops that are grasses (including corn) and has been the target of a lengthy, expensive eradication campaign (Eplee 2001).

Introduction of vectors can also spread not only introduced pathogens (e.g. the mosquitoes vectoring avian malaria in Hawaii) but also native ones. For example, the native trematode *Cyathocotyle bushiensis*, an often deadly parasite of ducks, has reached new regions along the St. Lawrence River recently as its introduced intermediate host, the Eurasian faucet snail (*Bithynia tentaculata*), has invaded (Sauer *et al.* 2007). Introduced parasites or pathogens and vectors can interact in complicated ways to devastate a native host species. Chinese grass carp (*Ctenopharyngodon idella*) infected with the Asian tapeworm *Bothriocephalus acheilognathi* were introduced to Arkansas in 1968 to control introduced aquatic plants and spread to the Mississippi River. There the tapeworm infected native fishes, including a popular bait fish, the red shiner (*Notropis lutrensis*). Fishermen or bait dealers then carried infected red shiners to the Colorado River, from which by 1984 they had reached a Utah tributary, the Virgin River. In the Virgin River, the tapeworm infected and killed many woundfin (*Plagopterus argentissimus*), a native minnow already threatened by dams and water diversion projects (Moyle 1993).

Parasites and pathogens have also been used successfully in biological control projects against introduced target hosts. For instance, the South American cassava mealybug in Africa, discussed above, has been partly controlled by an introduced South American parasitic wasp, *Epidinocarsis lopezi* (Norgaard 1988), while the European yellow clover aphid (*Therioaphis trifolii*), a pest of both clover and alfalfa, is controlled in California by three introduced parasitic wasps, *Praon palitans, Trioxys utilis*, and *Aphelinus semiflavus* (Van Den Bosch *et al.* 1964). The New World myxoma virus, introduced to mainland Europe (where the European rabbit is native) and Great Britain and Australia (where the rabbit is introduced), initially caused devastating mortality (over 90%). However, the initially virulent viral strains evolved to be more benign, while in Great Britain and Australia, rabbits evolved to be more resistant to the virus. Mortality has thus decreased in each successive epidemic (Bartrip 2008).

7.1.7 Hybridization

If introduced species are sufficiently closely related to native species, they may be able to mate and exchange genes with them, and a sufficient amount of genetic exchange (introgression) can so change the genetic constitution of the native population that we consider the original species to have disappeared—a sort of genetic extinction. This process is especially to be feared when the invading species so outnumbers the native that a native individual is far more likely to encounter the introduced species than a native as a prospective mate. The last gasp of a fish native to Texas, *Gambusia amistadensis*, entailed the species being hybridized to extinction through interbreeding with introduced mosquito fish *G. amistadensis* (Hubbs and Jensen 1984), while several fishes currently on the United States Endangered Species List are threatened at least partly by hybridization with introduced rainbow trout. The North American mallard (*Anas platyrhynchos*), widely introduced as a game bird, interbreeds extensively with many congeneric species and threatens the very existence of the endemic New Zealand grey duck (*A. superciliosa superciliosa*) and the Hawaiian duck (*A. wyvilliana*), as well as, perhaps, the yellowbilled duck (*A. undulata*) and the Cape shoveller (*A. smithii*) in Africa (Rhymer and Simberloff 1996, Matthews and Brand 2004a). European populations of the white-headed duck (*Oxyura leucocephala*) restricted to Spain, are threatened by hybridization and introgression with North American ruddy ducks (*O. jamaicensis*) (Muñoz-Fuentes *et al.* 2007). The latter had been introduced years earlier to Great Britain simply as an ornamental; they subsequently crossed the Channel, spread through France, and reached Spain.

Availability and increasing sophistication of molecular genetic techniques has led to the recognition that hybridization and introgression between introduced and native species is far more common than had been realized. Such hybridization can even lead to a new species. In the cordgrass (*Spartina*) case discussed above, occasional hybrids were initially sterile, until a chromosomal mutation (doubling of chromosome number) in one of them produced a fertile new polyploid species, which became highly invasive (Thompson 1991). A similar case involves Oxford ragwort (*Senecio squalidus*), a hybrid of two species from Italy, introduced to the Oxford Botanical Garden ca. 1690. *S. squalidus* escaped, first spread through Oxford, and then during the Industrial Revolution through much of Great Britain along railroad lines, producing sterile hybrids with several native British species of *Senecio*. A chromosomal mutation (doubling of chromosome number) of a hybrid between *S. squalidus* and *S. vulgaris* (groundsel) produced the new polyploid species *S. cambrensis* (Welsh groundsel) (Ashton and Abbott 1992).

It is possible for hybridization to threaten a species even when no genetic exchange occurs. Many populations of the European mink (*Mustela lutreola*) are gravely threatened by habitat destruction. North America mink (*M. vison*), widely introduced in Europe to foster a potential furbearing industry, have escaped and established many populations. In some sites, many female European mink hybridize with male American mink, which become sexually mature and active before the European mink males. The European mink females subsequently abort the hybrid embryos, so no genes can be exchanged between the species, but these females cannot breed again during the same season, a severe handicap to a small, threatened population (Maran and Henttonen 1995).

7.1.8 Chain reactions

Some impacts of introduced species on natives entail concatenated chains of various interactions: species A affecting species B, then species B affecting species C, species C affecting species D, and so forth. The spread of the Asian parasitic tapeworm from Arkansas ultimately to infect the woundfin minnow (*Plagopterus argentissimus*) in Utah is an example. However, chains can be even more complex, almost certainly unforeseeable. An example involves the devastation of European rabbit populations in Britain by New World myxoma virus, described above. Caterpillars of the native large blue butterfly (*Maculina arion*) in Great Britain required development in underground nests of the native ant *Myrmica sabuleti*. The ant avoids nesting in overgrown areas, which for centuries had not been problematic because of grazing and cultivation. However, changing land use patterns and decreased grazing led to a situation in which rabbits were the main species maintaining suitable habitat for the ant. When the virus devastated rabbit populations, ant populations declined to the extent that the large blue butterfly was extirpated from Great Britain (Ratcliffe 1979). In another striking chain reaction, landlocked kokanee salmon (*Oncorhynchus nerka*), were introduced to Flathead Lake, Montana in 1916, replacing most native cutthroat trout (*O. clarki*) and becoming the main sport fish. The kokanee were so successful that they spread far from the lake, and their spawning populations became so large that they attracted large populations of bald eagles (*Haliaeetus leucocephalus*), grizzly bears (*Ursus arctos horribilis*), and other predators. Between 1968 and 1975, opossum shrimp (*Mysis relicta*), native to large deep lakes elsewhere in North America and in Sweden, were introduced to three lakes in the upper portion of the Flathead catchment in order to increase production of kokanee; the shrimp drifted downstream into Flathead Lake by 1981 and caused a sharp, drastic decline in populations of cladocerans and copepods they preyed on. However, the kokanee also fed on these prey, and kokanee populations fell rapidly, in turn causing a precipitous decline in local bald eagle and grizzly bear numbers (Spencer *et al.* 1991; Figure 7.5).

7.1.9 Invasional meltdown

An increasing number of studies of invasion effects have pointed to a phenomenon called "invasional meltdown" in which two or more introduced species interact in such a way that the probability of survival and/or the impact of at least one of them is enhanced (Simberloff and Von Holle 1999). In the above example of an introduced faucet snail (*Bithynia tentaculata*), vectoring a native trematode parasite of ducks and thereby expanding the trematode's range, a recent twist is the arrival of a European trematode (*Leyogonimus polyoon*). *Bithynia* also vectors this species, which has turned out also to be lethal to ducks (Cole and Friend 1999). So in this instance, the introduced snail and the introduced trematode combine to produce more mortality in ducks than either would likely have accomplished alone. This is but one of myriad instances of meltdown.

Sometimes introduced animals either pollinate introduced plants or disperse their seeds. For instance, figs (*Ficus* spp.) introduced to Florida had until ca. 20 years ago remained where they were planted, the species unable to spread because the host-specific fig wasps that pollinate the figs in their native ranges were absent, so the figs could not produce seeds. That situation changed abruptly upon the arrival of the fig-wasps of three of the fig species, which now produce seeds. One of them, *F. microcarpa*, has become an invasive weed, its seeds dispersed by birds and ants (Kauffman *et al.* 1991). On the island of La Réunion, the red-whiskered bulbul (*Pycnonotus jocosus*), introduced from Asia via Mauritius, disperses seeds of several invasive introduced plants, including *Rubus alceifolius*, *Cordia interruptus*, and *Ligustrum robustrum*, which have become far more problematic since the arrival of the bulbul (Baret *et al.* 2006). The Asian common myna (*Acridotheres tristis*) was introduced to the Hawaiian islands as a biological

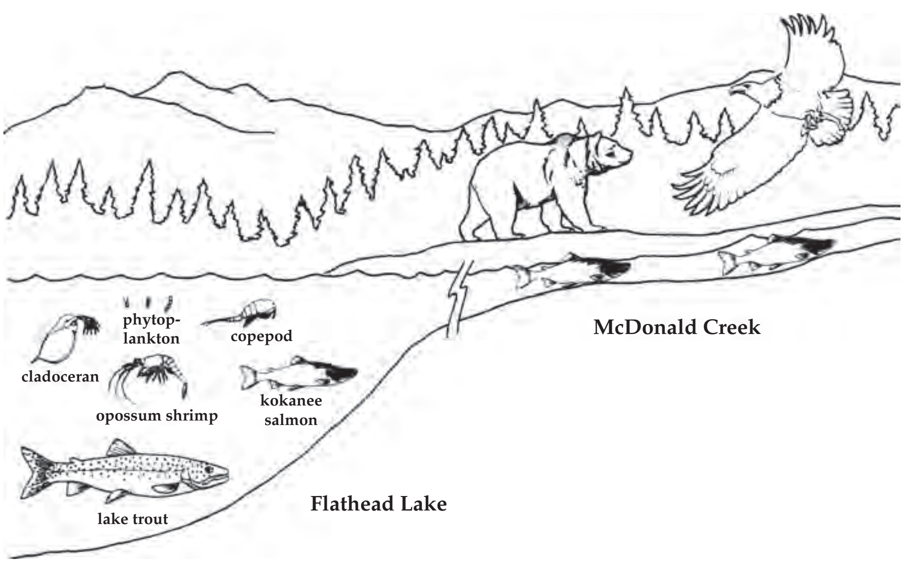

Figure 7.5 Shrimp stocking, salmon collapse, and eagle displacement. Reprinted from Spencer et al. (1991) © American Institute of Biological Sciences.

control for pasture insects but has ended up dispersing one of the worst weeds, New World *Lantana camara*, throughout the lowlands and even into some native forests (Davis *et al.* 1993). Also in Hawaii, introduced pigs selectively eat and thereby disperse several invasive introduced plant species, and by rooting and defecating they also spread populations of several introduced invertebrates, while themselves fattening up on introduced, protein-rich European earthworms (Stone 1985).

Habitat modification by introduced plants can lead to a meltdown process with expanded and/or accelerated impacts. As noted above, the nitrogen-fixing *Morella faya* (firetree) from the Azores has invaded nitrogen-deficient volcanic regions of the Hawaiian Islands. Because there are no native nitrogen-fixing plants, firetree is essentially fertilizing large areas. Many introduced plants established elsewhere in Hawaii had been unable to colonize these previously nutrient-deficient areas, but their invasion is now facilitated by the activities of firetree (Vitousek 1986). In addition, firetree fosters increased populations of introduced earthworms, and the worms increase the rate of nitrogen burial from firetree litter, thus enhancing the effect of firetree on the nitrogen cycle (Aplet 1990). Finally, introduced pigs and an introduced songbird (the Japanese white-eye, *Zosterops japonicus*) disperse the seeds of the firetree (Stone and Taylor 1984, Woodward *et al.* 1990). In short, all these introduced species create a complex juggernaut of species whose joint interactions are leading to the replacement of native vegetation.

Large, congregating ungulates can interact with introduced plants, pathogens, and even other animals in dramatic cases of invasional meltdown. For instance, Eurasian hooved livestock devastated native tussock grasses in North American prairie regions but favored Eurasian turfgrasses that had coevolved with such animals and that now dominate large areas (Crosby 1986). In northeastern Australia, the Asian water buffalo (*Bubalus bubalis*), introduced as a beast of burden and for meat, damaged native plant communities and eroded stream banks. The Central American shrub *Mimosa pigra* had been an innocuous minor component of the vegetation in the vicinity of the town of Darwin, but the water buffalo, opening up the flood plains, created perfect germination sites of *Mimosa* seedlings, and in many areas native sedgelands became virtual monocultures of *M. pigra*. The mimosa in turn aided the water buffalo by protecting them from aerial hunters (Simberloff and Von Holle 1999).

Aquatic plants and animals can also facilitate one another. In North America, the introduced zebra mussel filters prodigious amounts of water, and the resulting increase in water clarity favors certain plants, including the highly invasive Eurasian watermilfoil (*Myriophyllum spicatum*). The milfoil then aids the mussel by providing a settling surface and facilitates the movement of the mussel to new water bodies when fragments of the plant are inadvertently transported on boat propellers or in water (Simberloff and Von Holle 1999).

Some instances of invasional meltdown arise when one introduced species is later reunited with a coevolved species through the subsequent introduction of the latter. The fig species and their pollinating fig wasps in Florida are an example; the coevolved mutualism between the wasps and the figs is critical to the impact of the fig invasion. However, meltdown need not be between coevolved species. The water buffalo from Asia and *Mimosa pigra* from Central America could not have coevolved, nor could the Asian myna and the New World *Lantana camara* in Hawaii.

7.1.10 Multiple effects

Many introduced species have multiple direct and indirect effects on native species, harming some and favoring others at the same time. For example, the round goby (*Neogobius melanostomus*), an Old World fish that arrived in ballast water, is widely recognized in the North American Great Lakes as a harmful invader, feeding on native invertebrates and eggs and larvae of several native fishes. It also competes for food and space with other native fish species. However, the round goby also feeds on the harmful zebra mussel and related quagga mussel (*Dreissena bugensis*), although the impact on their populations is not known. It also now is by far the main food source for the threatened endemic Lake Erie water snake (*Nerodia sipedon insularum*), constituting over 92% of all prey consumed. Further, snakes that feed on the goby grow faster and achieve large size, which may well decrease predation on the snake and increase population size (King *et al.* 2006). On balance, almost all observers would rather not have the round goby in this region, but it is well to bear in mind the complexity of its impacts.

7.2 Lag times

Introduced species may be innocuous in their new homes for decades or even centuries before abruptly increasing in numbers and range to generate major impacts. The case of the hybrid cordgrass *Spartina anglica*, discussed above, is an excellent example. The introduced progenitor, North American *S. alterniflora*, had been present in Great Britain at least since the early nineteenth century and had even hybridized with the native *S. maritima* occasionally, but the hybrids were all sterile until one underwent a chromosomal mutation ca. 1891, producing a highly invasive weed (Thompson 1991). Brazilian pepper (*Schinus terebinthifolius*) had been present in Florida since the mid-nineteenth century as isolated individual trees, but it became invasive only when it began to spread rapidly ca. 1940 (Ewel 1986). Giant reed (*Arundo donax*) was first introduced from the Mediterranean region to southern California in the early nineteenth century as a roofing material and for erosion control, and it remained restricted in range and unproblematic until the mid-twentieth century, when it spread widely, becoming a fire hazard, damaging wetlands, and changing entire ecosystems (Dudley 2000). The Caribbean brown anole lizard (*Anolis sagrei*) first appeared in Florida in the nineteenth century, but it was restricted to extreme south Florida until the 1940s, when its range began an expansion that accelerated in the 1970s, ultimately to cover most of Florida (Kolbe *et al.* 2004).

Many such invasion lags remain mysterious. For instance, the delay for giant reed in California has yet to be explained. In other instances, a change in the physical or biotic environment can account for a sudden explosion of a formerly restricted introduced species. The spread of Brazilian pepper in Florida after a century of harmless presence was caused by hydrological changes—draining farmland, various flood control projects, and lowering of the water table for agricultural and human use. As described earlier, the sudden invasion by long-present figs in south Florida was spurred by the arrival of pollinating fig wasps. In some instances, demography of a species dictates that it cannot build up population sizes rapidly even if the environment is suitable; trees, for example, have long life cycles and many do not begin reproducing for a decade or more.

As genetic analysis has recently rapidly expanded with the advent of various molecular tools, it appears that some, and perhaps many, sudden expansions after a lag phase occur because of the introduction of new genotypes to a previously established but restricted population. The brown anole population in Florida was augmented in the twentieth century by the arrival of individuals from different parts of the native range, so that the population in Florida now has far more genetic diversity than is found in any native population. It is possible that the rapid range expansion of this introduction results from introductions to new sites combined with the advent of new genotypes better adapted to the array of environmental conditions found in Florida (Kolbe *et al.* 2004). The northward range expansion of European green crab (*Carcinus maenas*) along the Atlantic coast of North America was produced by the introduction of new, cold-tolerant genotypes into the established population (Roman 2006).

An improved understanding of lag times is important in understanding how best to manage biological invasions (Boggs *et al.* 2006). It is not feasible to attempt active management (see next section) of all introduced species—there are simply too many. Typically in each site we focus on those that are already invasive or that we suspect will become invasive from observations elsewhere. However, if some currently innocuous established introduced species are simply biological time bombs waiting to explode when the right conditions prevail in the future, the existing approach clearly will not suffice.

7.3 What to do about invasive species

By far the best thing to do about invasive introduced species is to keep them out in the first place. If we fail to keep them out and they establish populations, the next possibility is to attempt to find them quickly and perhaps to eradicate them. If they have already established and begun to spread widely, we may still try to eradicate them, or we can instead try to keep their populations at sufficiently low levels that they do not become problems.

7.3.1 Keeping them out

Introductions can be either planned (deliberate) or inadvertent, and preventing these two classes involves somewhat different procedures. In each instance, prevention involves laws, risk analyses, and border control. For planned introductions, such as of ornamental plants or new sport fish or game species, the law would be either a "white list," a "black list," or some combination of the two. A white list is a list of species approved for introduction, presumably after some risk analysis in which consideration is given to the features of the species intended for introduction and the outcome in other regions where it has been introduced. The most widely used risk analyses currently include versions of the Australian Weed Risk Assessment, which consists of a series of questions about species proposed for introduction and an algorithm for combining the answers to those questions to give a score, for which there is a threshold above which a species cannot be admitted (Pheloung *et al.* 1999). A black list is a list of species that cannot be admitted under any circumstances, and for which no further risk analysis is needed. Examples of black lists include the United States Federal Noxious Weed list and a short list of animals forbidden for entry to the US under the Lacey Act.

For such lists to be effective, the risk analyses have to be accurate enough, and the lists sufficiently large, that the great majority of species that would become invasive are actually identified as such and placed on black lists or kept off white lists. There are grave concerns that neither criterion is met. For instance, the black list of the Lacey Act is very short, and many animal species that have a high probability of becoming invasive if introduced are not on the list. The risk assessment tools, on the other hand, all yield some percentage of false negatives—that is, species assessed as unlikely to cause harm, therefore eligible for a white list, when in fact they will become harmful. Much active research (e.g. Kolar and Lodge 2002) is aimed at improving the accuracy of risk analyses—especially lowering the rate of false negatives while not inflating the rate of false positives (species judged likely to become invasive when, in fact, they would not).

For inadvertent introductions, one must first identify pathways by which they occur (Ruiz and Carlton 2003). For instance, many marine organisms are inadvertently carried in ballast water (this is probably how the zebra mussel entered North America). Insects stow away on ornamental plants or agricultural products. The Asian longhorned beetle (*Anoplophora glabripennis*), a dangerous forest pest, hitchhiked to North America in untreated wooden packing material from Asia, while snails have been transported worldwide on paving stones and ceramics. The Asian tiger mosquito (*Aedes albopictus*) arrived in the United States in water transported in used tires. Once these pathways have been identified, their use as conduits of introduction must be restricted. For ballast water, for example, water picked up as ballast in a port can be exchanged with water from the open ocean to lower the number of potential invaders being transported. For insects and pathogens carried in wood, heat and chemical treatment may be effective. For agricultural products, refrigeration, and/or fumigation are often used. The general problem is that each of these procedures entails a cost, and there has historically been opposition to imposing such costs on the grounds that they interfere with free trade and make goods more expensive. Thus it remains an uphill battle to devise and to implement regulations sufficiently stringent that they constrict these pathways.

Whatever the regulations in place for both deliberate and unplanned introductions, inspections at ports of entry are where they come into play, and here a variety of detection technologies are available and improvements are expected. Trained sniffer dogs are commonplace in ports in many countries, and various sorts of machinery, including increasingly accurate X-ray equipment, are widely in use (Baskin 2002). Although technologies have improved to aid a port inspector to identify a potential invader once it has been detected, in many nations these are not employed because of expense or dearth of qualified staff. Also, improved detection and identification capabilities are only half of the solution to barring the introduction of new species either deliberately or by accident (as for example, in dirt on shoes, or in untreated food). The other half consists of penalties sufficiently severe that people fear the consequences if they are caught introducing species. Many nations nowadays have extensive publicity at ports of entry, on planes and ships, and sometimes even in popular media, that combine educational material about the many harmful activities of invasive species and warnings about penalties for importing them.

7.3.2 Monitoring and eradication

The key to eradicating an introduced species before it can spread widely is an early warning-rapid response system, and early warning requires an ongoing monitoring program. Because of the great expense of trained staff, few if any nations adequately monitor consistently for all sorts of invasions, although for specific habitats (e.g. waters in ports) or specific groups of species (e.g. fruit fly pests of agriculture) intensive ongoing monitoring exists in some areas. Probably the most cost-effective way to improve monitoring is to enlist the citizenry to be on the lookout for unusual plants or animals and to know what agency to contact should they see something (see Figure 7.6 and Plate 8). Such efforts entail public education and wide dissemination in popular media and on the web, but they can yield enormous benefits. For instance, the invasion of the Asian longhorned beetle to the Chicago region was discovered by a citizen gathering firewood who recognized the beetle from news reports and checked his identification on a state agency website. This early warning and a quick, aggressive response by authorities led to successful regional extirpation of this insect after a five-year campaign. Similarly, the invasion in California of the alga *Caulerpa taxifolia* was discovered probably within a year of its occurrence by a diver who had seen publicity about the impact of this species in the Mediterranean. This discovery led to successful eradication after a four-year effort, and citizens have been alerted to watch for this and other non-native algal species in both Mediterranean nations and California.

Many introduced species have been successfully eradicated, usually when they are found early but occasionally when they have already established widespread populations. The keys to successful eradication have been as follows; (i) Sufficient resources must be available to see the project through to completion; the expense of finding and removing the last few individuals may exceed that of quickly ridding a site of the majority of the population; (ii) Clear lines of authority must exist so that an individual or agency can compel cooperation. Eradication is, by its nature, an all-or-none operation that can be subverted if a few individuals decide not to cooperate (for instance, by forbidding access to private property, or forbidding the use of a pesticide or herbicide); (iii) The biology of the target organism must be studied well enough that a weak point in its life cycle is identified; and (iv) Should the eradication succeed, there must be a reasonable prospect that reinvasion will not occur fairly quickly.

In cases where these criteria have been met, successful eradications are numerous. Many are on islands, because they are often small and because reinvasion is less likely, at least for isolated islands. Rats have been eradicated from many islands worldwide; the largest to date is 113 km^2. Recently, large, longstanding populations of feral goats and pigs have been

Figure 7.6 Maryland's aquatic invasive species. Poster courtesy of the Maryland Department of Natural Resources.

eradicated from Santiago Island (585 km^2) in the Galapagos (Cruz *et al.* 2005). The giant African snail has been successfully eradicated from sites in both Queensland and Florida (Simberloff 2003). Even plants with soil seed banks have been eradicated, such as sand bur (*Cenchrus echinatus*) from 400 ha Laysan Island (Flint and Rehkemper 2002). When agriculture or public health are issues, extensive and expensive eradication campaigns have been undertaken and have often been successful, crowned by the global eradication of smallpox. The African mosquito (*Anopheles gambiae*), vector of malaria, was eradicated from a large area in northeastern Brazil (Davis and Garcia 1989), and various species of flies have been eradicated from many large regions, especially in the tropics (Klassen 2005). The pasture weed *Kochia scoparia* was eradicated from a large area of Western Australia (Randall 2001), and the witchweed eradication campaign in the southeastern United States mentioned above is nearing success. These successes suggest that, if conservation is made a high enough priority, large-scale eradications purely for conservation purposes may be very feasible.

A variety of methods have been used in these campaigns: males sterilized by X-rays for fruitflies, chemicals for *Anopheles gambiae* and for rats, hunters and dogs for goats. Some campaigns that probably would have succeeded were stopped short of their goals not for want of technological means but because of public objections to using chemicals or to killing vertebrates. A notable example is the cessation, because of pressure from animal-rights groups, of the well-planned campaign to eradicate the gray squirrel before it spreads in Italy (Bertolino and Genovese 2003).

7.3.3 Maintenance management

If eradication is not an option, many available technologies may limit populations of invasive species so that damage is minimized. There are three main methods—mechanical or physical control, chemical control, and biological control. Sometimes these methods can be combined, especially mechanical and chemical control. In South Africa, the invasive Australian rooikrans tree (*Acacia cyclops*) can be effectively controlled by mechanical means alone—cutting and pulling roots—so long as sufficient labor is available (Matthews and Brand 2004a). Sometimes chemical control alone can keep a pest at low numbers. The Indian house crow (*Corvus splendens*), is an aggressive pest in Africa, attacking native birds, competing with them for food, preying on local wildlife, stripping fruit trees, and even dive-bombing people and sometimes stealing food from young children. It can be controlled by a poison, Starlicide, so long as the public does not object (Matthews and Brand 2004a). Many invasive plants have been kept at acceptable levels by herbicides. For instance, in Florida, water hyacinth was drastically reduced and subsequently managed by use of the herbicide 2,4-D, combined with some mechanical removal (Schardt 1997). For lantana in South Africa, a combination of mechanical and chemical control keeps populations minimized in some areas (Matthews and Brand 2004a). A South African public works program, Working for Water, has had great success using physical, mechanical, and chemical methods to clear thousands of hectares of land of introduced plants that use prodigious amounts of water, such as mesquite (*Prosopis* spp.) and several species of *Acacia* (Matthews and Brand 2004a). Similarly, in the Canadian province of Alberta, Norway rats have been kept at very low levels for many years by a combination of poisons and hunting by the provincial Alberta Rat Patrol (Bourne 2000).

However, long-term use of herbicides and pesticides often leads to one or more problems. First is the evolution of resistance in the target species, so that increasing amounts of the chemical have to be used even on a controlled population. This has happened recently with the use of the herbicide used to control Asian *Hydrilla verticillata* in Florida (Puri *et al.* 2007), and it is a common phenomenon in insect pests of agriculture. A second, related problem is that chemicals are often costly, and they can be prohibitively expensive if used over large areas. Whereas the market value of an agricultural product may be perceived as large enough to warrant such great expense, it may be difficult to convince a government agency that it is worth controlling an introduced species affecting conservation values that are not easily quantified. Finally, chemicals often have non-target impacts, including human health impacts. The decline of raptor populations as DDT residues caused thin eggshells is a famous example (Lundholm 1997). Many later-generation herbicides and pesticides have few if any non-target impacts when used properly, but expense may still be a major issue.

These problems with pesticides have led to great interest in the use of classical biological control—deliberate introduction of a natural enemy (predator, parasite, or disease) of an introduced pest. This is the philosophy of fighting fire with fire. Although only a minority of well-planned biological control projects actually end up controlling the target pest, those that have succeeded are often dramatically effective and conferred low-cost control in perpetuity. For instance, massive infestations of water hyacinth in the Sepik River catchment of New Guinea were well controlled by introduction of the two South American weevils that had been used for this purpose in Lake Victoria, *Neochetina eichhorniae* and *N. bruchi* (Matthews and Brand 2004b). A recent success on the island of St. Helena is the control of a tropical American scale insect (*Orthezia insignis*) that had threatened the existence of the endemic gumwood tree (*Commidendrum robustum*). A predatory South American lady beetle (*Hyperaspis pantherina*) now keeps the scale insect population at low densities (Booth *et al.* 2001). Even when a biological control agent successfully controls a target pest at one site, it may fail to do so elsewhere. The same two weevils that control water hyacinth in New Guinea and Lake Victoria had minimal effects on the hyacinth in Florida, even though they did manage to establish populations (Schardt 1997).

However, in addition to the fact that most biological control projects have not panned out, several biological control agents have attacked non-target species and even caused extinctions—the cases involving the cactus moth, rosy wolf snail, small Indian mongoose, mosquitofish, and thistle-eating weevil have been mentioned earlier. In general, problems of this sort have been associated with introduced biological control agents such as generalized predators that are not specialized to use the specific target host. However, even species that are restricted to a single genus of host, such as the cactus moth, can create problems.

Summary

- Invasive species cause myriad sorts of conservation problems, many of which are complicated, some of which are subtle, and some of which are not manifested until long after a species is introduced.
- The best way to avoid such problems is to prevent introductions in the first place or, failing that, to find them quickly and eradicate them.
- However, many established introduced species can be managed by a variety of technologies so that their populations remain restricted and their impacts are minimized.

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Relevant websites

- World Conservation Union Invasive Species Specialist Group: http://www.issg.org/index.html.
- National Invasive Species Council of the United States: http://www.invasivespecies.gov.
- National Agriculture Library of the United States: http://www.invasivespeciesinfo.gov.
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